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136

**THE ROLE OF WATER SALINITY
IN STRUCTURING EASTERN BALTIC
COASTAL FISH COMMUNITIES**

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LIST OF ORIGINAL PAPERS

This dissertation is based on the following papers, which are referred to in the text by their Roman numerals.

- I Albert, A., Vetemaa, M. & Saat, T. 2004. Effects of salinity on the development of Peipsi whitefish *Coregonus lavaretus maraenoides* Poljakow embryos. *Annales Zoologici Fennici* 41 (1): 85–88.
- II Albert, A. Vetemaa M. & Saat T. 2006. Laboratory-based reproduction success of ruffe, *Gymnocephalus cernuus* (L.), in brackish water is determined by maternal properties. *Ecology of Freshwater Fish*, 15: 105–110.
- III Albert, A. & Einarsson, H.A. Selectivity of gillnet series in sampling of perch (*Perca fluviatilis* L.) and roach (*Rutilus rutilus* L.) in the coastal sea of Estonia. Manuscript.
- IV Vetemaa, M., Eschbaum, R., Verliin, A., Albert, A., Eero, M., Lillemägi, R., Pihlak, M. & Saat, T. 2006. Annual and seasonal dynamics of fish in the brackish-water Matsalu Bay, Estonia. *Ecology of Freshwater Fish*, 15: 211–220.
- V Vetemaa M., Eschbaum R., Albert, A. & Saat T. 2005. Distribution, sex ratio and growth of *Carassius gibelio* (Bloch) in coastal and inland waters of Estonia (north-eastern Baltic Sea). *Journal of Applied Ichthyology* 21: 287–291

Author's contribution to the papers:

In Papers I and II, I participated in planning the experiments, carried out the experiments and data analysis and was responsible for writing the manuscripts. In Paper III, I participated in performing the data analysis and was responsible for writing the manuscript. In Papers IV and V, I was involved in data collection and analysis and participated in finishing the manuscripts.

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INTRODUCTION

The Baltic Sea is a semi-enclosed water area, and the second largest brackish water basin in the world. In the southern Baltic Sea, the surface layer salinity is usually 3–12‰, but it is as low as 1–6‰ in the northern Baltic Sea (Fig.1). The water is almost fresh in the river estuaries. Besides horizontal gradient, salinity also varies vertically: a halocline occurs at the depth of 50–70 m. Under the halocline, salinity is somewhat higher, 10–22‰, and is irregularly subjected to hypoxia or anoxia and the presence of H₂S. The hydrography of the sea is largely regulated by the sporadic inflows of saline North Sea water via the narrow entrance of the Danish straits in the south-west, and intermediate stagnation periods; the average retention time is 25–30 years (Voipio 1981; Ojaveer & Pihu 2003).

The coastal waters of Estonia have low salinity (1–9‰, usually 5–7‰); they are often shallow, especially in the West-Estonian Archipelago Sea (Väinameri) and the Gulf of Riga area. Water temperature in shallow areas reaches 26–28°C in hot summers, and these areas are ice-covered in the winter.

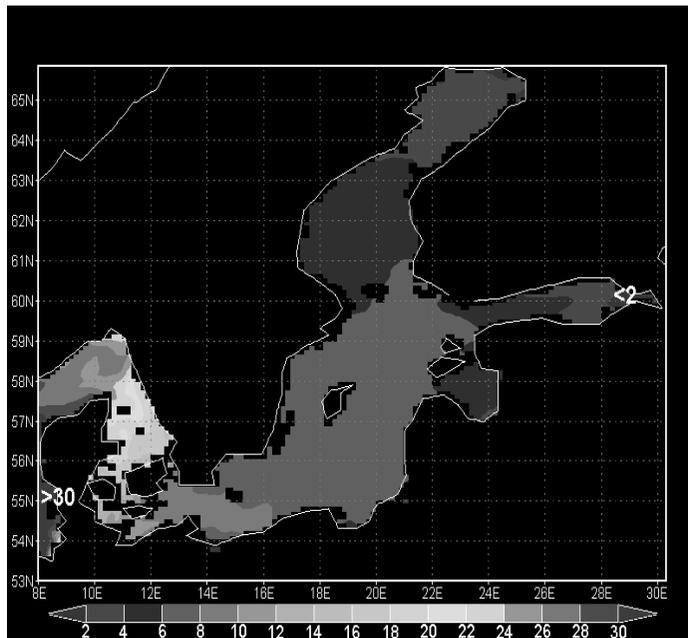


Figure 1. Surface salinity (‰) in the Baltic Sea (based on baltic.mersea.eu.org).

The Baltic Sea is a relatively young one on the geological time scale: the fish have been able to adapt to current abiotic conditions for 7000–10000 years (Ignatius *et al.* 1981). After the last glaciation period, a freshwater lake was

formed, which was followed by a short marine period and then a second freshwater period lasting until about 7500 years before the present day, at which time it became brackish (Tulkki 1984). Fish species have immigrated to the sea at different times by different ways; the distribution pattern of various species reflects their original habitat and salinity tolerance. Thus, the number of marine species is highest in areas near the Danish Straits and diminishes eastwards and northwards, while the number of freshwater species increases when salinity decreases. The marine species, which were not able to adapt to low salinity, failed to colonise the sea and other species, whose better plasticity enabled them to cope with the salinity levels, succeeded (Voipio 1981). At the same time, freshwater species, which had the possibility to reproduce at more favourable freshwater inlets, colonised the shallow coastal areas where the current species' composition somewhat resembles the European lowland freshwater waterbodies (Matena 1995; Eklöv 1997; Holmgren & Appelberg 2000; Irz *et al.* 2002). Selection pressure on species, adapting to the brackish conditions of the sea, has probably been strong and salinity has been the major evolutionary force.

A lot of salinity-related literature is provided on economically important species such as cod, Baltic herring and sprat, which inhabit mainly the open zone of the Baltic Sea. However, a much smaller amount of knowledge has been published on the fish and fish assemblages, especially freshwater species, in the shallow coastal areas in relation to the brackish-water characteristics of the sea.

The present thesis intends to investigate the effects of abiotic factors, especially salinity, on the freshwater species inhabiting the coastal areas of the eastern Baltic Sea with the emphasis on embryonic salinity tolerance of freshwater species, changes in egg size in different environments and effects of water salinity on spatial distribution of freshwater fish and fish assemblages.

The central objectives of the research papers were therefore to study 1) the effect of salinity on the embryonic stage of freshwater species (Papers I and II), and 2) distribution of fish species and communities (Papers IV and V) in relation to key environmental factors. An additional aim was to evaluate the effectivity and reliability of methodology used in the presented studies IV and V (Paper III). The methodology was established for coastal fish surveys (Thoresson 1996) and has been used in Estonia since 1992 (Saat *et al.* 2003a) in order to assess the trends in the fish population and assemblages. Yet, how well the results reflect the actual abundance of the main species has not been previously estimated.

ADAPTATION TO UNUSUAL SALINITY CONDITIONS

The brackish (2–8‰) coastal waters of the eastern part of the sea are inhabited by several freshwater species like the northern pike *Esox lucius*, European perch *Perca fluviatilis*, roach *Rutilus rutilus*, etc. It is known, that the embryonic period is the most sensitive to environmental factors during ontogeny (Depêche & Billard 1994), which limits the environment suitable for reproduction (for example, unfavourable salinity causes malformation and the death of embryos, Paper I). Adult specimens of some freshwater species can tolerate the brackish waters of the open Baltic Sea. However, they are unable to reproduce under such salinity conditions, and need to migrate to areas of lower salinity, e.g. estuaries, or even into fresh river waters for spawning (Paper IV). At the same time, the higher embryonic salinity tolerance of other species allows them to reproduce at higher salinities (6–8‰). These salinity values (6–8‰) are considered the critical values for embryonic development of various freshwater species (Karås & Hudd 1993; Lehtonen *et al.* 1996; Neuman *et al.* 1996; Westin & Limburg 2002). Embryonic salinity tolerance of some species has been estimated via laboratory experiments (Table 1).

Table 1. Embryo salinity tolerance of some freshwater-originating species. BW indicates brackish-water, and FW freshwater population.

Species		Salinity tolerance limit (‰)	Reference
Common whitefish	<i>Coregonus lavaretus</i>	10.2	(Jäger <i>et al.</i> 1981)
BW ruffe	<i>Gymnocephalus cernuus</i>	9.0	(Vetemaa & Saat 1996)
Perch	<i>Perca fluviatilis</i>	7.4	(Klinkhardt & Winkler 1989)
Pikeperch	<i>Sander lucioperca</i>	7.0	(Klinkhardt & Winkler 1989)
Pike	<i>Esox lucius</i>	6.9	(Westin & Limburg 2002)
Gibel carp	<i>Carassius gibelio</i>	6.0	(Vetemaa <i>et al.</i> 2003)
FW ruffe	<i>Gymnocephalus cernuus</i>	6.0	(Vetemaa & Saat 1996)
Common carp	<i>Cyprinus carpio</i>	5.0	(Neudecker 1975)
Peipsi whitefish	<i>C. lavaretus maraenoides</i>	4.8	(Paper I)
Roach	<i>Rutilus rutilus</i>	4.1	(Klinkhardt & Winkler 1989)

Many studies have demonstrated that adult specimens of freshwater species can tolerate higher salinity, e.g. grass carp *Ctenopharyngodon idella* (> 9‰; Cross 1970; Kilambi & Zdinak 1980), roach, ide *Leuciscus idus* (>15‰; Thiel *et al.* 1995) and pikeperch (33‰; Brown *et al.* 2001). Moreover, fish can even benefit from moderately increased salinity, which may result in higher growth rates (Bœuf & Payan 2001). Adult specimens of common whitefish inhabit both the North and the Baltic Sea, but for juveniles the salinity limit is 15–20‰, and

larvae can tolerate salinity up to 12.5‰ for a longer time (de March 1989). Embryos of common whitefish hatch at salinity up to 10.2‰ (Jäger *et al.* 1981). However, for the Lake Peipsi whitefish the limit for viable hatching is 4.8‰ (Paper I). Lake Peipsi whitefish invaded Peipsi shortly after the last glaciation, before the passage of fish was blocked by the Narva River waterfall (Hang & Miiel 1999). So this subspecies of whitefish evolved during the last 9000 years exclusively in the freshwater conditions in isolation from other populations of the common whitefish, which probably has led to the lower embryonic salinity tolerance.

In addition, the embryonic growth rate of freshwater species increases in brackish water compared to a freshwater environment. Brackish water decreases osmotic and ionic gradients between body fluid and external environment and less energy is needed for osmoregulation (Lam & Sharma 1985). In brackish water ruffe the longest larvae hatched at 3‰ (Vetemaa & Saat 1996), in common carp at 1.5–3‰ (Lam & Sharma 1985) and in pikeperch at 2‰ (Albert 2003). Regarding Lake Peipsi whitefish the longest larvae hatched at 1.9–3.5‰, however, the survival rate was highest at lower salinities (Paper I). The fact that freshwater might not be the optimal environment for reproduction of freshwater species is also supported by studies where the highest embryo survival rates and most viable larvae have been detected at salinities 1–3‰ (Bein & Ribic 1994; Vetemaa & Saat 1996; Vetemaa *et al.* 2003).

On the basis of the study by Jäger *et al.* (1981), and Paper I, it can be concluded that the embryonic salinity tolerance of Lake Peipsi whitefish is about two times lower than the tolerance of the common whitefish. It is lower than in the case of percids and gibel carp (Vetemaa *et al.* 2003) inhabiting the Baltic Sea, but higher than embryonic salinity tolerance of roach (Klinkhardt & Winkler 1989), which is also abundant in coastal areas of the north-eastern Baltic Sea (Ådjers *et al.* 2006; Paper III; Paper IV). There is also a significant difference between the salinity tolerance of freshwater and brackish-water populations of ruffe (Table 1; Vetemaa & Saat 1996; Paper II). Despite a geologically short period of time, freshwater fish in the Baltic Sea area seem to have adapted to the prevailing salinity conditions. At the same time, the magnitude of this adaptation varies. For example, percids seem to have adapted to a greater extent than cyprinids.

VARIATIONS IN EGG CHARACTERISTICS OF FISH SPECIES INHABITING THE BALTIC SEA

Several studies have been carried out with the aim to reveal the differences in reproductive parameters of marine fish inhabiting the Baltic Sea, when compared to North Sea or Atlantic populations. Development of flounder *Platichthys flesus* eggs has found to be unsuccessful in the northern Baltic Sea at salinities $< 6\text{‰}$ (Nissling *et al.* 2002). The same figure applies for sprat *Sprattus sprattus* (Veldre 1986), but Baltic herring *Clupea harengus membras* can reproduce in less haline waters (3–5‰, Ojaveer 1981). However, in the process of adaptation the Baltic herring has lost its ability for successful embryonic development in the ocean salinities (Ojaveer 1981). Baltic Sea populations of another marine species, turbot *Psetta maxima*, have shown viable hatching in laboratory conditions at salinities 7–15‰, whereas for the North Sea turbot populations the optimum salinity conditions were $\geq 20\text{‰}$ (Nissling *et al.* 2006). In case of the Baltic cod *Gadus morhua callarias* successful spawning is limited to areas where salinity is at least 11–12‰. Such conditions occur regularly in the Bornholm basin, but only sporadically in the Gotland and Gdansk basins, where the depths are only filled with oxygen-rich water of high salinity after inflows of haline waters from the North Sea (Dickson & Branden 1993). More commonly the deep layers of these basins are filled with anoxic stagnating water masses and eggs, which sink, are determined for death. Therefore, egg buoyancy seems to be the key factor regulating successful spawning and, consequently, the year-class strength of cod in the Baltic Sea (Nissling *et al.* 1994).

Compared to the pelagic eggs of marine fishes inhabiting the world oceans, the pelagic eggs of fish living in the Baltic Sea are larger and have a decreased specific gravity (Solemdal 1967; Nissling & Westin 1991). The lower specific gravity of marine fishes (cod, flounder) in the Baltic Sea has been associated with decreased chorion thickness and higher water content (Riis-Vestergaard 1982; Nissling & Westin 1991; Thorsen *et al.* 1996). An increased ability of Baltic cod to hydrolyse a larger share of the egg yolk proteins to free amino acids, compared to that of marine cod eggs, is supposed to be imperative for the establishment of egg buoyancy in the brackish Baltic Sea, and thus to be an important genetic factor contributing to isolation of Baltic cod from the other Atlantic cod *Gadus morhua* stocks (Thorsen *et al.* 1996).

Flounders produce pelagic eggs in the Atlantic Ocean. The species has adapted to the brackish environment of the Baltic Sea, forming there three distinguishable populations (Nissling *et al.* 2002). Two populations spawn in the deep basins of the western part of the sea, and have pelagic eggs (minimum salinity requirements 9–12‰). The third population is constituted by flounder which spawn in the less haline eastern part and have demersal eggs, which

develop normally at salinities $\geq 6\text{‰}$ (however, the fertilisation rate is high up to 10–15‰). Pelagic eggs are significantly larger than demersal. Successful reproduction at low salinities has made the flounder the most abundant pleuronectid in the Baltic (Nissling *et al.* 2002). In the case of cod it has been found that the chemical stimulants released by the eggs are of significance to sperm motility, and ovarian fluid extends the stimulating encounter region around the egg (Litvak & Trippel 1998). So despite the unfavourable environmental conditions (i.e. decreased salinity), in the presence of maternal substances, Baltic cod sperm still becomes activated and achieves fertilisation (Westin & Nissling 1991).

There are a few studies concerning the effect of environmental and maternal variables on the egg size of freshwater fish (e.g. Daoulas & Kattoulas 1985; Sehgal & Toor 1991; Huang *et al.* 1999; Katayama 2001; Johnston & Leggett 2002). In anadromous species it has been found that females, who were kept in sea water (25–30‰), produced larger eggs compared to females kept in the freshwater environment (Atse *et al.* 2002).

The model species for our studies, dealing with salinity tolerance of eggs from different populations (Paper II) was ruffe, a widespread freshwater percid, whose abundance has increased about 3.5 times in some areas of the Estonian coastal sea over the last 10-year period (Vetemaa *et al.* unpublished). Due to rapid population growth, supported by early maturation and high fecundity, the ruffe are able to become rapidly abundant almost everywhere they occur (Saat *et al.* 2003b). This demersal spawner, which inhabits both brackish and fresh waters, has differences in egg size between those two environments: eggs of freshwater (Lake Peipsi) ruffe were significantly smaller compared to eggs from coastal areas of the Baltic Sea (Paper II). It is possible to infer that thereby the fecundity is higher in the freshwater population of ruffe.

Wootton (1992) has stated that there is only a weak relationship between maternal body size and egg size in teleosts generally, except for some fish, e.g. Salmonidae. Nevertheless, female characteristics are found to influence egg size in various fish species. For example, both egg size and fecundity improved with an increase in female length, weight and condition factors in haddock *Melanogrammus aeglefinus* (Trippel & Neil 2004). Egg size and quality have also been positively associated with female size and age in the wild population of Atlantic cod (Solemdal 1997; Marteinsdottir & Steinarsson 1998). Also, in the case of freshwater cyprinid- *Rutilus rubilio*, and in Japanese smelt *Hypomesus nipponensis* (Lake Ogawara) egg size has been shown to increase with the increasing size and age of the spawners (Daoulas & Kattoulas 1985; Katayama 2001). In earlier studies of the egg size of ruffe, a positive correlation between egg size and female size has been documented (Pihu 1963; Smirnov 1977; Koncevaya & Frantova 1980). However, in the case of ruffe from the Estonian coastal sea and Lake Peipsi, egg size was independent of female length and age (Paper II).

It has been found that, in some batch spawning species, the average egg diameter in consecutive clutches decreases, which has been associated with diminishing resources of the female (Hsiao *et al.* 1994; Marteinsdottir & Steinarsson 1998; Trippel & Neil 2004). In the case of ruffe, which also spawns in batches, this phenomenon was found to be evident only in the freshwater population (Paper II). In brackish-water ruffe, the egg size remained constant (Paper II), which can be related to the better condition of brackish-water ruffe, or with a need for larger eggs to ensure the viability of successors.

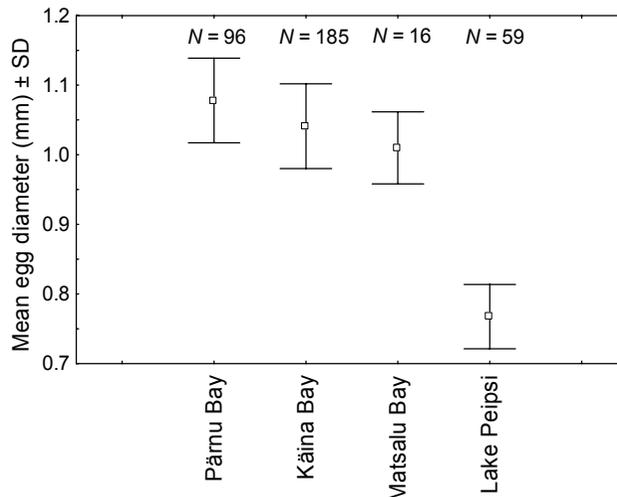


Figure 2. Egg size of three brackish-water, and one freshwater ruffe, populations (Paper II, Albert *et al.* unpublished).

Fish populations, transferred to new habitats, might exhibit a shift in egg size and that has been interpreted as an adaptation to changing environmental conditions (Stearns 1983; Kinnison *et al.* 1998). Differences in egg size are thought to reflect adaptation by the spawning stock to varying conditions met by early larvae (Hinckley 1990). An investigation of walleye *Stizostedion vitreum* eggs across different populations and latitudes showed that egg size is quite stable for a given population and may be determined by particular environmental conditions (Johnston & Leggett 2002).

Einum and Fleming (2002) have found intrapopulation variation in egg size to be larger in fish with demersal eggs and larvae than those with pelagic eggs and/or larvae, and suggest that the lack of significant differences between marine and freshwater species within reproductive types and the pattern of variance observed could not be ascribed to differences between freshwater and marine environments. Comparing the freshwater and brackish-water populations of ruffe we found that intrapopulation differences in egg size of ruffe were insignificant compared to interpopulation variation (Paper II).

Laboratory experiments with Indian major carp *Labeo rohita* showed that size of larvae at hatching, survival until exogenous feeding, larval growth rate and survival during starvation were positively correlated with egg size (Sehgal & Toor 1991). Large eggs generally result in large larvae (e.g. differences in larval size of freshwater and brackish-water ruffe; Paper II; Fig. 3) with wider mouth gape, longer visual reactive distance and greater swimming speed than is typical for their smaller conspecifics (Heming 1982; Miller *et al.* 1988). These traits, in addition to large size as such, are likely to have higher survival value in nature, e.g. in terms of earlier initiation of exogenous feeding and increased efficiency to forage and/or to avoid predators (Heming 1982; Huang *et al.* 2000). On the other hand, if egg predation is size dependent or daily mortality rate is higher in the embryonic than in the larval period, producing large eggs and an extended embryonic period are the cost for being large at hatching (Miller *et al.* 1995). Small size and low energy reserves may explain the higher mortality and slower growth of embryos developed in unfavourable salinity conditions (Huang *et al.* 2000).

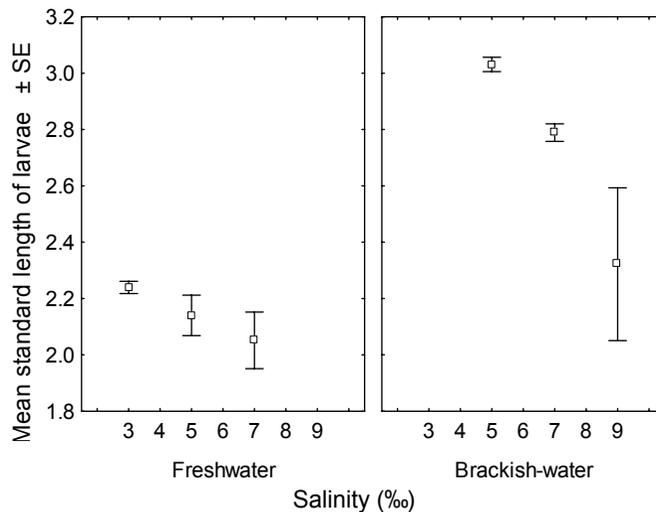


Figure 3. Standard length at hatching of freshwater and brackish-water ruffe larvae developed at different salinities (Paper II). Note that the lowest salinity is 3‰ for freshwater and 5‰ for brackish-water larvae.

For Paper II, we carried out reciprocal crossing experiments to find out if there is any paternal influence on the embryonic salinity tolerance. One could assume that at least at later stages, when organs are developed on the basis of genetic information provided by both parents, the salinity tolerance would also be affected by contribution of the paternal genes. However, no significant differences in the success of embryonic development of eggs of freshwater or brackish-water females fertilised with sperm of freshwater- and brackish-water-

originated males were found at any critical developmental stage (fertilisation, gastrulation, hatching) in different salinities. Survival at all tested salinities depended only on female origin with embryos of brackish-water females showing higher salinity tolerance. This indicates that, in the case of the ruffe, egg properties are decisive in the embryo salinity tolerance (Paper II).

Although the mechanisms behind the increased egg size of freshwater species in the brackish environment are unknown, it is yet possible to conclude that adaptation to salinity conditions in the Baltic Sea is, to a large extent, determined by changes in egg characteristics.

RELIABILITY OF COASTAL FISH SAMPLING METHODOLOGY

When the salinity tolerance was investigated via laboratory experiments, the dynamics and trends of fish assemblages' distribution were studied *in situ* using the proper fishing gears. To evaluate the reliability of the methodology, applied in the regular coastal fish monitoring in Estonia, and also in the presented studies IV and V, a selectivity analysis was carried out (Paper III).

The Estonian Marine Institute of the University of Tartu has conducted routine coastal fish monitoring using gillnet series in Estonian coastal waters since 1992 (Saat *et al.* 2003a). The main objectives are to obtain fisheries-independent data on abundance and year-class strength of important commercial species and determine trends in the coastal fish populations and assemblages related to natural variation and large-scale environmental changes. The same objectives are also met elsewhere in the Baltic Sea where coastal fish monitoring is carried out (Appelberg *et al.* 2003). In addition, the same gear and methods have been applied with the aim to study the seasonal and spatial distribution of fish (Papers IV and V). Moreover, gillnets have been used also in environmental impact assessment in Estonian coastal areas (Saat & Eschbaum 2002).

Gillnets are passive gears (i.e. the fish have to swim into the net to get caught) mainly used for fishing in shallower waters, and also for research purposes, e.g. in shallow coastal areas or lakes (Sparre & Venema 1998; Lucas & Baras 2000). The catch process has been divided into three phases: first the range of fish and the use of fishing gear must overlap in time and space; secondly the fish must encounter the nets, and thirdly, be caught and retained in the nets. The first two phases are essentially dependent on fish distributions and behavioural patterns, while in the latter the specific characteristics of the fishing gear and morphology of the fish play a main role (Parrish 1963; Holst *et al.* 1998).

It is widely acknowledged, that gillnets are very size-selective (Hamley 1975; Nielsen & Johnson 1983). As gillnets are passive gears, the fish, which move more and fast, have a larger probability of encountering the gear than less and slow moving fish (Sparre & Venema 1998). Hence, the length distribution of fish available for the net may differ from the length distribution of the entire population (Millar & Fryer 1999; Finstad *et al.* 2000). Therefore, the results can be biased and not reflect the exact abundance of all species and age groups (Hamley 1975; Kurkilahti & Rask 1996; Kurkilahti *et al.* 2002; Appelberg *et al.* 2003).

However, other commonly used fish sampling techniques are generally not applicable in the shallow coastal areas. Trawling is not possible due to shallowness and the stony bottom, and large commercial seine-nets are not suitable due to the abundant stones and/or dense vegetation in many areas. Therefore, gillnet sampling is still the most widespread method in studying coastal fish assemblages in the northern Baltic Sea.

Originally, the standardised mesh sizes (17, 21, 25, 30, 33 and 38 mm measured from knot-to-knot) were designed for coastal monitoring considering mainly the two abundant species in the coastal fish communities – perch and roach (Neuman *et al.* 1997; Saat *et al.* 2003a), but also with the aim to give reliable comparable information about other species inhabiting the sea. According to Jensen (1986), a geometric series of mesh sizes is recommended for use if an equal efficiency for fish of a certain length interval is wanted. However, reducing the number of nets in the current net series has been found unnecessary when considering perch and roach (e.g. Fig. 5; Paper III).

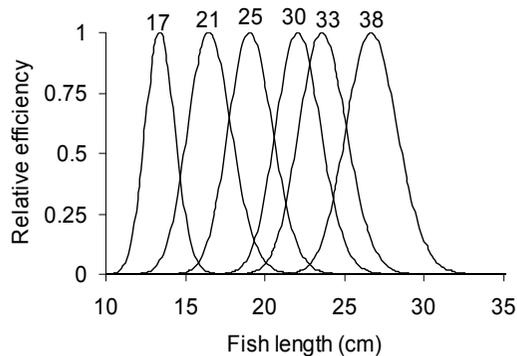


Figure 5. Modelled selection curves of different mesh sizes over the gillnet series of 17–38 mm using perch data (Paper III).

Nevertheless, the results of Paper III assert that the use of the gillnet series, for assessing population structure, may result in bias with regard to interpretations of size structure, and hence, further biological interactions, if the sampling bias is not taken into account. Yet the time series of samples obtained with the

gillnet series provide valuable information about relative changes in the population structure, which usually is the main issue for the monitoring.

In Estonia, besides monitoring with gillnets, experimental fishing is occasionally undertaken with other equipment, such as trap nets and beach seines (Paper IV). Therefore, it is known that small-sized fish species and younger age-classes are insufficiently covered in gillnets when using a minimum mesh size of 17 mm in the study area.

To be more accurate, the fish <12 cm of total length are rarely caught with the typical gillnet series of 17–38 mm (Paper III). There are two possible explanations. Most obviously, the mesh sizes are too big to catch smaller fish. The second explanation is related to the above-mentioned circumstance that fish, moving quickly, have a larger probability of encountering the gear than slowly moving fish. It is known that larger fish move faster than small fish of the same species (the swimming speed can be approximated by constant times a power function of a length; Wardle 1996) and cover larger areas (Millar & Fryer 1999). While combined with a larger mass, it results in an increased likelihood of entanglement (Finstad *et al.* 2000). Therefore, the fishing effort with passive gear like gillnets should actually be progressively higher towards smaller mesh sizes.

Based on the selectivity pattern calculations (Paper III) a standard-sized gillnet, with mesh size 14 mm (measured from knot to knot), has been added to the series used in the Estonian regular coastal fish monitoring in order to get supplementary information on e.g. recruitment without discontinuation of the present long-term data sets (Paper III). The preliminary results (from years 2006–2007) show that the 14 mm net has resulted both in catching additional smaller size groups of perch and roach, as well as provided valuable data on smaller-sized species like black goby *Gobius niger*, greater sandeel *Hyperoplus lanceolatus*, gudgeon *Gobio gobio* etc., which were almost absent in the catches before.

In conclusion, the methodology employing the gillnet series, with the aim to obtain information on composition of fish fauna and abundance of different species (Papers IV and V), can be considered sufficiently reliable for studying and comparing the fish communities in the Estonian coastal areas.

SMALL-SCALE DISTRIBUTION OF FISH ASSEMBLAGES

Salinity is a key factor determining the distribution of fish species in the Baltic Sea: the number of marine species is highest in areas near the Danish Straits and diminishes eastwards and northwards, while the number of freshwater species increases when salinity decreases. However, in the shallow Estonian coastal sea a steep horizontal salinity gradient is also especially evident in several

geographically small areas, e.g. bays, and the composition of fish assemblages varies along the gradient. We defined the small-scale to be at the bay level, and larger-scale to be the coastal sea area level (e.g. Gulf of Finland).

The model study area for small-scale fish distribution, Matsalu Bay (Paper IV), is one of the largest bays and the only real delta estuary in Estonia. A horizontal salinity gradient from shallow (1 m) almost freshwater (0–2‰) inner part, to deeper (3 m) brackish-water (4–6‰) outer part, occurs in the bay, and therefore provides diverse environmental conditions.

It has been shown in several studies that species' diversity in estuaries changes temporally (seasonally) and spatially according to changes in the water temperature and salinity (e.g. Thiel *et al.* 1995; Araújo *et al.* 1999; Jaureguizar *et al.* 2006). Thiel *et al.* (1995) showed that temperature was the best predictor of the total fish abundance in the Elbe estuary, while salinity influenced the species' richness and total biomass. Salinity is confirmed to also have a major impact on the species' richness in the archipelago zone of the Gulf of Finland, as marine species like turbot, flounder, sprat and viviparous blenny *Zoarces viviparus* are known to occur only occasionally in the least haline regions both of the Gulf on Finland (Lappalainen *et al.* 2000) and the Gulf of Bothnia (Pitkänen 1994). Neuman (1982) found that the boundary between freshwater and marine species shifts towards deeper and more open areas in summer in the archipelagos of the Bothnian Sea. Abundance dynamics of marine species, presented in Paper IV, supports the previous findings: marine species like flounder, Baltic herring and viviparous blenny entered the shallow Matsalu Bay only during the cold period (Paper IV). The key factor behind these relocations can be considered to be water temperature. However, contrary to the study by Neuman (1982) several rather typical marine species (e.g. cod, turbot, shorthorn sculpin *Myoxocephalus scorpius*) were never found in Matsalu Bay. One possible reason lies in the fact that during summers even the bottom layers of the shallow Väinameri warm up. So, the closest cold-water sanctuary is geographically too far away to make winter migration into this area energetically reasonable.

Abiotic factors like water salinity and temperature have been stated to have a decisive effect on survival of larval and juvenile fish in marine estuaries (Harris *et al.* 2001), whereas in lake littoral zones and rivers biotic factors like macrophyte abundance and heterogeneity often play a major role (Weaver *et al.* 1997). The young-of-the-year (YOY) fish beach seine data, from Finnish coastal bays, showed a shift from freshwater species' dominance in the inner areas to marine species' dominance in the more exposed outer areas, which suggests that salinity is an important factor controlling YOY fish species richness and composition along horizontal inshore-offshore exposure and salinity gradient (Lappalainen & Urho 2006). Smaller perch and roach were also less abundant in the coastal areas with higher salinity levels (6–7‰; Albert *et*

al. unpublished), which can be associated with lower salinity tolerance of juveniles (Mehner 1993; Bein & Ribí 1994).

As mentioned above, in shallow bays of the north-eastern Baltic Sea the horizontal salinity gradient explains well the main changes in the fish assemblages. However, in parallel with the salinity gradient, other conditions like water depth, vegetation density and coverage usually also change. Therefore, it is not easy to distinguish the effects of all these factors on the fish species' distribution. In the Matsalu Bay the abundance of fish species fluctuated a lot during the regular midsummer sampling over the ten-year research period (1994–2003), and concerning the most of the species caught, no clear trend appeared that could be explained by some abiotic, biotic or anthropogenic factor (Paper IV). Lappalainen *et al.* (2000) found that the supply of suitable food is a very important factor determining the composition of fish communities in the archipelago zone during mid- and late summer. The results of Paper IV also suggest that factors such as water temperature, water depth, food and shelter possibilities, etc. play an even more important role than salinity in the small-scale distribution of species in the north-eastern Baltic Sea.

RECENT CHANGES IN LARGER-SCALE FISH SPECIES DISTRIBUTION

It is not likely that large-scale changes have taken place in the coastal sea during the 15 years of coastal gillnet monitoring (since 1992). However, some conclusions can be drawn from this data series: firstly, the share of cyprinids in the catches has increased (Eschbaum *et al.* 2004; Paper IV), and secondly, a new invasive species – gibel carp – has appeared in the catches and become biomass dominant in some coastal areas (Paper V).

The first record of gibel carp in the Estonian coastal sea (near the southern border) dates from 1985. After that time the species has expanded its distribution, and in 1997 was caught from the Gulf of Finland (Paper V). It was detected in the southern coast of Finland in 2005 (Urho & Pennanen, unpublished data). The current distribution of gibel carp in the Baltic Sea is limited to the eastern areas of surface salinity $\leq 8\text{‰}$, and the western extent of gibel carp occurrence is most probably Poland where it can be found in the almost freshwater Vistula Lagoon, but very seldom in the open and therefore colder and deeper waters of the Baltic Sea (Paper V). Laboratory experiments have shown that viable larvae hatched at salinities up to 6‰, but the survival was highest at 3‰. Hatched larvae were also the longest at 3‰ (Vetemaa *et al.* 2003).

The increase in the cyprinid abundance has been explained by several factors: decrease in predatory fish (pike, pikeperch) abundance, eutrophication of coastal areas (Lappalainen *et al.* 2000) and higher average yearly tempera-

tures (Fig. 4). The rapid expansion of gibel carp was most probably enhanced by the latter: the species became widely abundant in the commercial catches in the period of 1999–2004 that followed unusually warm summers in 1989–1991 (Paper V).

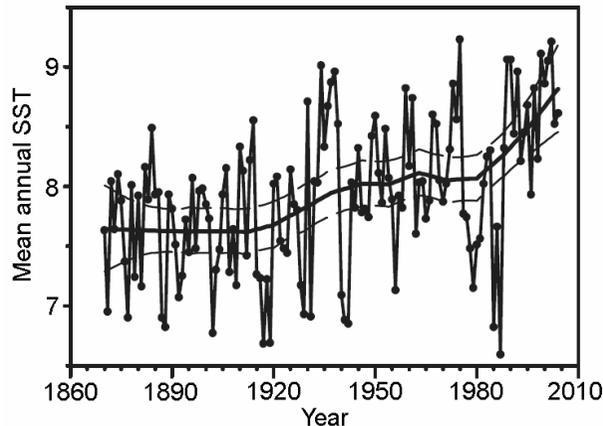


Figure 4. Mean annual sea surface temperature (SST) in the central Baltic Sea (MacKenzie & Schiedek 2007).

Forecasted climate changes in northern Europe will likely affect both the temperature and salinity of the Baltic Sea, causing it to become warmer and fresher (Döscher & Meier 2004; MacKenzie *et al.* 2007). These long-term effects are likely to result in a shift in native fishes' distribution as well as in the expansion of invasive species. Several other invasive non-native freshwater species besides gibel carp have a high potential to expand their distribution northwards in the Baltic Sea under those conditions. The number of native species, adapted to the brackish Baltic Sea, is lower than in fresh or marine waters, and it has been suggested that species-poor systems generally have a lower stability and capacity to cope with disturbances in the environment compared to the high diversity systems (Johnson *et al.* 1996).

An adult European invasive species stone moroko *Pseudorasbora parva* has been shown to tolerate salinities of <13.7‰ and there is accordingly a limited potential for this species to disperse into new river systems via brackish waters (Scott *et al.* 2007). However, the salinity of coastal waters of the Baltic does not exceed this magnitude (Fig. 1), and once it has entered the Baltic Sea system, it has no barriers for further distribution inside the system. Salinity conditions might restrain another potential pest, Chinese sleeper *Percottus glenii*, from advance in the Baltic Sea. Until now the lack of reproduction grounds in the Baltic Sea may have held back the expansion of the round goby *Apollonia melanostoma* (referred to as *Neogobius melanostomus* in several publications)

in the sea (Almqvist *et al.* 2007). Still, the species has already been spotted in many places ranging from Poland to Finland, including Estonia (Ojaveer 2006).

The introduction and expansion of species can modify ecosystems by altering community composition (Gurevitch & Padilla 2004), population size and age structure, food webs, but also by introduction of new parasites and pathogens (Gozlan *et al.* 2005). Some possible positive effects of water temperature increase in the Baltic Sea have also been predicted. For example expansions of the distribution areas of several commercially important warm-water species like bream and pikeperch (Lappalainen & Lehtonen 1997). However, such a scenario is desirable only strictly from the point of view of commercial fisheries and possible side-effects of this scenario on the ecosystem on the whole are by far not yet clear.

In conclusion, although the present and possible future salinity characteristics are the key factor determining the large-scale distribution of marine and freshwater species in the Baltic Sea, some other factors, e.g. global warming may also have significant impact.

SUMMARY

In the current thesis I investigated the role of abiotic factors, especially salinity, on the freshwater fish species inhabiting the Baltic Sea area with the emphasis on embryonic salinity tolerance, changes in egg size in different environments, and effects of water salinity on spatial distribution of freshwater fish and fish assemblages.

1. Lake Peipsi whitefish *Coregonus lavaretus maraenoides* has, since the last glacial period, evolved exclusively in freshwater conditions, apart from the other populations of common whitefish. Laboratory experiments showed that its embryo's, as the most sensitive stage, salinity tolerance is significantly lower than in the common whitefish population inhabiting the Baltic Sea (Paper I). Also, significant differences between the salinity tolerance of freshwater and brackish-water populations of ruffe *Gymnocephalus cernuus* were confirmed (Paper II). Despite the geologically short period of time, fish in the Baltic Sea area seem to have adapted to the prevailing salinity conditions.
2. Earlier studies have shown that, if compared to the pelagic eggs of marine fishes in the North Sea, the pelagic eggs of fish inhabiting the Baltic Sea are larger and have decreased specific gravity. In Paper II, I showed that the demersal eggs of freshwater percid ruffe had considerable differences in size, and subsequently also in larval size, between the brackish-water and freshwater populations. The crossing experiments with both freshwater and brackish-water females and males showed that survival at all tested salinities depended only on the female origin, with embryos of brackish-water females

showing higher salinity tolerance (Paper II). This indicates that, in the case of the ruffe, egg properties are decisive in the embryo salinity tolerance. Although the mechanisms, behind the enlargement of eggs of freshwater species in the brackish environment, are unknown, it is yet possible to conclude that the adaptations to salinity conditions of the Baltic Sea are greatly determined by changes in egg characteristics.

3. Investigation of the selectivity of the gillnet series used in the Estonian coastal fish monitoring (Paper III) asserts that this method, while used in assessing fish population structure, may result in biases with regard to interpretations of size structure, and hence, further biological interactions, if the sampling bias is not taken into account. Yet it is difficult to use other, less selective gears due to the shallowness, rocky and/or stony bottom prevailing in the north-eastern coastal Baltic Sea. However, the selectivity model used in Paper III shows satisfactory coverage of size groups larger than 12 cm for the main species, caught with the gillnet series used in coastal fish monitoring in Estonia, perch *Perca fluviatilis* and roach *Rutilus rutilus*. Most importantly, the time series of data obtained using the gillnetting method provides valuable information about relative changes in population structure, which is the main issue in the monitoring. Thus, the employed methodology (with the changes suggested in Paper III) can be considered to be sufficiently reliable for studying the fish communities in the Estonian coastal areas.
4. In the shallow Estonian coastal sea, a steep horizontal salinity gradient is especially evident in several geographically small areas, e.g. bays, and the composition of fish assemblages varies significantly along the gradient. How the fish assemblages' composition in a shallow bay is changing, seasonally and annually, was investigated in Paper IV. The results suggest that factors such as water temperature, water depth, food and shelter possibilities, etc. play an even more important role than salinity in the small-scale distribution of species in the eastern Baltic Sea.
5. One of the most remarkable recent changes in the composition of coastal fish assemblages is linked to the expansion of a non-indigenous species gibel carp *Carassius gibelio* (Paper V). One of the main triggers, in this rapid expansion of area of distribution, is considered to be the small but still significant recent increase in the average temperature of the sea, creating more favourable reproduction conditions for this warm-water cyprinid. Forecasted climate changes in northern Europe will probably affect both the temperature and salinity of the Baltic Sea, causing it to become warmer and fresher, and likely result in shift in the native fishes' distribution, as well as in the expansion of invasive species. So, although the present and possible future salinity characteristics are the key factor determining the large-scale distribution of marine and freshwater species in the Baltic Sea, some other factors, e.g. global warming may also have considerable impact.

SUMMARY IN ESTONIAN

Vee soolsuse roll Läänemere idaosa rannikumere kalastiku kujunemisel

Riimveelise Läänemere idaosa suhteliselt madalas rannikumeres ulatub soolsus kuni 9‰, olles keskmiselt 5–7‰. Jõgede suudmealadel on vesi peaaegu mage (<2‰). Mereliikide, sealhulgas kalade, liigirikkus on suurim Taani väinade piirkonnas ning see väheneb põhja ning ida suunas, kusjuures väiksema soolsusega kaldaäärseid piirkondi asustavad ka mitmed mageveeliigid. Läänemeri on geoloogilises ajaskaalas noor meri ning seda asustavad liigid on saanud selle praeguste keskkonnatingimustega kohaneda alla kümne tuhande aasta. Paljude mere – ja magevee kalaliikide täiskasvanud isendid on riimvee suhtes tolerantsed, kuid edukaks paljunemiseks peavad siirduma vastavalt kas kõrgema (süvikud) või madalama soolsusega (estuaarid, jõed) aladele. Kalade ontogeneesi jooksul on embrüonaalne staadium kõige tundlikum ebasobivate keskkonnatingimuste suhtes, mis seab kindlad piirid paljunemineks sobivale keskkonnale. Siiski on mõned mageveest pärinevad kalaliigid võimelised kudema kõrgema soolsusega (6–8‰) merealadel, mida peetakse mageveeliikide embrüonaalse soolsustaluvuse kriitiliseks piiriks. Käesoleva dissertatsiooni eesmärgiks oli analüüsida, kas ja kuidas Läänemere piirkonda asustavad liigid on kohastunud ebasoodsate soolsustingimustega ning samuti selgitada, kui suur roll on soolsusel rannikumere peamiselt mageveeliikidest koosneva kalastiku kujunemisel.

1. Peipsi siig *Coregonus lavaretus maraenoides* on Läänemere kaldaäärseid piirkondi asustava merisiia *Coregonus lavaretus* alamliik, kes on pärast viimast jääaega seoses rändevõimaluse kadumisega Läänemerest elanud vaid magevees. Laborikatsetega selgitati, et Peipsi siia embrüonaalse kui kõige tundlikuma eluperioodi soolsustaluvus on oluliselt väiksem kui merisiial (artikkel I). Katsed kinnitasid ka seda, et kiisa *Gymnocephalus cernuus* rannikumerd ja Peipsi järve asustavate populatsioonide soolsustaluvus on erinev (artikkel II). Niisiis võib väita, et hoolimata geoloogiliselt lühikesest ajavahemikust on Läänemere piirkonda asustavad kalad adapteerunud vastavate soolsustingimustega.
2. Varasemad uuringud on näidanud, et võrreldes Põhjamerd asustavate mere- liikide (nt. tursk *Gadus morhua*, lest *Platichthys flesus*) pelaagilise marjaga on nende Läänemeres elavate liigikaaslaste mari suurema läbimõõduga ning suurenenud ujuvusega. Et teada saada, kas ka mageveeliikide puhul võib erineva soolsusega keskkonnas optimaalne munaraku suurus varieeruda, uuriti kiisa vastavaid parameetreid. Leiti, et kiisa demersaalne mari (mõõdeti küpseid ootsüüte) ning samuti sellest koorunud vastsed olid meres elavatel kiiskadel oluliselt suuremad kui mageveepopulatsiooni kaladel (artikkel II).

Magavee- ja merekiiskade ristamiskatsed näitasid, et embrüote ellujäämus erinevatel soolsustel sõltus vaid emase päritolust, kusjuures ellujäämus kõrgematel soolsustel oli oluliselt kõrgem riimveest pärit emaste embrüotel. Seega on võimalik järeldada, et muutused Läänemere piirkonda asustavate kalaliikide embrüonaalses soolsustaluvuses on tõenäoliselt suurel määral tingitud just ootsüütide omaduste muutustest.

3. Hindamaks artiklites IV ja V kasutatud andmete kogumise meetodikat, analüüsiit kuuest erineva silmasuurusega nakkevõrgust koosneva jada selektiivsusust sellega kõige sagedamini püütavate kalaliikide ahvena *Perca fluviatilis* ja särje *Rutilus rutilus* näitel (artikkel III). Tulemused näitasid, et kuigi nakkevõrgud on väga selektiivne püügivahend, ning püütud kalade pikkuseline ning vanuseline jaotus ei pruugi peegeldada kalapopulatsiooni tegelikku struktuuri, on nende kalaliikide puhul antud võrguseeria püükides pikkusklassid >12 cm küllaltki rahuldavalt esindatud. Samas on teiste, vähem selektiivsete püügivahendite (nagu traalide ja suurte nootade) kasutamine Läänemere kirdeosa valdavalt madalas kariderohkes ja kohati tiheda veetaimestikuga rannikumeres piiratud või võimatu. Kokkuvõttes annavad nakkevõrkudega standardmeetodikat jälgides kogutud andmerekad väärtuslikku informatsiooni suhteliste muutuste kohta populatsioonides ja võimaldavad võrrelda eri alade kalastikku. Niisiis võib öelda, et artiklite IV–V puhul kasutatud meetodika on sobiv ning piisavalt usaldusväärane kirjeldamiseks Eesti rannikumere kalakooslusi. Seda eriti juhul, kui võrgujadale lisada võrk silmasuurusega 14 mm, mida on soovitatud artiklis III ja tegelikult rannikumere seires ka juba kasutusele võetud.
4. Eesti rannikumere mitmetele piirkondadele on iseloomulik suhteliselt järsk horisontaalne soolsuse gradient, mida mööda muutub ulatuslikult ka kalastik (domineerivad liigid, liikide arvukus jne.). Sellised piirkonnad on näiteks lahed: Matsalu laht, Saunja laht jt. Seda, kuidas ja mil määral kalastik niisuguses piirkonnas aastaringselt ning aastate jooksul muutub, uuriti artiklis IV Matsalu lahe näitel. Tulemused näitasid, et kuigi soolsus on peamine tegur, mis määrab kalaliikide leviku piirid Läänemeres, on mingi geograafiliselt väikse piirkonna kalastiku struktuuri (liigiline koosseis, dominantliigid eri aastaegadel jne.) täpse väljakujunemise juures olulisemad veetemperatuur, sügavus, taimestiku parameetrid ning sobivate toiduobjektide ja varjupaikade olemasolu.
5. Kõige ilmekamaks hiljutiseks muutuseks Läänemere idaosa kaldalähedaste alade kalastiku liigilises koosseisus on võõrliigi hõbekogre *Carassius gibelio* arvukuse järsk tõus viimase 20 aasta jooksul (artikkel V). Üheks peamiseks teguriks selle liigi eduka leviku taga võib pidada keskmise veetemperatuuri tõusu suveperioodil ning sellega kaasnevaid sobivamaid sigimistingimusi selle soojalembese kalaliigi jaoks. Prognoositud kliimamuutused Euroopa põhjaosas mõjutavad tõenäoliselt ka Läänemere veetemperatuuri ja soolsust, muutes mere soojemaks ja magedamaks. Selle üheks tagajärjeks võivad olla

muutused kohalike kalaliikide levikus ning invasiivsete võõrliikide leviala laienemine. Prognooside realiseerumisel võivad siia ilmuda liigid, kes on soojalembesed, aga madalam soolsus seab nende paljunemisele piirid ning eelise saavad mageveekalad.

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Selectivity of gillnet series in sampling of perch (*Perca fluviatilis* L.) and roach (*Rutilus rutilus* (L.)) in the coastal sea of Estonia

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ABSTRACT

The selectivity pattern of perch and roach for a 6 net gillnet series (mesh sizes 17, 21, 25, 30, 33 and 38 mm) was studied using the gamma model. Data were collected in 1995–2004 during routine coastal fish monitoring surveys in Estonia covering 6 permanent monitoring areas along the coastline. Gamma curves were fitted to the length distributions of different mesh sizes using all strata and relative abundances of the length groups in the gillnet catches were derived. Based on relative abundances the estimated length distributions were calculated, and the representativeness of different length groups in the catches was evaluated. Size groups 17–27 cm of perch and roach were overrepresented in the catches using the gillnet series and the size groups <12 cm were covered insufficiently. Adding nets with smaller mesh sizes to the series would cover more sufficiently smaller size groups and small-sized species without discontinuation of long-term data series.

Key words: selectivity, gillnets, coastal fish monitoring

INTRODUCTION

The Estonian Marine Institute of University of Tartu has conducted routine coastal fish monitoring using a gillnet series at standard stations in Estonian coastal waters since 1992 (Saat *et al.* 2003). This method is used also in Latvia, Lithuania and Sweden (Ådjers *et al.* 2001; Appelberg *et al.* 2003). The main objective of the monitoring is to determine trends in coastal fish populations

and assemblages related to natural variation and large-scale environmental changes (Appelberg *et al.* 2003). In addition, the same method has been applied to study seasonal and spatial distribution of fish and it has been used in environmental impact assessment as well (Saat & Eschbaum 2002).

Originally, the standardised mesh sizes (17–38 mm measured from knot-to-knot) were designed for coastal monitoring considering mainly the two abundant species in the coastal fish communities – perch and roach (Neuman *et al.* 1997; Saat *et al.* 2003), but also with the aim to give reliable comparable information about other species inhabiting the sea. Besides monitoring with gillnets, experimental fishing is occasionally undertaken using other gears like fyke nets and hand seines. Therefore it is known that small-sized fish species and younger age-classes are insufficiently covered in gillnets' catches when using minimum mesh size of 17 mm (measured from knot to knot) in the study area (Saat & Eschbaum 2002; Vetemaa *et al.* 2006).

It is also known, that the overall selectivity of a gillnets series may be such that certain size groups may be over- or underrepresented (Hamley 1975; Holst *et al.* 1998; Appelberg *et al.* 2003). As gillnets are passive gears, the fish which move more and fast, have a larger probability of encounter with the gear than less and slow moving fish (Sparre & Venema 1998). Hence the length distribution of fish encountering the gear may differ from the length distribution of the entire population (Millar & Fryer 1999; Finstad *et al.* 2000). Selectivity may affect any estimates that imply random sampling, e.g. length-weight regressions, sex ratios, capture-recapture estimates of population size, and calculations of growth, age distribution as well as mortality (Hamley 1975).

Previous studies concerning gillnet selectivity of perch and roach have been focusing on freshwater environment, e.g. lake and reservoir littoral zones (gillnet series: Jensen, 1986; Nordic-type multimesh gillnets: Kurkilahti & Rask 1996; Finstad *et al.* 2000; Kurkilahti *et al.* 2002) or multimesh gillnets in the coastal areas of the Baltic (Appelberg *et al.* 2003). There are not many studies available on estimated size distributions. Finstad *et al.* (2000) compared the age and length distributions of Arctic char from gillnet catches and estimated directly from mark-recapture experiments. The results of their study show strong underestimation of smaller-sized fish when sampling with gillnets. The study of gillnet selectivity of cod population in the North Sea showed the same tendency (Hovgård *et al.* 1999).

The purpose of the present study was therefore to i) study the gillnet selectivity pattern of perch and roach over the gillnet series in areas where these species occur; ii) calculate the estimated length distributions based on the selectivity pattern; iii) find the gaps in the present gillnet series according to the selectivity pattern, and based on available length distribution of perch and roach in the coastal areas of Estonia, suggest additional mesh sizes for the gillnet series. Studying the selectivity patterns of two different species enables better evaluation of gillnet series used in the coastal fish monitoring.

MATERIAL AND METHODS

Study areas

Routine coastal fish monitoring using gillnets was initiated in 1992 off the south-eastern coast of Hiiumaa Island as HELCOM warm water fish monitoring area. Later this monitoring was extended to other permanent study areas including the gulfs of Riga and Finland (Saat *et al.* 2003). During the first years, the catch was not recorded separately by each net and data from these years are excluded from the current study. Data from all six areas were included in the present study (Fig. 1): 1. Kihnu (1997–2004), 2. Vilsandi (1997–2004), 3. Matsalu (1995–2004), 4. Hiiumaa (1998–2004), 5. Käsnu (1997–2004), 6. Vaindloo (1997–2004).

Gillnetting

The survey is conducted in July-August each year, starting from Kihnu in the south and ending in Vaindloo in the north. In the Hiiumaa area (area 4) the location of stations is fixed, in other areas the locations are selected each day according to weather conditions and differ between years, so for each setting occasion the position of the station is recorded.

The series of nets used consists of 6 bottom gillnets with mesh sizes 17, 21, 25, 30, 33 and 38 mm, measured from knot to knot. The nets are 1.8 m (6 feet) deep and made of multifilament nylon. Each net consists of a 60 m long stretched net bundle, which is attached to a 27 m floating line (35 cm between floats, buoyancy 6g/m) and a 33 m lead line (weight 2.2 kg/100 m). Hanging ratio is therefore approximately 0.5. Yarn thicknesses are no. 210/2 (2 filaments each weighing 210 g per 10 000 m) for 38–33 mm and no. 110/2 for all other sizes (Neuman *et al.* 1997). Colour is green, dark blue or grey irrespective of the mesh size. Buoys and weights are used at the both end of station. The nets are tied together at the upper corner in random order.

Nets are set between 17:00 to 20:00 at the depth of 2–5 m parallel to the coastline and lifted the following morning between 7:00 and 10:00. Catch of each net is recorded separately. All fish are measured individually (total length to nearest mm).

Fish retention is unknown and assumed to be equal throughout the series. The proportion of catch enmeshed in different ways is not recorded. In case of perch it is known that the bigger fish can be entangled by spiny dorsal fins or by gill cover. Roach is typically caught gilled or wedged.

Statistical analysis

Selection pattern calculations were based on fish length. The raw length data in millimetres were transformed to 0.5 cm length groups.

To estimate the selectivity of the gillnet series, the gamma function was used for the modelling (Millar & Fryer 1999; Hovgård & Lassen 2000):

$$S(\lambda | \alpha, \beta) = \left[\frac{l}{(\alpha-1)\beta} \right]^{(\alpha-1)} \exp \left[\alpha - 1 - \frac{l}{\beta} \right] \quad (1)$$

where λ was length/mesh size, α and β (k *mesh size) were the parameters estimated in the fitting process, and l was the length of fish.

As there were rather few fish in some strata, the bootstrapping method (Elfron 1979, cited in: Haddon 2001) was used to estimate the best selection curves. Length distribution from each stratum was resampled for each mesh size separately. The value of α was estimated from the pooled data and estimated α was then used in fitting k for each bootstrap sample. The number of bootstrap iterations was 1000. *Alpha* and mean value of k from bootstrapping analysis was used to calculate the optimal length for each mesh size:

$$(\alpha-1)\beta \quad (2)$$

The selectivity curves obtained were used to calculate the estimated length distributions (in mm) from the catches using the gamma lines (l) of every mesh size. The pooled results of all mesh sizes (l) were used to estimate the relative abundance of each size of fish in the population according to Gulland and Harding (1961): for a length l , if a mesh size m has a relative efficiency of ${}_mP_l$, and catches ${}_mN_l$ fish, then the abundance in the population is proportional to:

$$\frac{\sum_m {}_mN_l}{{}_mP_l} \quad (3)$$

For the estimated length distribution calculations, the maximum ${}_mP_l$ was taken as 1 and the ${}_mP_l$ was divided with $\max {}_mP_l$:

$$\frac{\sum_m {}_mN_l}{\sum_m ({}_mP_l \cdot \max_m P_l^{-1})} \quad (4)$$

The results were transformed to 1 cm length groups for better graphical presentation. For the evaluation of the representative length distributions from the gillnet series used, the pooled selection curves of different mesh sizes were used. The suggestions of additional mesh sizes are based on the estimated parameters (α , k) of existing mesh sizes.

RESULTS

Perch

Altogether length data of 25704 perch caught with gillnet series from all six areas were used in the bootstrapping iterations (Table 1). The pooled length distribution was dominated by the length groups 13–24 cm (Fig. 2).

The 50% selection range (W , calculated as 75% relative efficiencies) increased progressively as the mesh size increased (Table 1, Fig. 3). Length distribution of mesh size 38 mm showed higher proportion of smaller length groups available for the gillnets in the study areas and scarceness of bigger fish in some study areas (e.g. Kihnu). Selection curves of mesh sizes 30 and 33 mm showed some overlapping, but the optimal lengths over all net series showed rather even coverage of length groups (Fig. 3). The summarized selectivity curves showed that size groups 17–27 cm of perch were overrepresented in the gillnet catches (Fig. 4).

Roach

Altogether length data of 19981 roach caught with gillnet series from three areas were used in the bootstrapping iterations (Table 2). The pooled length distribution was dominated by the length groups 14–25 cm (Fig. 2).

The 50% selection range increased progressively in mesh sizes 17–25 cm, and showed no pattern in mesh sizes 30–38 mm (Table 2, Fig. 3). The optimal length for the biggest mesh size 38 mm according to gamma model was smaller than for 33 mm, the gamma function fitted poorly to the length distribution in the catches of mesh size 38 mm and showed the scarceness of fish of optimum length and larger (Table 2). Although the optimal length was overlapping in mesh sizes 33–38 mm, the length distribution was wider in 38 mm net (Fig. 3) and the net catches more larger fish than smaller mesh sizes.

The summarized selectivity curves showed that size groups 17–27 cm of roach were overrepresented in gillnet catches (Fig. 4) as well as in case of perch, reflecting the length distribution of raw data (Fig. 2).

Estimated length distributions

We used the data from the Matsalu study area in 2004 in order to compare the length distributions from gillnet catches with the estimated length distributions based on the summarized selection curves (Fig. 5). Using the method of pooled selectivity curves of different mesh sizes the number of smaller and bigger fish in the catches could not be estimated because of fewer fish caught.

In case of roach gamma model fitted poorly to length distribution of mesh size 38 mm. When using the parameters estimated for mesh size 30 mm, also in mesh size 38 mm, the optimal length for roach would be 29.2 cm instead of

24.2 (Table 2). As can be seen in Figure 2, there were almost no roach caught of this size. Therefore the estimated length distributions of roach were based on mesh sizes 17–33 mm.

The length range of fish caught reflected the optimal lengths of smallest and biggest mesh size. The optimal length for mesh size 17 mm was 13.4 cm for perch (Table 1) and 14.5 cm for roach (Table 2) and for mesh size 38 mm 26.7 in perch and 24.2 cm in roach.

The length distributions also showed the strongest underestimation of the 15 cm perch in the catches. The peaks in estimated and gillnet length distributions coincided more or less in perch (Fig. 5). Regarding roach the relative underestimation of smaller fish in gillnets catches was much higher (Fig. 5).

DISCUSSION

This study showed the differences in selectivity pattern of gillnet series in sampling of perch and roach and the differences in the length distributions of gillnet catches and in estimated size distribution of the population.

The length distribution of perch and roach caught with gillnets was not the same, although similar (Fig. 2), and presumably reflected the most abundant size groups in the study areas. The differences between selection patterns of the species studied can be explained with the differences in the body morphology: the roach has a softer body and can be more compressed whilst perch has strong fins and harder, less compressible body (Pihu *et al.* 2003; Vetemaa *et al.* 2003). The girth of perch and roach of the same size, although not measured in this study, could also be different. That might be one explanation why the roach captured in the same mesh size are longer than perch. But also with the differences in the distribution pattern: e.g. in the Matsalu study area perch was homogeneously distributed and abundant all over the bay, the larger fish preferring shallower areas in the inner part of the bay, whereas the abundance and size of roach increased towards deeper areas of the outermost part of the bay. So the preferred areas the different size groups of roach and perch could be covered by the different sampling effort.

According to the gamma model used the size groups 17–27 cm of perch and roach are overrepresented using the current gillnet series. Due to some skewness of data, that is not covered by the model it can be assumed, that the overrepresentation is not so high at size groups 17–25 cm in perch and 17–22 cm in roach. However, Hovgård *et al.* (1999) found that the estimated size distributions of cod were largely independent of the choice of the selectivity model used. Figure 2 also shows that there are not many fish bigger than 25 cm caught with the gillnet series and probably the size groups 17–25 cm are actually dominating in the study areas.

Hamley (1975) suggested that each way fish is captured should be described as normal curve and the total selectivity by the sum of these curves. In entangling (perch, mesh sizes 17, 21 and 25 mm) and probably snagging (perch, mesh 38 mm; roach mesh sizes 30, 33, 38 mm) it is likely that the skewed side could be described as second curve. As the way of capture is not recorded, it would be hypothetical to separate the length distributions according to this. An experimental study would enable more accurate assumptions on different curves for each mesh size.

The estimated length distributions (Fig. 5) even out the over- and under-representations of the selective length distributions of size groups 12–28 cm in the gillnet catches according to the pooled selectivity curves (Fig. 4). The above estimates of selection pattern are nevertheless indirect and length distributions should therefore be regarded as estimates only.

A direct estimation of target species catchability and net selectivity could be done by:

- a) A comparison with gear of known selectivity. In present case it is very difficult to do this kind of estimation as the study areas are shallow and using the different type of gear is limited. The gears used besides gillnets are usually trap nets and beach seines with unknown selectivity and escapement rate. Using sonars or detonations with limited power (Sandström & Karås 2002) would probably give unselective results, but only in limited space.
- b) Fishing a known population, e.g. releasing tagged fish into the environment before the gillnetting is begun. In practice direct estimations are seldom used because of the expense of providing known populations of fish. Also the tagging mortality should be either avoided or recorded, and the tags used for selectivity studies should not increase the catchability of fish. Tagging would however provide us with better estimations of selectivity of the gillnet series.

The study asserts that the use of gillnet series for assessing population structure may result in biases with regard to interpretations of size structure, and hence, further biological interactions, if the sampling bias is not taken into account. However, time series of samples obtained with gillnet series may give valuable information about relative changes in population structure, which actually is the main issue for the monitoring.

As mentioned above, fish < 12 cm are not caught in the gillnet series. This is in accordance with findings of Finstad *et al.* (2000), and Hovgård *et al.* (1999), who described the same tendency in sampling with gillnets. The main explanation is that the mesh sizes are too big to catch smaller fish. Also the swimming distance and speed of fish may have an effect. It is known that larger fish move faster than small fish of the same species (the swimming speed can be approximated by constant times a power function of a length; Wardle 1996)

and cover larger areas (Millar & Fryer 1999), and combined with a larger mass, increased energy for entanglement (Finstad *et al.* 2000). Therefore the fishing effort with passive gears like gillnets should be progressively higher towards smaller mesh sizes.

The present gillnet series overestimates to some extent the size groups 17–27 cm, especially in roach as mentioned above. Reducing the number of nets (e.g. mesh size 33 mm) would lead to opposite – underestimation of larger size groups (23–26 cm). However, as there are rather few fish that were caught with nets with mesh size 38 mm, no reason is seen to add larger mesh sizes to the existing series. According to Jensen (1986), a geometric series of mesh sizes is recommended for use if an equal efficiency for fish of a certain length interval is wanted. As the present gillnet series provides coverage sufficient enough of fish > 12 cm, the optimal solution would be adding smaller mesh sizes. As roach captured in the same mesh size are longer than perch, the need for smaller mesh sizes is obvious especially when sampling roach. Herewith the discontinuation of long-term data series can also be avoided.

Based on the parameters derived from existing series, two additional gillnets with smaller mesh sizes are suggested to the existing series: 11.5 and 14 mm (Figure 6). The series follows a geometric series with ratio between mesh sizes being approximately 1.2 for mesh sizes 11.5–30 mm.

Adding smaller mesh sizes to the existing series should be also followed by having more gillnet stations to shallower water. The smaller mesh sizes hopefully catch better not only smaller size-classes of perch and roach, but also the small-sized species like black goby (*Gobius niger*) and great sandeel (*Hyperoplus lanceolatus*), which are known to be abundant (R. Eschbaum, personal communication). The negative side is the possibility to catch myriads of sticklebacks. Sampling with supplementary gillnets would also give experimental and more direct evaluation on the length distribution estimated here and allow more accurate estimation of selectivity in the future.

Conclusions

- i. Size groups 17–27 cm of perch and roach are overrepresented in the catches using the gillnet series and the size groups < 12 cm are covered insufficiently.
- ii. The estimated length distributions even out the over- and underestimations in size groups 12–28 cm.
- iii. Reducing the number of nets or adding larger mesh sizes is not needed when considering species like perch and roach.
- iv. The optimal solution in terms of continuing the long-term dataset is adding nets with smaller mesh sizes to the present gillnet series.
- v. For better estimations of selectivity and evaluation of gillnet series the experimental studies e.g. recording the different ways the fish are captured and tagging experiments are recommended.

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TABLES

Table 1. The optimal length, parameters, the 50% selection range (W) derived from bootstrapping and the number of perch used in bootstrapping.

Mesh size (mm)	17	21	25	30	33	38
Optimal length (cm)	13.38	16.47	19.04	22.05	23.58	26.66
α	207.27	146.25	187.96	242.98	249.88	276.15
k	0.0038	0.0054	0.0041	0.0030	0.0029	0.0026
W (cm)	1.4	2.0	2.0	2.1	2.2	2.4
No of fish (raw data)	5870	6882	6314	4014	2020	604

Table 2. The optimal length, parameters, the 50 % selection range (W) derived from bootstrapping and the number of roach used in bootstrapping.

Mesh size (mm)	17	21	25	30	33	38
Optimal length (cm)	14.53	17.80	20.71	23.04	24.25	24.16
α	157.61	96.12	108.72	234.81	357.53	94.13
k	0.0055	0.0089	0.0077	0.0033	0.0021	0.0068
W (cm)	1.7	2.7	3.1	2.3	1.9	3.8
No of fish (raw data)	3403	5538	5711	3537	1541	251

FIGURES



Figure 1. Study areas along the coastline of Estonia: 1 – Kihnu, 2 – Vilsandi, 3 – Matsalu, 4 – Hiiumaa, 5 – Käsmu, 6 – Vaindloo.

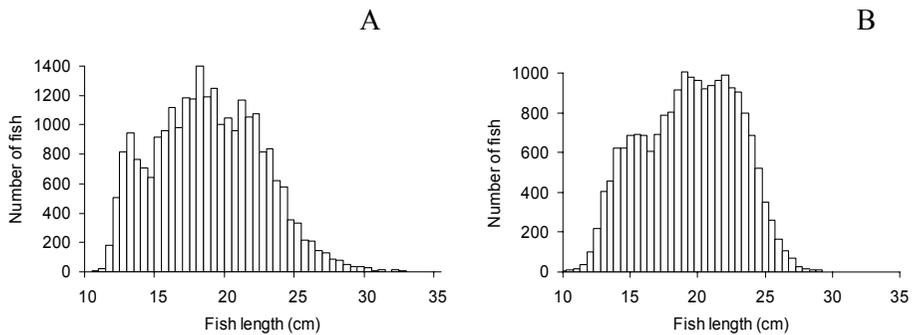


Figure 2. Length distributions of fish in 0.5 cm groups sampled with gillnet series and used in the selectivity calculations. A – perch ($N=25704$), B – roach ($N=19981$).

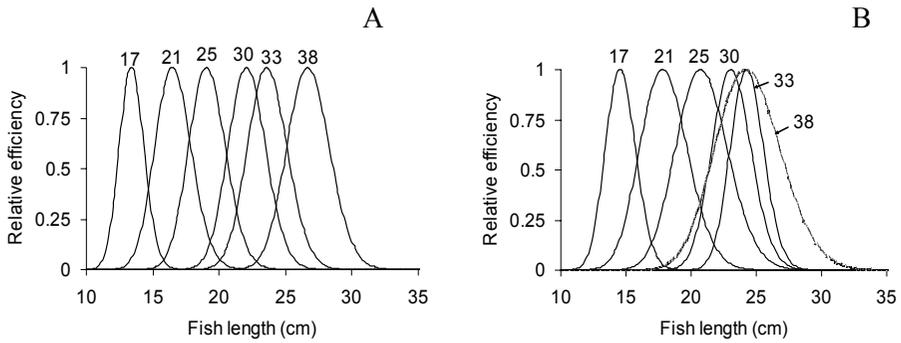


Figure 3. Gamma curves of different mesh sizes of perch (A) and roach (B) over the gillnet series.

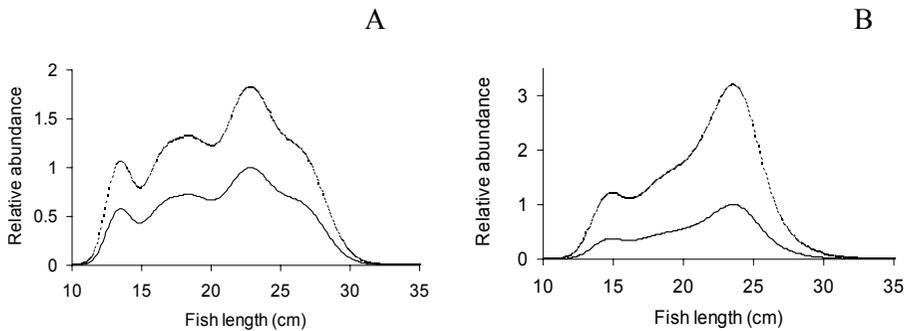


Figure 4. Relative abundance of the length groups (cm) of perch (A) and roach (B) in the gillnet catches (dotted line) and transformed abundance with maximum at 1 (whole line) according to the selection pattern of different mesh sizes.

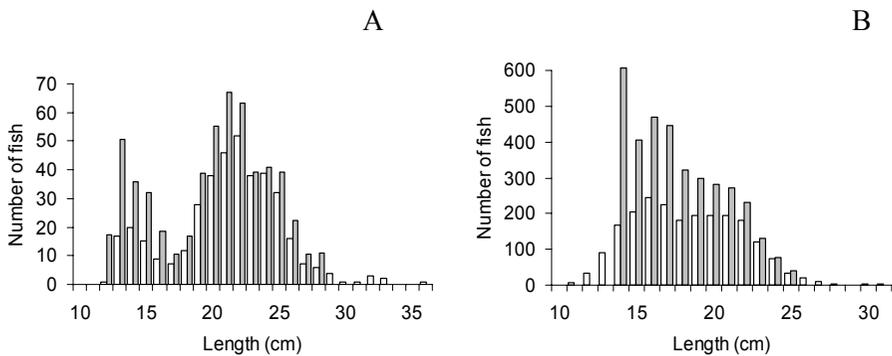


Figure 5. Length distribution of gillnet catches (white) and estimated from the pooled selectivity pattern (grey) of perch (A) and roach (B) in Matsalu study area in 2004.

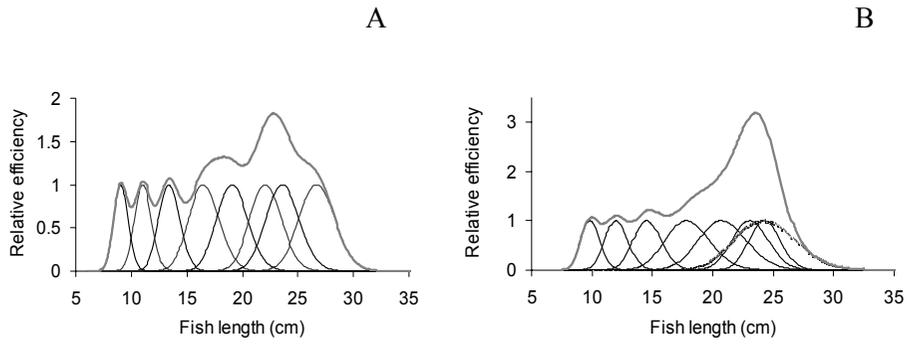


Figure 6. Existing gillnet series with two suggested additional mesh sizes: 11.5 and 14 mm. A – perch, B – roach. Grey line – summarised selectivity curves.

Vetemaa, M., Eschbaum, R., Verliin, A., Albert, A., Eero, M., Lillemägi, R., Pihlak, M. & Saat, T. 2006. Annual and seasonal dynamics of fish in the brackish-water Matsalu Bay, Estonia. *Ecology of Freshwater Fish*, 15: 211–220.

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Vetemaa M., Eschbaum R., Albert, A. & Saat T. 2005. Distribution, sex ratio and growth of *Carassius gibelio* (Bloch) in coastal and inland waters of Estonia (north-eastern Baltic Sea). *Journal of Applied Ichthyology* 21: 287–291

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II Research history

1. Research interests
Reproduction of freshwater fishes in the Baltic Sea; water salinity as a factor affecting fish assemblages' composition and distribution; dynamics of coastal fish.
2. Publications
 1. Albert, A., Vetemaa, M. & Saat, T. 2004. Effects of salinity on the development of Peipsi whitefish *Coregonus lavaretus maraenoides* Poljakow embryos. *Annales Zoologici Fennici* 41 (1): 85–88.
 2. Eschbaum, R., Saat, T., Vetemaa, M., Verliin, A., Eero, M., Albert, A. & Spilev, H. 2004. Changes in Estonian coastal fish assemblages during recent years (Eesti rannikumere kalastiku muutused viimastel aastatel). *Estonia Maritima* 6: 73–109. In Estonian with English summary.

3. Albert, A., Möller, T. & Vetemaa, M. 2005. Flora of Matsalu Inner Bay: species composition and changes during last decade (Matsalu siselahe taimestik: liigiline koosseis ja muutused viimasel kümnendil). Loodusevaatlusi 2004–2005: 19–32. In Estonian with English summary.
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5. Vetemaa M., Eschbaum R., Albert, A. & Saat T. 2005. Distribution, sex ratio and growth of *Carassius gibelio* (Bloch) in coastal and inland waters of Estonia (north-eastern Baltic Sea). Journal of Applied Ichthyology 21: 287–291
6. Vetemaa, M., Eschbaum, R., Verliin, A., Albert, A., Eero, M., Lillemägi, R., Pihlak, M. & Saat, T. 2006. Annual and seasonal dynamics of fish in the brackish-water Matsalu Bay, Estonia. Ecology of Freshwater Fish, 15: 211–220.
7. Albert, A. Vetemaa M. & Saat T. 2006. Laboratory-based reproduction success of ruffe, *Gymnocephalus cernuus* (L.), in brackish water is determined by maternal properties. Ecology of Freshwater Fish, 15: 105–110.

3. Conference thesis

1. VIII International Symposium on the Biology and Management of Coregonid Fishes. 26–29.08.2002 Rovaniemi, Finland. Oral presentation “Effects of salinity on the development of Peipsi whitefish *Coregonus lavaretus maraenoides* embryos” by Albert, A., Vetemaa, M.
2. ICES Annual Science Conference. 24–27.09.2003 Tallinn, Estonia. Oral presentation “Invasion of gibel carp into the Estonian coastal sea” by Vetemaa, M., Albert, A., Eschbaum, R., Saat, T.
3. Behaviour and ecology of freshwater fish: Linking ecology and individual behaviour. 22–26.08.2004 Silkeborg, Denmark. Poster presentation “Is the reproduction success of ruffe (*Gymnocephalus cernuus* (L.)) in moderate salinities determined by maternal properties?” by Albert, A., Vetemaa, M., Saat, T.
4. XI European Congress of Ichthyology. 6–10.09.2004 Tallinn, Estonia. Poster presentation “Seasonal dynamics of fish in brackish-water Matsalu Bay, Western Estonia” by Vetemaa, M., Eero, M., Lillemägi, R., Eschbaum, R., Verliin, A., Albert, A., Saat, T.
5. XII European Congress of Ichthyology. 9–13.09.2007 Cavtat (Dubrovnik), Croatia. Poster presentation “Reproduction characteristics of spawning population of brackish-water ruffe *Gymnocephalus cernuus* (L.) in Käina Bay (eastern Baltic Sea)” by Albert, A., Vetemaa, M., Saat, T.
6. XII European Congress of Ichthyology. 9–13.09.2007 Cavtat (Dubrovnik), Croatia. Oral presentation “Effects of cormorants on fish populations in a shallow eastern Baltic bay” by Eschbaum, R., Vetemaa, M., Verliin, A., Albert, A., Taal, I., Saat, T.
7. ICES Annual Science Conference. 17–21.09.2007 Helsinki, Finland. Oral presentation “Spatial variation in size distribution of two freshwater species, European perch (*Perca fluviatilis* L.) and roach (*Rutilus rutilus* L.), in the shallow coastal area of the NE Baltic Sea” by Albert, A.

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II. Teaduslik ja arendustegevus

1. Peamised uurimisvaldkonnad
Mageveekalade sigimise edukus Läänemeres; vee soolsus kui kalastiku liigilist koosseisu ja levikut mõjutav tegur; rannikumere kalastiku dünaamika.
2. Publikatsioonide loetelu
 1. Vetemaa, M., Eschbaum, R., Verliin, A., Albert, A., Eero, M., Lillemägi, R., Pihlak, M. & Saat, T. 2006. Annual and seasonal dynamics of fish in the brackish-water Matsalu Bay, Estonia. *Ecology of Freshwater Fish*, 15(2), 211–220.
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3. Konverentside teesid

1. VIII International Symposium on the Biology and Management of Coregonid Fishes. 26–29.08.2002 Rovaniemi, Soome. Suuline ettekanne “Effects of salinity on the development of Peipsi whitefish *Coregonus lavaretus maraenoides* embryos” Albert, A., Vetemaa, M.
2. ICES Annual Science Conference. 24–27.09.2003 Tallinn, Eesti. Ettekanne “Invasion of gibel carp into the Estonian coastal sea” Vetemaa, M., Albert, A., Eschbaum, R., Saat, T.
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4. XI European Congress of Ichthyology. 6–10.09.2004 Tallinn, Eesti. Posterettekanne “Seasonal dynamics of fish in brackish-water Matsalu Bay, Western Estonia” Vetemaa, M., Eero, M., Lillemägi, R., Eschbaum, R., Verliin, A., Albert, A., Saat, T.
5. XII European Congress of Ichthyology. 9–13.09.2007 Cavtat (Dubrovnik), Horvaatia. Posterettekanne “Reproduction characteristics of spawning population of brackish-water ruffe *Gymnocephalus cernuus* (L.) in Käina Bay (eastern Baltic Sea)” Albert, A., Vetemaa, M., Saat, T.
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7. ICES Annual Science Conference. 17–21.09.2007 Helsinki, Soome. Suuline ettekanne “Spatial variation in size distribution of two freshwater species, European perch (*Perca fluviatilis* L.) and roach (*Rutilus rutilus* L.), in the shallow coastal area of the NE Baltic Sea” Albert, A.

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