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PRESS

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LIST OF ORIGINAL PUBLICATIONS

I Ojaveer, H. 1997. Environmentally induced changes in distribution of fish aggregations on the coastal slope in the Gulf of Riga. pp. 170–183. *In* Proceedings of the 14th Baltic Marine Biologists Symposium, Pärnu, Estonia, 5–8 August 1995. Ed. by E. Ojaveer. Estonian Academy Publishers, Tallinn.

II Ojaveer, H. Application of experimental trawl data for estimation of fish stock dynamics in the Gulf of Riga (Baltic Sea). Submitted to ICES Journal of Marine Science.

III Ojaveer, H., and A. Lankov. 1997. Adaptation of eelpout, *Zoarces viviparus* (L.), to spatially changing environment on the coastal slope of the Gulf of Riga (Baltic Sea). ICES CM/EE:03.

IV Ojaveer, H., A. Lankov, A. Lumberg, and A. Turovski. 1997. Forage fishes in the brackish Gulf of Riga ecosystem (Baltic Sea). pp. 293–309. *In* Forage Fishes in Marine Ecosystems. Alaska Sea Grant College Program, University of Alaska Fairbanks, AK-SG-97-01.

V Ojaveer, H., and A. Lumberg. 1995. On the role of *Cercopagis* (*Cercopagis*) *pengoi* Ostroumov in Pärnu Bay and the northeastern part of the Gulf of Riga ecosystem. Proceedings of the Estonian Academy of Sciences. Ecology, 5: 20–25.

VI Ojaveer, H. Exploitation of biological resources of the Baltic Sea by Estonia in 1928–1995. Limnologica, in press.

VII Svedäng, H., H. Ojaveer and E. Urtans. 1997. Interpretation of the otolith structures in viviparous blenny *Zoarces viviparus*. Journal of Applied Ichthyology, 13: 137–142.

ABSTRACT

The organisms inhabiting the brackish Baltic Sea can roughly be divided into three major groups: freshwater organisms, marine boreal euryhaline eurytherm species and glacial relicts. Owing to the rather short period of the existence of the sea, the species belonging to these groups have largely retained the adaptations to their pre-immigration habitats. Therefore, the distribution of freshwater fish is mostly restricted to the near-coastal areas, marine species are found over the whole basin and cold-water species (incl. glacial relicts) usually dwell in deep water-layers, during the warm season below the thermocline. However, to these groups a fourth group of organisms — non-indigenous species introduced through human activities into the Baltic Sea, should be added. Among these, the most recent invader, the cladoceran *Cercopagis pengoi*, has a high abundance in the warm season and constitutes a substantial part of the diet of several fish species in the Gulf of Riga.

In general, in utilization of forage reserves, the different groups of organisms are also restricted to spatially separate parts of the Gulf of Riga. The basic part of the energy (in the form of nourishment) for the maintenance of the ecosystem and the biological production is derived from frontal zones. The permanent fronts at the Pärnu River estuary and in the Irbe Sound area, as well as at the seasonal thermocline (especially in the intense mixing zones), attract large fish aggregations. Higher indices for their stomach fullness and a lower percentage of empty stomachs were recorded in and near the thermocline. Direct relationship between fish and their food abundance need not always exist as fish can graze down higher food concentrations. Therefore, fish feeding activity is a better indication of fish feeding conditions and is used in this study.

In the relatively young Baltic Sea, intense adaptation processes of the immigrants are mainly triggered by the availability of energy (food) resources. In order to get access to energetically important prey species, the older age-groups of marine boreal herring have transferred to deeper cold water, whereas young smelt (a cold-water species) is distributed in warm water above the thermocline. Originally the cold-water eelpout has developed as a specific warm-water ecological group in the shallow Pärnu Bay which is rich in prey organisms. These differ from the eelpout which is found in the cold-water in the Ruhnu Deep in otolith characters, number of vertebrae, growth rate, etc.

Under the present conditions of intense exploitation of a number of marine biological resources, changes in the abundance of at least of a number of fish stocks should be assessed. The presently applied single-species VPA does not meet these requirements. The results of the present work indicate that, based on regular experimental bottom trawl surveys, the long-term abundance dynamics of fish stocks can be evaluated. This applies also to currently non-assessed and

non-target species. Advanced stock assessment methods that consider fish stocks as constituents of the ecosystem, where trophic relationships (i.e., predation) play a vital role, should be developed. One such method, consisting in the indexing of monthly complete trawl surveys of commercial as well as prey species and comparing and interpreting the results in space and time, is suggested in this work.

Since 1974, important fluctuations in the abundance of marine fishes (e.g., herring, sprat, cod), glacial relicts (e.g., fourhorned sculpin, smelt, eelpout) as well as in fishes of freshwater origin (e.g., pikeperch, bream, bleak) have taken place in the Gulf of Riga. These have probably been caused by a number of factors, which could be classified as internal impacts (natural deviations in the environment, anthropogenic effects) and external influences (saline water inflows, presence or absence of cod) affecting the ecosystem.

1. INTRODUCTION

The Gulf of Riga is one of the most eutrophied areas in the Baltic (HELCOM 1997). It also supports a high fish production and accounts for about 4% of the total fish landings in the Baltic Sea (for the Baltic herring, the percentage caught in the Gulf of Riga is over 12%). Certain fishes (e.g., pikeperch and smelt) are mainly caught in the Pärnu Bay area, which currently provides livelihood for more than 800 fishermen. However, the basin has a much broader importance for Estonia than the direct monetary profit from the fishery alone. Other important uses of the basin include recreation, maritime transport, and, in former times, seal hunting.

The importance of the Gulf of Riga is also reflected in the scientific efforts devoted to investigations of the ecosystem, which date back to the early 1920s. In the thermine cruises, started by K. Frisch and H. Riikoja in 1923, several abiotic and biotic parameters were determined. Studies on phytobenthos (started in 1847), zooplankton (since 1956), fish larvae (from 1946), nektobenthos (systematic investigations between 1974–1994), regular studies in fish fauna (since 1974, with some gaps) and recording of fish catches (since the turn of the century) are all examples of systematic studies of the biota of the Gulf of Riga. These investigations were accompanied by the simultaneous recording of the key abiotic parameters of the ecosystem (e.g., Sidrevics *et al.* 1993). Most of this research has been dedicated to developing a better understanding of the factors influencing the dynamics of commercial fish stocks (Rannak 1954, Erm 1967, Kornilovs 1993, Gaumiga *et al.* 1997).

Synthesis of the scientific knowledge accumulated to the present allowed Ojaveer and Elken (1997) to draw the conclusion that the Gulf of Riga could be treated as an ecologically functioning sub-system in the multi-basin Baltic Sea. This means that both scientific efforts and management principles should be applied separately for this ecosystem.

The current study should be seen as a continuation and intensification of investigations of the ecosystem of the Gulf of Riga in the following three directions:

1. The distribution pattern of main fish species in the Gulf of Riga, including some microevolutionary aspects.
2. The identification of the main regions (hydrodynamic frontal zones) responsible for the existence and production in the whole ecosystem.
3. The application of experimental trawl data for the estimation of fish stock dynamics, including presently non-target and non-assessed species.

2. THE ENVIRONMENT OF THE GULF OF RIGA AND THE LOCATION OF THE RESEARCH AREA

The relatively enclosed Gulf of Riga; with an average depth of 20 m, long-term mean surface area of 16 330 km^2, and a volume of 424 km^3 (Berzinsh 1995) is situated in the northeastern of the Baltic Sea. On the northwestern side, it is bordered by Saaremaa and Muhu islands (Figure 1). The deepest part of the Gulf of Riga (*ca.* 60 m) is located southeast of Ruhnu Island. Small islands and several banks are found in the northern part while the comparatively large Gretagrund Bank with Ruhnu Island is situated in the central part of the Gulf.

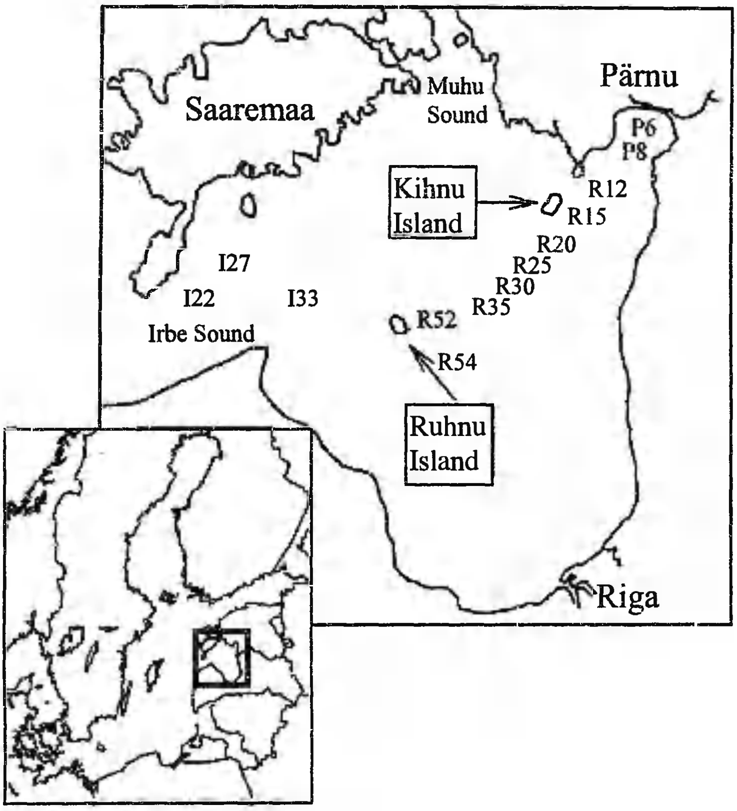

Figure 1. Location of sampling sites in the Gulf of Riga. Numbers denote the depth of a given station.

The Gulf of Riga receives runoff from a huge drainage area (134 000 km^2). The volume of the annual freshwater inflow is 31 km^3 (Yurkovskis *et al.* 1993). Approximately 84% of the total freshwater input enters the southern part of the basin (Andrushaitis *et al.* 1995), mainly via four Latvian rivers: Daugava, Lielupe, Gauja and Salaca. The rather limited water exchange with other parts of the Baltic, which is generally wind-driven, takes place through Irbe (sill depth *ca.* 20m) and Muhu (sill depth *ca.* 5m) sounds. The annual amount of water flow through the sounds is estimated at about 360 km^3 (Petrov 1979) and 147 km^3 (Berzinsh *et al.* 1994). Thus, the theoretical residence times of the water in the Gulf of Riga are 1.2 and 2.4 years, respectively.

Both cyclonic and anticyclonic types of circulation and turnover of water masses have been observed in the basin (Pastors 1967) with the cyclonic type dominating both in the surface and bottom water layers (Berzinsh 1995).

Low and variable salinity — 0.5–2.0 psu in spring in coastal zone and 7.5–7.7 psu in deeper layers close to Irbe Sound (Auninsh 1966) — can be explained by the relative isolation of the Gulf from the open Baltic, and high and variable river discharge. Due to its shallowness, the Gulf of Riga lacks a permanent halocline and, thus, a distinct nutricline. This feature makes nutrients accessible for biological transformation processes through regular mixing of the whole water column during the cold season. Mean long-term water temperature is 0.0 (annual variation from –1.1 to 2.1) for winter and 12.0°C (variability range 10.4–14.2) for summer (Berzinsh 1995).

The strongest (quasi)permanent hydrological fronts are found close to the river mouths and Irbe Sound (Berzinsh 1995, Lips 1995). The biggest horizontal gradients are formed in the eastern part of the Gulf during the warm season. Intense vertical mixing occurs in the western regions and the Irbe Sound, due to the water exchange processes with open parts of the Baltic Sea.

A very important feature of the oceanographic regime of the Gulf of Riga is its relatively high nitrogen content (2–3 times higher) as compared to other parts of the Baltic Sea. Phosphorus is believed to be the limiting nutrient in the Gulf of Riga ecosystem (Yurkovskis *et al.* 1993).

Long-term and seasonal dynamics of the hydrological parameters of the Gulf of Riga are determined by several factors, which can be classified into three types (for further details see Berzinsh *et al.* 1994, Berzinsh 1995):

1. Geographical location and the related climatic features;
2. Occasional, periodic or quasiperiodic deviations of different parameters, in particular those of climatic origin (e.g., temperature, precipitation, air pressure, water exchange in sounds);
3. Anthropogenic factors that cause changes in oceanographic (mainly hydrochemical) characteristics.

The main mechanisms forming the oceanographic regime of the Gulf of Riga are atmosphere-surface water layer interactions (which are transmitted to the water column by turbulence and convective mixing processes) and water inflow from rivers and the open Baltic which create density gradients and density driven circulation (Berzinsh 1995).

For studying environmentally related spatial distributions of fish aggregations, the survey area was designed to cover most of the depth range on the coastal slope in the Gulf of Riga. This was achieved on the transect from Pärnu Bay to Ruhnu Deep (Figure 1). The stations locations were determined from depth rather than fixed by strictly recorded coordinates. With the addition of the sampling sites in Irbe Sound, the entire survey area embraced (quasi)-permanent hydrological frontal regions in Irbe Sound (stations I22, I27 and I33) and Pärnu River estuary (stations P6 and P8) as well as the seasonal thermocline (stations R12–R30). Seasonal variability in the life cycle of the fish populations in the Gulf of Riga (wintering, spawning and feeding concentrations) was recorded through surveys organised monthly on this transect.

3. ORIGIN AND EVOLUTION OF THE ORGANISMS INHABITING THE BALTIC SEA

3.1. General

A series of glaciations in the Pleistocene resulted in the fauna of the brackish Baltic Sea being poor compared to similar seas in other regions (e.g., in the Caspian Sea). The glacier that covered the Baltic basin during the last Ice Age started to retreat about 15,000 years ago. Salinity conditions similar to those prevailing today have occurred for about the last 3,000 years (Ignatius *et al.* 1981). This is a short period of time in the evolutionary scale for the establishment of an ecosystem with complex biological interactions and adaptations of the organisms. Moreover, in a changing brackish environment populated by organisms of different origin (e.g., marine and freshwater) these evolutionary processes take probably more time than at stable salinities. Therefore, the biota of the Baltic Sea is still undergoing a rather rapid development both in terms of new invasions (e.g., Paper V, Salemaa and Hietalahti 1993, Lagzdins and Pallo 1994, Skora 1996) and adaptation of the species already dwelling there (Papers I and III). It is suggested here that this should be considered as a normal process of evolution of a relatively young brackish ecosystem.

3.2. Origin and distribution of the organisms

The organisms found in the Baltic Sea originate from different types of environments: from marine areas, freshwater bodies of the surrounding continent and the Caspian-Black Sea basin. They have immigrated into the Baltic basin during various stages of the development of the Baltic Sea since the deglaciation started (Ignatius *et al.* 1981). Some of the first organisms that invaded the cold and oxygen-rich postglacial Baltic Sea still survive and have retained their original requirements to the environment. Their distributions are confined to the regions such as the Gulf of Riga, Gulf of Finland and Gulf of Bothnia where the corresponding niche has retained. The species in the Baltic Sea can be roughly divided into three groups: marine boreal, freshwater and relict organisms on the basis of where they originated (Paper I).

The settlement of immigrants in a new area can be successful only if they can reproduce there and have viable offspring. Concerning reproduction, the ecological groups of fishes have largely retained their environmental requirements formed before their establishment in the Baltic Sea — freshwater species spawn in the coastal zone, marine boreal species at higher salinities and glacial relicts at low temperatures. However, both with respect to temperature and salinity, adaptations of these ecological groups to the conditions in the Baltic Sea are obvious, driven probably by seeking of higher survival rate for their offspring (Ojaveer 1988).

The feeding ecology and especially the distribution pattern of species clearly depend on their origin. Freshwater and estuarine fishes predominantly occupy the shallow coastal zone above the seasonal thermocline while marine boreal euryhaline species are abundant above or in the mixing zone of the seasonal temperature front and the complex of cold-water fish (including the glacial relicts) usually dwell below the seasonal thermocline (Figure 2). A schematic diagram, showing the general distribution pattern of the most abundant representatives of these main components of the fish fauna on the coastal slope in the Gulf of Riga in relation to the seasonal thermocline during the feeding period is given in Figure 3. In this figure smelt (*Osmerus eperlanus eperlanus*) represents the glacial relicts; herring (*Clupea harengus membras*) and sprat (*Sprattus sprattus balticus*) the marine boreal euryhaline fish and pikeperch (*Stizostedion lucioperca*) and sticklebacks (*Gasterosteus aculeatus* and *Pungitius pungitius*) the freshwater and estuarine species.

3.3. Some adaptational considerations

The distribution and adaptations of marine euryhaline species (e.g., herring, sprat, cod (*Gadus morhua callarias*) and flounder (*Platichthys flesus*)), to brackish conditions in the Baltic have been studied rather thoroughly. The investigations indicate that marine species (mostly herring and cod, but also sprat) have successfully adapted to very diverse regional environmental variability. This has resulted in the development of a complicated stock structures in these species (e.g., Ojaveer 1988, Shvetsov *et al.* 1995). In addition, two distinct cod stocks exist in the Baltic (Bagge *et al.* 1994). Other species of marine fishes have been studied less intensively, probably due to the in much smaller commercial importance. Certain non-commercial species such as gobies (*Pomatoschistus* spp.) and straight-nosed pipefish (*Nerophis ophidion*) are clearly tolerant to a wide range of environmental conditions and can endure both low salinity and increasing eutrophication. They have successfully adapted to the environment in the productive coastal zone (e.g., the Pärnu River estuary) and are only seldom found in deeper regions (Paper II).

Fishes of fresh- or brackishwater origin mostly occupy the shallow coastal zone. Their distribution is generally restricted by salinity conditions. However, migration into deeper waters of pikeperch from the very shallow Pärnu River estuary is observed in summer. This is probably connected with the seaward migration of herring, the pikeperch's main prey in this area.

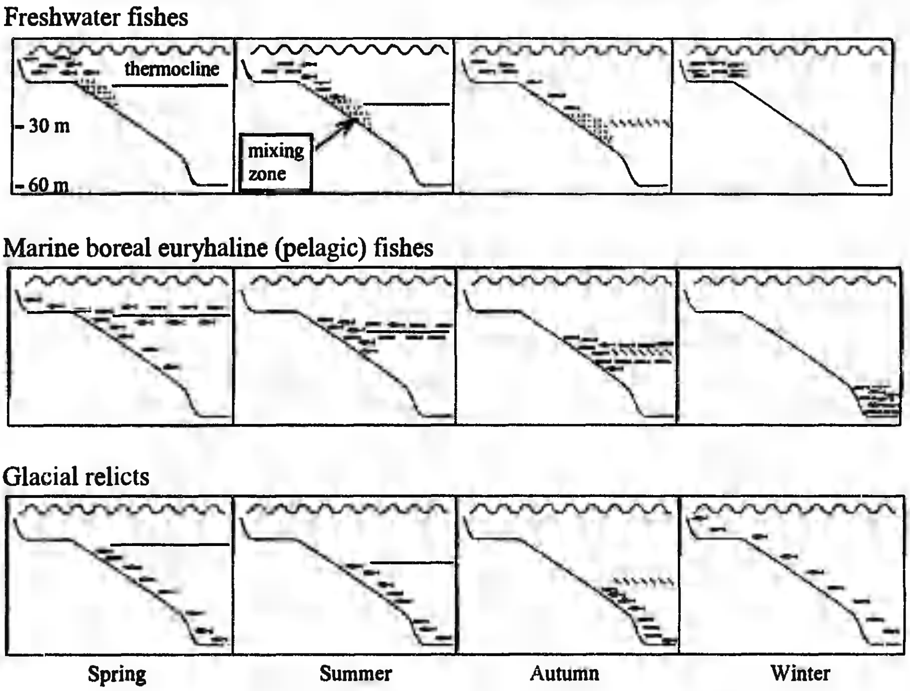

Figure 2. Spatio-temporal dynamics of representatives of three groups of natural immigrants of fishes of the Baltic Sea.

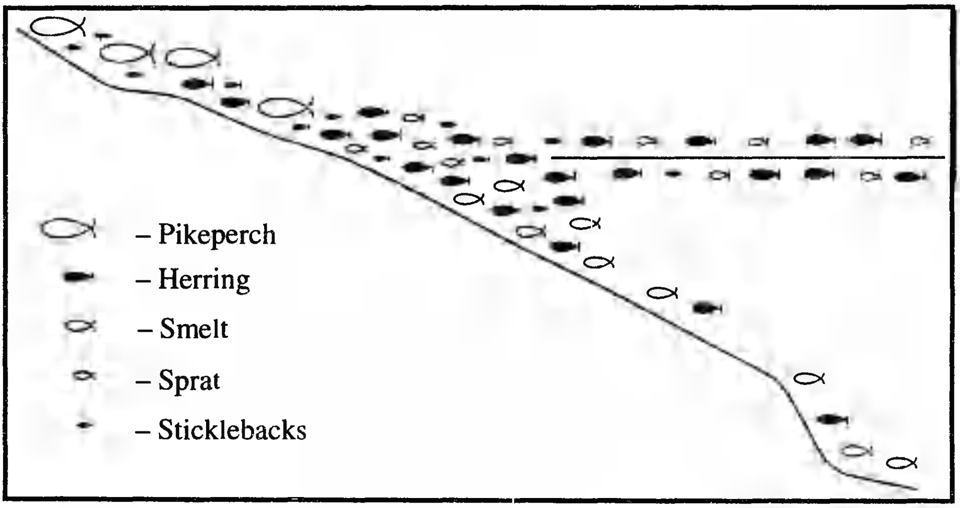

Figure 3. Schematic illustration of the general distribution pattern of the most abundant fishes on the coastal slope in the Gulf of Riga. For details see Section 3.2.

The glacial relicts of marine origin that invaded Northern Europe by easterly routes have undergone repeated physiological adaptations to fresh and again to brackish-water conditions (e.g., Segerstråle 1966). Those adaptations have been fixed both morphologically and genetically. Thus, a wide capacity for adaptation of glacial relicts with regard to rather diverse salinity and also oxygen (Fischer *et al.* 1992) conditions have convincingly been demonstrated. Until recently, the distribution area of glacial relicts has been believed to be generally restricted to cold water layers. However, Hansson (1980) found the typical glacial relict fourhorned sculpin (*Myoxocephalus quadricornis*) in upper water layers above the seasonal thermocline during summer.

For the present study, eelpout (*Zoarces viviparus*) was chosen for investigations on adaptation of fishes to the Baltic environment. In the first phase, the otolith formation pattern of the species was examined. This led to a revision in the interpretation of the eelpout's otolith structures. In contrast to earlier studies (Kristoffersson and Oikari 1975), we found that the opaque otolith material was mainly deposited in spring and summer (during the main feeding period of the fish) and hyaline in autumn and winter. Two important events during the early life history of the fish — hatching and birth — were both registered in fish otoliths by the formation of the corresponding hyaline rings (Paper VII). The ageing of eelpout carried out in the rest of the study was performed according to this new information.

The present investigation also revealed that the adaptation of eelpout, originally probably a stenotherm cold-water inhabitant, has lead to the formation of two phenotypically distinct and spatially separated ecological groups in the Gulf of Riga. The group populating deeper regions (i.e., below the seasonal thermocline) dwells in cold-water stenotherm conditions. The other group, which differs from the stenotherm fraction in, among other things, its otolith characters, number of vertebrae and growth rate occurs in the shallow Pärnu Bay area where much greater annual temperature variability is recorded. The phenomenon was not known before the current study. The fish occupying the transitional zone between the main distribution centres of these two groups, i.e., the region around the seasonal thermocline, display an intermediate or a mixed pattern of the parameters measured (Paper III). The distributions of smelt also shows evidence of adaptation of this group to the local conditions. In the northeast Gulf of Riga, young smelt (age-groups 0 and 1) were usually, but not alone, found in the warm water layers above the seasonal thermocline during the feeding period (Paper I).

It is suggested here that the driving force for the above adaptations is that newly colonized areas present a richer and energetically more valuable food supply than already colonized areas (Paper III). Compared to deeper water layers, shallower regions are characterised by higher production of food items. This probably favours the invasion of benthos-feeding cold-water inhabitants (e.g., smelt and eelpout) into such regions. On the other hand, herring, which are generally considered to be pelagic planktivores in the ocean, penetrate during summer into deeper and colder regions in order to find food of higher caloric content, i.e., large cold-water calanoid copepods and nektobenthic organisms (e.g., Ojaveer 1988). Thus, the above-named species appear to have changed their distribution patterns according to the distribution and availability of their most valuable food organisms. Those fish species that are less adaptable with regard to changes of evolutionarily developed species-specific predator-prey relationships or adaptations to different environmental parameters (e.g., temperature and salinity) have retained their distribution patterns with respect to the environment from which they originate. Such species include sprat, most of the glacial relicts as well as freshwater and estuarine species.

In the case of eelpout's adaptation process to eurytherm conditions in shallower areas, it is suggested here that natural selection is probably the strongest in the transition area between the two distinct environments (i.e., in the region of the seasonal thermocline) (Paper III).

3.4. Continued immigration to the Baltic and its implication for ecosystem dynamics

Owing to their transport in ballast waters, transfers of non-indigenous species have markedly increased during recent decades (e.g., Carlton and Geller 1993, Carlton *et al.* 1995). Very recently, the appearance of a new inhabitant of the Baltic Sea, the cladoceran *Cercopagis pengoi* (Ostroumov, 1891), also called water flea, was observed in the Gulf of Riga (Paper V). The natural distribution of this species is mainly in brackish-water environments in the Ponto-Caspian region (Mordukhai — Boltovskoi and Rivier 1987). From there, *Cercopagis pengoi* has apparently been introduced into the Baltic Sea, most likely by means of ship ballast waters.

In order to succeed in a new environment, it is important that the newcomer find favourable living conditions in the new habitat. The water flea has found them in shallower areas and become a part of the Gulf's food-web. It is preyed upon by adult herring, sticklebacks, bleak (*Alburnus alburnus*) and juvenile smelt. The animal, however, appears to be too large to be consumed by young (0-group) individuals of the above-named species (Paper V). Several other fishes, whose distribution areas overlap to a greater or lesser extent to that of *C. pengoi* (i.e., pikeperch, vimba bream (*Vimba vimba*), white bream (*Blicca bjoerkna*) and sprat) were not found to feed upon this prey item.

The invasion of *Cercopagis pengoi* into the Gulf of Riga clearly influences the abundance dynamics and condition of fish stocks differently. Warm-water freshwater and estuarine species (e.g., bleak and sticklebacks) and euryhaline planktivorous herring, whose distribution areas overlap with that of *C. pengoi*, may have directly profited from this invasion through improved feeding conditions in warm summer months. As the distribution of cold-water species (e.g., smelt) exhibit only a slight overlap with *C. pengoi*, its occurrence will not have substantial direct impact on the stock size of fishes in this category. The influence of this cladoceran upon the zooplankton community in the research area is as yet unknown.

4. PRODUCTIVITY ZONES IN THE GULF OF RIGA

4.1. General

The distribution and productivity of organisms in marine ecosystems are heterogeneous. According to the general view, elevated biological activity, both in terms of standing stock and/or production, often occurs in the regions with a rapid variation of 'auxiliary energy' of oceanographic processes (including various fronts, currents, upwellings and turbulence). The development of the hydrological formations depends on solar activity, transmitted into the water directly (heat input), or indirectly (as the momentum from the wind) (Mann and Lazier 1991). In addition, differences in water density (salinity) can also give rise to formation of frontal structures.

Elevated chlorophyll biomass and/or primary productivity occur, at least intermittently, within or close to hydrological fronts (e.g., Pingree *et al.* 1975, Savidge 1976, Richardson 1985, Richardson *et al.* 1986a, Munk 1993). Peaks in copepod productivity and abundance of copepod eggs have been observed in mixed and, particularly, in frontal waters whereas zooplankton abundance is not always higher in these regions (e.g., Kiørboe and Johansen 1986, Kiørboe *et al.* 1988). The latter phenomenon has been explained by the influence of both currents and former oceanographic conditions and also by zooplankton population dynamics. As to fish stocks in frontal areas, the abundances of fish eggs and larvae are higher and the development, growth and survival of eggs and larvae are often better in frontal than in neighbouring areas (Richardson *et al.* 1986b, Munk *et al.* 1995, Grioche and Koubbi 1997). Raid (1989) suggested that the aggregation of larvae and young fish in frontal areas is probably due to more favourable long-term average feeding conditions there.

Upwelling areas (which are often synonymous with frontal regions) are also important as aggregation areas for adult fish, where especially high landings are taken (e.g., Crawford *et al.* 1989). Extensive upwelling regions do not exist in the Gulf of Riga. Local coastal upwelling, however, occurs during long-lasting offshore winds.

Thus, various oceanographic characteristics and processes can give rise to regions of primary significance with regards to biological productivity of marine ecosystems. Such regions may play a key role in the process of recruitment to several fish stocks as well as determine the growth rates of exploitable fish populations.

4.2. Permanent hydrological fronts

In the Gulf of Riga, permanent hydrological fronts are situated in river estuaries including that of the Pärnu River, where the strongest and most permanent hydrochemical gradients can also be found. The transition area between the Gulf of Riga and the Baltic Proper, the Irbe Sound, has been thoroughly studied with regard to water exchange. The results published by Lips (1995) allow the conclusion that a quasipermanent but migrating salinity front of complicated horizontal and vertical structure exists in this area.

The Pärnu River estuary and its bordering areas support very high production of zoobenthos (Kotta and Kotta 1995) and fish (Paper I) as compared to the deeper regions of the Gulf of Riga. This area is clearly dominated by freshwater species with the addition of some of the marine euryhaline component. In the region, important spawning grounds and larval retention areas of the Gulf of Riga herring, pikeperch, smelt and other species are situated. Thus, year-class abundance of these fish stocks is mainly formed here (Erm 1967, Shestakov 1967, Rannak 1970).

The Irbe Sound is characterised by a salinity front with mild vertical temperature stratification during the warm season (Paper I). This area (stations I22 and I27, Figure 2) is, during the warm season, an important region for the aggregation of feeding juvenile clupeoids, probably due to the good feeding conditions (important factors are probably the food supply as well as the abiotic environment). The biomass and abundance of clupeoid's prey — zooplankton — did not always exceed that at other stations with smaller fish catch rates. However, food availability also depends on the distribution of prey organisms. As stated by Kiørboe and Johansen (1986), the distribution of zooplankton is a function of both current and former oceanographic conditions and zooplankton dynamics. They also noted that, considering our present knowledge, it is difficult to understand distribution of older copepod stages.

4.3. Seasonal thermocline

As the water temperature of the upper water layers rises in the spring, the seasonal thermocline is formed at depths of 8–12 m (stations P8-R12, Figure 1) on the coastal slope in the Gulf of Riga. From its formation, the distributions of the main fish aggregations are closely related to it. During the whole course of thermocline development, the fishes inhabiting the coastal slope of the Gulf of Riga were mainly concentrated in the mixing zone at the seasonal thermocline (see Figure 2). The mixing zone is the region where an active upwelling of waters from below the thermocline takes place. There, the fish catches were significantly higher than those at adjacent stations (Paper IV).

In the Gulf of Riga, solar radiation and winds are the most important processes affecting the thermal depth structure and the stability of the water column. After its formation in spring, the seasonal thermocline gradually descends during the warm season until it disappears at the onset of homothermium in autumn. However, persistent northeast winds during the summer transport warm water masses out of Pärnu Bay causing inflow of cold waters from deeper layers, which results in an intensification of the seasonal thermocline ($\Delta t_{max} = 7.0°C$ has been measured at the depth of from 5 to 6 m) even in the Bay. Pelagic fish shoals closely follow the movements of the thermocline.

It is likely that the affinity of fish aggregations with the mixing zones of different water masses is related to more favourable feeding and abiotic conditions in these regions during the main feeding period. Ojaveer and Kalejs (1974) argued that, due to permanent upwelling of nutrient-rich waters (mainly phosphates) from below the thermocline, these regions are characterised by elevated plankton production and, thus, provide a rich food supply for plankivorous fishes. In addition, environmental conditions (temperature) seem to favour the aggregation of fish species with different temperature preferences (e.g., sprat, herring and smelt) around the mixing zone.

A positive correlation between fish food and fish abundance need not always be found at important feeding grounds as high standing stocks of fish can graze down food organisms (e.g., zooplankton), thus resulting in a negative correlation. Therefore, fish feeding activity (the percentage of fish with empty stomachs and stomach fullness index) and the size of fish aggregations are better measures of fish feeding conditions. This study shows that significantly lower numbers of empty stomachs of adult clupeoids were observed in the mixing zone at the seasonal thermocline than above and below it. However, this generalization cannot be made for smelt and sticklebacks. The stomach fullness index of herring and smelt caught in the mixing zone tended to be higher than that in adjacent areas (Paper IV). Thus, the aggregation of pelagic fishes in the mixing zone at the seasonal thermocline is probably due to the richer food supply (zooplankton), which generally results in elevated feeding activity of fish.

It can be concluded that with regard to the long-term maintenance and production of biocoenoses in the ecosystem of the Gulf of Riga in general, a notable part of the energy transfer to higher trophic levels takes place in hydrographically active zones — in the permanent and seasonal frontal areas. In addition, these regions are of essential importance in the formation of exploitable productivity of fish stocks.

5. ESTIMATION OF FISH STOCK DYNAMICS AND THE FACTORS RESPONSIBLE FOR STOCK FLUCTUATIONS

5.1. General

As it was already mentioned in the Introduction, the ecosystem of the Gulf of Riga should be considered as an autonomously functioning part of the Baltic Sea. Therefore, its biological resources (including fish stocks) should also be treated separately. At present, only the most important commercial fish stocks (herring, sprat and cod), permanently or periodically inhabiting the basin, are assessed. According to the current assessment methods and management regime, the fish of the Gulf of Riga are dealt with as a part of much larger regions (ICES 1996). This is not always scientifically justified. The stock dynamics of other commercial fishes, mostly of local importance, has been followed on the basis of commercial catch statistics (Paper VI, Winkler 1991, Erm *et al.* 1992), a method which often is of questionable reliability and takes into account only the recruited part of the stock. The dynamics of the non-commercial fish stocks (e.g., sticklebacks, gobies and bleak) have received almost no scientific attention. In the Baltic, however, where the species diversity is low, the importance of non-commercial and less abundant species in mediating the energy flow is probably greater than in other aquatic ecosystems.

There is no doubt that conventional single-species assessment models, even if they are appropriate and applicable (which they are not), are inadequate for the assessment of the intensive fisheries today. It is obvious that the removal of a considerable amount of commercial (mainly predatory) fish out of the sea has a substantial impact on the predator-prey interactions and on the stocks which are taken incidentally as by-catch. When starting exploitation of a stock, it is clear that in addition to the abundance and structure of the exploited stock, its prey, competitors and predators will also be affected by the fishery. Thus, the whole ecosystem will be changed (Laevastu 1996).

Therefore, better fish stock estimation methods than those presently in use, are urgently needed. The current study provides one possible alternative solution for this problem: the use of experimental survey data, regularly collected on a transect through the main area of fish distribution (including feeding and wintering areas).

In the past, removal of fish by means of the commercial fishery was thought to be the most important factor affecting the stock dynamics of the exploited populations. The scientific knowledge accumulated recently points to a more complicated and not yet fully understood interaction of mechanisms responsible for changes in fish stocks. Based on the observation that several widely separated fish stocks have varied synchronously despite being managed differently, Mann (1993) concluded that physical factors, acting through the marine food web are probably the governing factors for fish stock change. Similarly, Cushing (1982) stated that most probably the well-known gadoid outburst in the North Sea during the 1960s was of climatic origin, mediated through the food web via plankton development that resulted in better feeding conditions for gadoid larvae and in several abundant year-classes. Environmental alterations in the marine ecosystem, induced by climatic changes or factors of anthropogenic origin, have been identified as possible causes of changes in fish stocks by many other fisheries scientists (e.g., Anttila 1973, Lehtonen and Hilden 1980, Corten 1986, Southward *et al.* 1988, Beamish 1993).

5.2. Description of the method proposed

Bottom trawl surveys with a generally similar sampling designs were conducted at fixed depths on the transect from Pärnu Bay to Ruhnu Deep on a monthly basis (Figure 1). In each haul, the species composition and abundance of fish species were determined. Due to minor changes in the stations (depths) sampled over the whole study period (1974–1986 and 1994–1996), certain grouping of the stations sampled were inevitable. Distributions of twelve of the most abundant fish taxa over the whole study area were analysed using abundance values or means, if there existed more than one observation per 'grouped station' per haul by stations (for methodological details see Paper II). As the first step, the catch per unit effort data were analysed by the following multiplicative model on logarithm transformed catch numbers:

$$\log(\text{catch}+1) = \text{Year} + \text{Month} + \text{Depth} + \text{Year*Month} + \text{Year*Depth} + \text{Month*Depth} + \varepsilon, \qquad (1)$$

where:

catch — the number of a certain fish caught per 30 min haul; 1 was added to all catches to allow for calculation of logarithms from zero values;

Year, Month and Depth — the year-effect, month-effect and depth-effect, respectively;

ε — the error term; and

Year*Month, Year*Depth and Month*Depth are interaction terms.

In order to circumvent the problems of the existence of statistically significant interactions that hinder clear interpretation of the main effects and a high number of zero catches for the majority of the fish taxa analysed, the monthly survey was chosen as one observation. Thus, for data analysis, the following GLM model was applied:

$$\log(\text{mean catch}+1) = \text{Year} + \text{Month} + \varepsilon, \qquad (2)$$

where mean catch is the monthly average catch by number of a species.

The year-effect in model (2) was used as an index describing the dynamics of fish stock abundance. Index values were calculated for the twelve most important species (the species that yielded a total catch of more than 500 individuals during the whole study period).

5.3. Advantages and weakness of the method

The results of the present estimate generally agreed with the results of the single-species VPA assessments of commercial species (herring, sprat, cod). The sampling and data treatment method also allows the estimation of stock dynamics and the condition of presently non-assessed and non-target species, amongst others, less abundant species (Figure 4). This is important for the evaluation of the state of an exploited ecosystem. When considering the possibilities of parallel data collection for other investigations (e.g., plankton, benthos, fish feeding and parasite studies), the current survey design provides a relatively inexpensive method of carrying out complex studies of the monitoring of marine biotic resources and studies on their interactions.

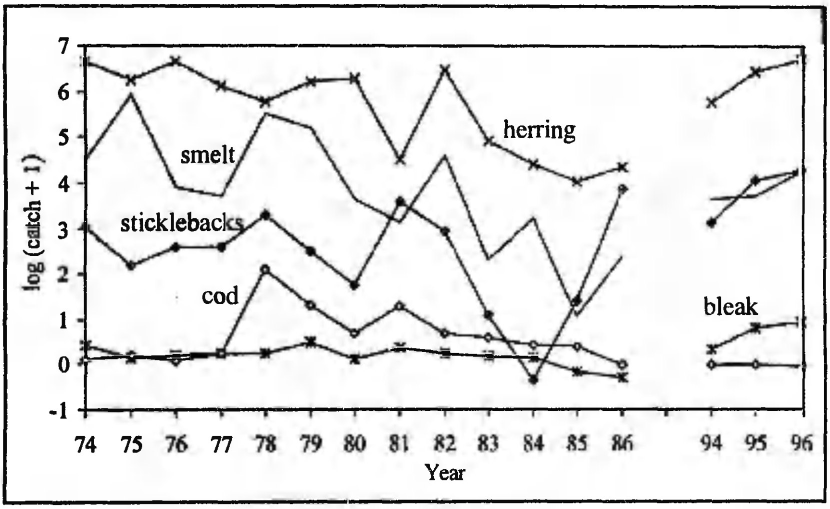

Figure 4. Long-term dynamics of selected fish stocks in the Gulf of Riga, based on model treatment of log-transformed experimental catches. For details see Paper II.

However, one should be aware that some freshwater fishes, that also occupy the shallow coastal zone, are less representatively sampled by this method than most of the marine and cold-water species. Support for this argument can be found from the poorer statistics indices of the GLM models (Paper II). Therefore, in order to get better stock estimates for those fish species, additional sampling with other and more relevant catch methods should accompany the proposed trawl surveys.

5.4. Dynamics of fish stocks and the factors responsible

5.4.1. Dynamics of fish stocks

The dynamics of twelve of the most abundant fish stocks estimated by means of the proposed method, reveal considerable differences between the fish groups of different origin (see Section 3). Generally, higher abundances of the marine pelagic (i.e., herring, sprat) and cold-water and marine demersal species (i.e., smelt, eelpout, cod) in the 1970s was followed by a marked decline in the 1980s. Recently, the stock condition of clupeoids has considerably improved whereas smelt and eelpout have shown only a slight increase in numbers and cod has been disappeared from the Gulf of Riga. Changes in the stock abundance of freshwater fishes (with a few exceptions) were less pronounced than of the fish mentioned above. Compared to the first study period, the abundance of pikeperch and bleak tended to be higher in recent years, whereas no clear changes in the catch rates of other species from the freshwater category studied were detected (Paper II). However, the relatively abundant sticklebacks exhibited, in general, an increase in the stock size over the study period. The dynamics in the abundance of less numerous species was estimated by means of comparing their average values during the two periods with the full-year survey coverage: 1974–1986 and 1994–1996. In general, the fish inhabiting shallower areas showed, opposite or smaller changes in the mean abundance values as compared to those of glacial relicts and marine demersal fishes (Paper II).

5.4.2. The factors affecting changes in fish stocks

The changes in fish stocks observed in Pärnu Bay and the Gulf of Riga are believed to be multifactorial. Changes in essential environmental parameters: water temperature, salinity, oxygen content and pollution load (Sidrevics *et al.* 1993, Berzinsh 1995, etc.) can have affected fish directly via physical interactions. In general, the changes observed have favoured freshwater and estuarine species, tolerant to eutrophication (i.e., sticklebacks, pikeperch, bream, bleak) and caused deterioration in the stock condition of species requiring saline and/or oxygen rich water (including most of the glacial relicts). This is also confirmed by the model estimates (Paper II).

Predation by cod, the only abundant large marine predatory fish in the Baltic, is probably partly responsible for the decline in several forage fish stocks (e.g., clupeoids, smelt, eelpout, gobies, sandeel) in the Gulf of Riga in the late 1970s and the early 1980s. According to Bagge (1981) and Uzars (1994), cod feeds on these species. The occurrence of cod in the Gulf of Riga depends on its stock size in the eastern Baltic, mediated through alterations in hydrological conditions chiefly in the southern part of the sea. These, in turn, are related to large-scale climate changes. Thus, the predation effect on the dynamics of various fish stocks is externally determined rather than governed by alterations in the Gulf of Riga ecosystem itself.

In addition, changes in some commercial fish stocks are likely to be affected primarily by (over)exploitation (pikeperch, eelpout) or by the integrated effect of exploitation and continuous reproduction failure, possibly due to increasing pollution of the marine environment (smelt, possibly eelpout) (Papers II and VI).

At this time, it can be suggested that an improved food resource could be a possible explanation for the observed recent increase in the stock size of non-commercial species, bleak and sticklebacks. These species were found to feed very actively upon a new introduction to the Baltic — the water flea *Cercopagis pengoi* (Paper V).

Separating the effects of anthropogenic influence from changes due to ‘natural’ factors, is often very difficult due to an inability to separate often masked effects of various causative factors and, also, a lack of proper long-term datasets.

In conclusion, the abundance of fish stocks is determined by the state of the whole ecosystem. This, in turn, is influenced by alterations in natural parameters, including climatic changes that affect various phenomena both within and outside (e.g., cod stock dynamics) of the Gulf of Riga, and anthropogenic influences (pollution and resource exploitation). Therefore, the state of the ecosystem and, especially, species interactions within the food web (as proposed, for instance, by Shepherd *et al.* 1984), should be taken into account when developing new methods for fish stock assessment.

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KALASTIKU KOOSSEIS NING KALAVARUDE DÜNAAMIKA LIIVI LAHE ÖKOSÜSTEEMIS

Kokkuvõte

Läänemerd asustavad organismid võib päritolu järgi jaotada kolmeks suureks rühmaks: mageveelised liigid, merelised eurühaliinsed eurütermsed organismid ning jääaja reliktid. Läänemere noore ea tõttu on nende rühmade esindajad üldjoontes säilitanud iseloomulikud immigratsioonieelsed adaptatsioonid. Seega, mageveelise päritoluga kalade leviku areaal hõlmab peamiselt kaldaäärset piirkonda, merelis-eurühaliinseid liike leidub kõikjal üle kogu Liivi lahe ning külmaveelised liigid, sh. jääaja reliktid, asustavad peamiselt sügavamaid piirkondi ja on suvel peamiselt allpool termokliini.

Viimasel ajal on inimmõju tõttu intensiivistunud uute liikide sissevool Läänemerre. See on toimunud peamiselt laeva ballastvete kaudu. Hiljutine tulnukliik, vesikirbuline *Cercopagis pengoi*, on leidnud sobiva elupaiga Liivi lahe kirdeosas, esinedes seal väga arvukalt suvel. Ta on muutunud mitmete kalade oluliseks toiduartikliks.

Enamik energiat Liivi lahe ökosüsteemi ülalpidamiseks ja bioloogilise produktsiooni tekkeks saadakse hüdroloogiliselt aktiivsetest piirkondadest — frontaaltsoonidest. Suuremad kalakoondised paiknevad püsivate hüdroloogiliste frontide läheduses (Pärnu jõe suudmealal ja Irbeni väinas) ning sesoonse termokliini, eriti selle aktiivse segunemistsooni piirkonnas. Kalade kõrgem toitumisintensiivsus ja suurem toitumisindeks ning väiksem tühjade magudega kalade osatähtsus viitab paramatele toitumistingimustele termokliini ümbruses ja selle segunemistsooni piirkonnas.

Organismide kohastumisprotsessid geoloogiliselt noores Läänemeres on suunatud nii paljunemise efektiivsuse tõstmisele kui ka energia- (toidu-) varude paiknemiskohtade hõivamisele. Energeetiliselt väärtuslikuma toidu otsinguil on boreaalse räime vanemad isendid nihkunud toitumisperioodil sügavamatesse (ja külmematesse) veekihtidesse allpool temperatuuri hüppekihti. Liigina külmaveelise meritindi noorjärgud aga hoiduvad soojematesse veekihtidesse ülalpool termokliini. Külmaveelise päritoluga emakalal on evolutsiooni käigus tekkinud sügaval külmas vees elavate isendite kõrvale eraldi ökoloogiline rühm, kes asustab rikkaliku toidubaasiga sooja ja madalat Pärnu lahte. Liivi lahes madalal ja sügaval elavad emakala rühmad erinevad üksteisest otoliitide struktuuri, keskmise selgroolülide arvu, kasvu parameetrite jt. näitajate poolest.

Praegustes mere-elusvarude intensiivse ekspluateerimise oludes tuleb lisaks senistele esmatähtsate töönduskalade (räim, kilu, tursk) varude suuruse hinnangutele analüüsida ka teiste kalade ning mereökosüsteemi funktsioneerimise seisukohast oluliste elusvarude dünaamikat. Praegusel ajal kasutusel olevad

meetodid aga selleks ei sobi. Käesolev töö näitab, et regulaarsetel katsetraalimistel kogutud andmete alusel saab hinnata mitme kalaliigi (sh. vähemoluliste ning töönduslikku tähtsuseta kalade) varude pikaajalist dünaamikat. Tulevikus peavad kalavarude suuruse hindamise meetodid käsitlema kala kui ökosüsteemi üht komponenti.

Uurimisperioodi kestel (alates 1974. a.) on muutunud oluliselt mitme merekala (tursk, räim, kilu), jääaja relikti (meritint, emakala) ja mageveekala (koha, viidikas) varude suurus. Nende tõenäolisi põhjusi võib jagada Liivi lahe sisesteks (keskkonnatingimuste looduslikud kõikumised Liivi lahes, inimreostus) ning välismõjudeks (soolase vee sissevool globaalsete kliimamuutuste tagajärjel, tursa esinemine või mitteesinemine).

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PUBLICATIONS

I

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ENVIRONMENTALLY INDUCED CHANGES IN THE DISTRIBUTION OF FISH AGGREGATIONS ON THE COASTAL SLOPE IN THE GULF OF RIGA

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Abstract. The species composition of fish is richer and their numbers and biomass are higher in the areas of hydrological fronts than in other areas, due to wide variation in abiotic conditions and relatively high abundance and variation in food organisms in these areas. This condition was found to be more pronounced during the feeding period.

Quasipermanent fronts in the Irbe Sound area and in the Pärnu River estuary attract constantly large fish concentrations.

Seasonal fronts, connected mainly with the existence of thermocline, cause regular shifts of large fish aggregations. From spring to autumn fish shoals are found around the thermocline. They descend and move on the coastal slope from near-coast areas towards the open part of the Gulf of Riga. With cooling of water and the onset of homothermium in autumn, freshwater and estuarine fish gather for wintering into areas influenced by river waters. The fish of marine boreal origin aggregate in the waterlayers of the highest temperature in the Ruhnu Deep and the cold-water species start their spawning migration towards the shallower areas on the coastal slope.

Introduction

Hydrological fronts are relatively narrow features with high temperature and salinity gradients. There is no general consensus with regard to their classification, factors responsible for their formation or chain of events taking place in a certain frontal system (Le Fevre, 1986; Mann and Lazier, 1991). Partial listing of the types of fronts more commonly occurring in coastal waters would be: tidal- (shallow-sea), shelf-break-, upwelling- and estuarine fronts, and fronts associated with geomorphic features (Mann and Lazier, 1991). Despite of different formation mechanisms, dynamics and factors having essential influence upon them, the frontal waters are regions of great biological significance. High phytoplankton standing stock at frontal locations have been considered to result from enhanced production (Munk, 1995), associated with high secondary and tertiary production (Ryther, 1969; Cushing, 1971). High commercial fish catches are also reported from these productive regions (Crawford *et al*., 1989). Thus, fronts can be considered as important aggregation areas of the marine living resources.

The importance of frontal regions in biological productivity has been also shown in the Baltic Sea (e.g. Ojaveer and Kalejs, 1974; Raid, 1989; John *et al*., 1995).

The present work was undertaken in order to investigate spatio-temporal distribution of fish assemblages in relation to hydrological fronts and some other environmental factors on the coastal slope in the Gulf of Riga (transect Pärnu Bay – Ruhnu Deep – Irbe Sound). Relevant background information about the Gulf of Riga is given by Yurkovskis *et al.* (1993) and Berzinsh (1995) .

Materials and Methods

Bottom trawlings (duration 30 minutes, trawling velocity 2 knots, estimated trawl opening area 40 m^2, mesh size in the codend 8 or 20 mm) were performed in the Gulf of Riga (Fig. 1) during day-time from May to November, 1994. In each catch, fish (excluding gobies) were identified to species, counted and the total weight of each species in the catch was calculated. Altogether 5811 fish were taken for further biological analyses (length and weight measurements; stage of gonad development; age, sex, and stomach content and stomach fullness determinations). The temperature of water layers and the oxygen concentration in the near-bottom water were measured with a portable thermo-oxymeter (MJ 94, Elke Sensor, Estonia). Salinity of the near-bottom water layer was determined as outlined by Koroleff (1979). Zooplankton was sampled from bottom to surface (large Juday net, mesh size 90 μm). The samples were preserved and analysed according to Lumberg (1976). Wet weights of individuals of different zooplankton taxa, used in biomass calculations, are given in Table 1.

Table 1

Wet weight (mg) of zooplankters, incl. that of copepods at different stages of development (Yashnov, 1934, Bodniek, 1954; Mordukhai-Boltovskoi, 1954; Kiselev, 1956)

Copepoda	Copepodites						
	Stage 1	Stage 2	Stage 3	Stage 4	Stage 5	Female	Male
Eurytemora hirundoides	0.005	0.009	0.011	0.013	0.020	0.030	0.025
Temora longicornis	0.005	0.009	0.011	0.013	0.040	0.040	0.040
Acartia bifilosa, A. longiremis	0.005	0.009	0.012	0.013	0.020	0.026	0.025
Centropages hamatus	0.005	0.009	0.011	0.013	0.040	0.080	0.080
Limnocalanus grimaldii	0.020	0.050	0.090	0.110	0.270	0.350	0.300
Pseudocalanus m. elongatus	0.007	0.013	0.018	0.033	0.066	0.087	0.075

	Weight		Weight		Weight
Nauplii cop.	0.003	*Keratella*	0.001	*Polyarthra*	0.001
Mesocyclops	0.020	*Synchaeta*	0.006	*Gastropoda*	0.010
Bosmina	0.013	*Cercopagis*	0.030	*Chydorus*	0.010
Evadne	0.040	*Balanus*	0.005	*Euchlanis*	0.006
Podon	0.030	*Daphnia*	0.013		

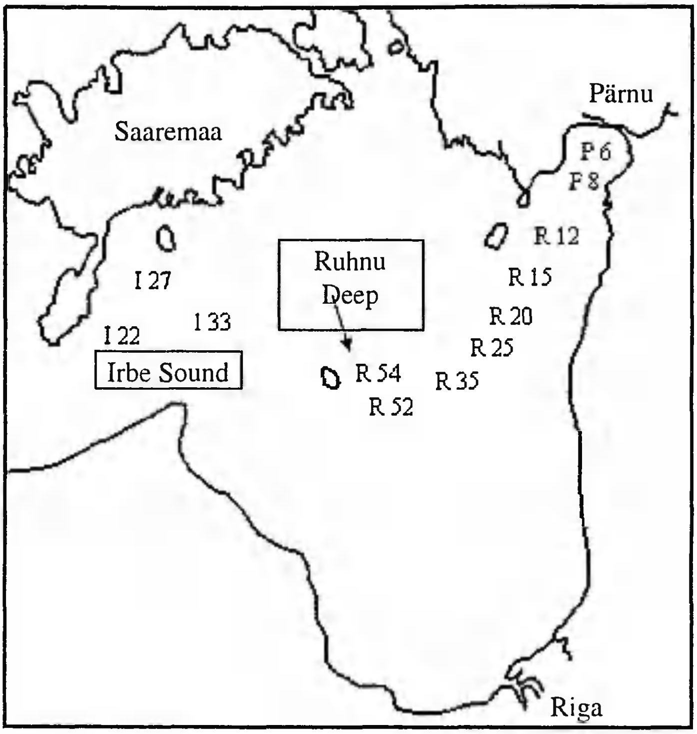

Figure 1. Location of sampling stations in the Gulf of Riga. Numbers indicate depth of a given station.

Results

Fish can be grouped, taking into account their origin, ecology and the distribution pattern on the coastal slope, into three different categories: freshwater and estuarine fish, inhabiting mainly the Pärnu Bay area; marine boreal fish, being more abundantly found above or in the upper part of the seasonal temperature front; and the complex of cold-water fish, inhabiting usually areas below the seasonal thermocline:

1. **Freshwater and estuarine fish***
    - pike-perch – *Stizostedion lucioperca* (L.)
    - perch – *Perca fluviatilis* (L.)
    - ruffe – *Acerina cernua* (L.)
    - vimba bream – *Vimba vimba* (L.)
    - bream – *Abramis brama* (L.)
    - white bream – *Blicca bjoerkna* (L.)
    - bleak – *Alburnus alburnus* (L.)
    - roach – *Rutilus rutilus* (L.)
    - dace – *Leuciscus leuciscus* (L.)

three-spined stickleback – *Gasterosteus aculeatus* (L.)
nine-spined stickleback – *Pungitius pungitius* (L.)

2. **Marine boreal fish**
herring – *Clupea harengus membras* (L.)
sprat – *Sprattus sprattus balticus* (Schneider)
flounder – *Platichthys flesus trachurus* Duncker natio *baltica* (Suworow)
straight-nosed pipefish – *Nerophis ophidion* (L.)
gobies – *Pomatoschistus* sp.

3. **Cold-water fish of marine and freshwater origin****
smelt – *Osmerus eperlanus eperlanus* (L.)
eelpout – *Zoarces viviparus* (L.)
four-horned sculpin – *Triglopsis quadricornis* (L.)
sea scorpion – *Cottus scorpius scorpius* (L.)
lumpsucker – *Cyclopterus lumpus* (L.)
seasnail – *Liparis liparis barbatus* (Ekström)

Spring In early May (Fig. 2, A), water surface temperature rises from the open parts of the Gulf of Riga towards Pärnu Bay and Ruhnu Island along both directions of the transect. Homothermium was still observed in Station R 30. Elevated zooplankton biomass occurred in the Irbe Sound area with maximum values up to 0.87 g m^{-3}, concomitant with increased biomass of copepods. The highest marine fish catches were taken in the Irbe Sound area (up to 48.4 kg, Station I 33) and also at the Stations R 30 and R 35 (8.0 and 25.6 kg, respectively). Older herring had started their spawning in Pärnu Bay in the beginning of May whereas the younger individuals remained for a longer period in prespawning and feeding aggregations in deeper layers (Station R 35). Freshwater fish were staying in waters influenced by the Pärnu River while the cold-water fish occurred mainly in the Ruhnu Deep (Station R 52).

In late May (Fig. 2, B), surface water temperature exceeded 6.0 °C all over the investigation area, the water mass was fairly unstable with no clearly existing thermocline. In comparison with those in early May, higher salinity values of bottom water layers were recorded (especially in Stations P 6 to R 15) indicating an inflow of water of higher salinity. During this cruise, higher zooplankton biomasses were observed in the Irbe Sound area (varied from 0.26 to 0.40 g m^{-3}) and at Stations R 30, R 35 and R 52 (0.23–0.28 g m^{-3}). In these stations, the share of the biomass of copepods in the total zooplankton biomass was up to 88% (Station I 27). In shallower stations (P 6 – R 20), zooplankton was still scanty. Most marine pelagic fish, mainly herring, had moved towards the spawning areas, but some of them still remained in deeper water layers (Station R 35). Again, the highest yield (43.5 kg) was taken from the Irbe Sound area. Freshwater fish were

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* Later in the text = freshwater fish.

** Like commonly accepted glacial relict four-horned sculpin (Segerstråle, 1966), these fish species prefer generally cold water (their reproduction takes predominantly place in the cold season) and require also a high water oxygen content. Thus, they have retained their mode of life prevailing during early historical stages of the Baltic Sea and in the areas they probably originate from.

found mainly in Pärnu Bay (Station P 6) and cold-water fish in deep layers with the temperature below 1 °C (Stations R 35 – R 54).

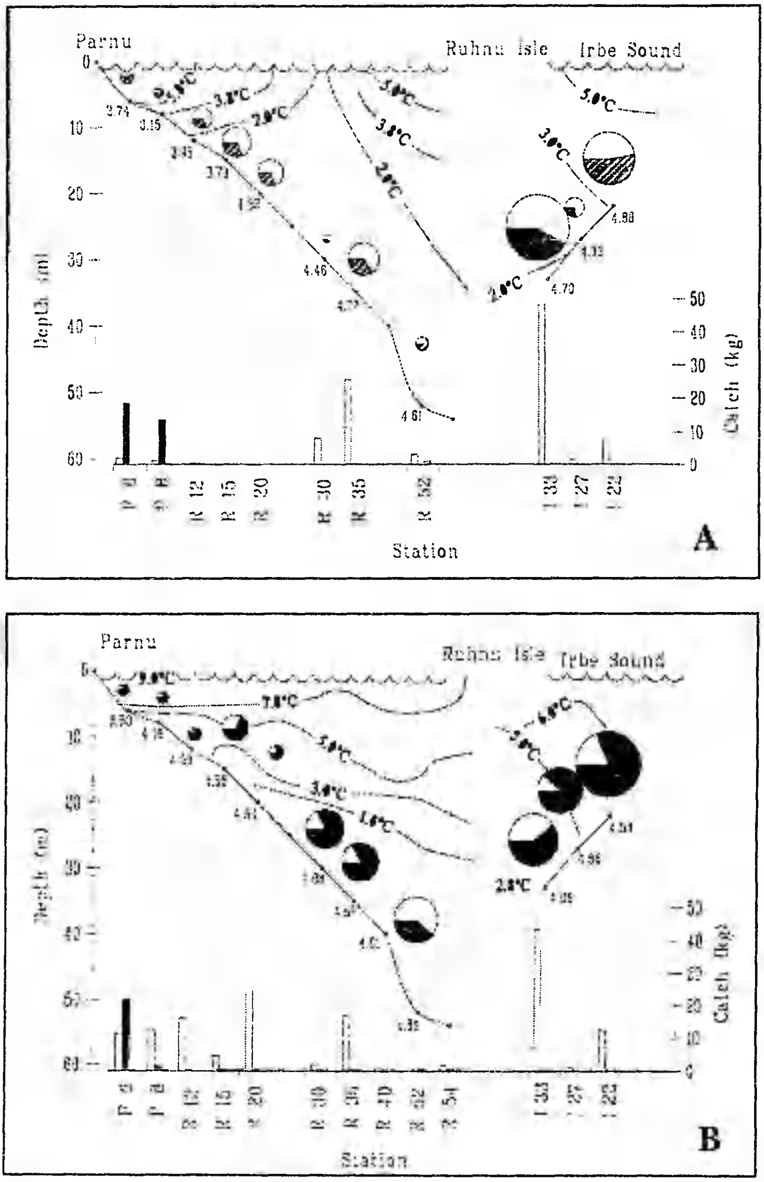

Figure 2. Water temperature (°C), salinity of the near-bottom water layer (‰), zooplankton biomass (g m^{-3}) and fish catches (kg) in the Gulf of Riga in spring: early May (A) and late May (B).○ – Zooplankton biomass: 1 mm in diameter = 0.10 g m^{-3} (A) and 0.04 g m^{-3} (B); ■ – copepods, □ – others.
□■□– fish of marine boreal origin, freshwater fish, and cold-water species, respectively.

Summer (Fig. 3, A) Primary and secondary seasonal temperature fronts (at the depths 12 and 25 m, respectively) matched well with higher fish yields (23.3 and 28.5 kg, respectively). Elevated fish catches were also obtained from the Pärnu

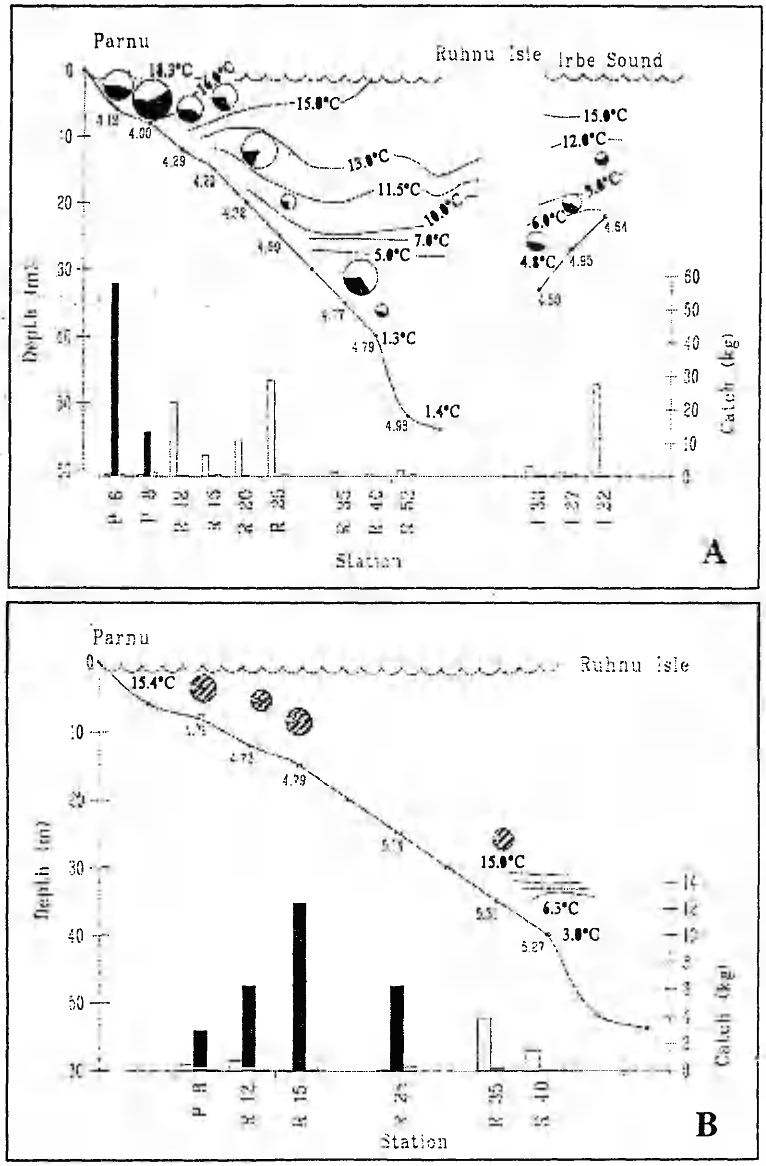

Figure 3. Water temperature (°C), salinity of the near-bottom water layer (‰), zooplankton biomass (g m^{-3}) and fish catches (kg) in the Gulf of Riga in summer (July, A) and autumn (September, B). Zooplankton biomass: 1 mm in diameter = 0.36 g m^{-3} (A) and 0.11 g m^{-3} (B). For other legend see Fig. 2.

River estuary and the Irbe Sound area (58.0 and 27.6 kg, respectively). Contrarily to the situation in May, the cold-water fish, although occurring in catches in relatively small amounts, slightly preferred shallower water (depth 8 and 12 m) with the temperature range 13–16 °C, probably due to redistribution of their nektobenthic food organisms. Although the total zooplankton biomass had considerably increased (variation 0.68–2.00 g m^{-3}), the share of copepods in the zooplankton community was noticeably lower (in the active feeding area 18.7–28.1%) than in other seasons investigated. It should be noted that no sharp temperature stratification was found in the sampling stations in the Irbe Sound area and the lowest zooplankton biomasses were observed in this region.

Autumn In September (Fig. 3, B), after late summer–early autumn storms, the mixed upper layer reached down to a depth of 30 m. The share of copepods in the total zooplankton community had again increased, reaching 98.7% in Station R 15. The total zooplankton biomass above the thermocline (0.26–0.43 g m^{-3}) did not exhibit any notable trends. Because of unfavourable weather conditions the number of stations sampled was reduced, therefore there are no numbers available for the Irbe Sound area. Higher freshwater fish catches occurred at the depths 12–25 m, those of marine pelagic fish were taken from deeper waters (35–40 m) below the seasonal thermocline. Cold-water fish were present in all hauls with elevated biomass values in Stations R 25 and R 35.

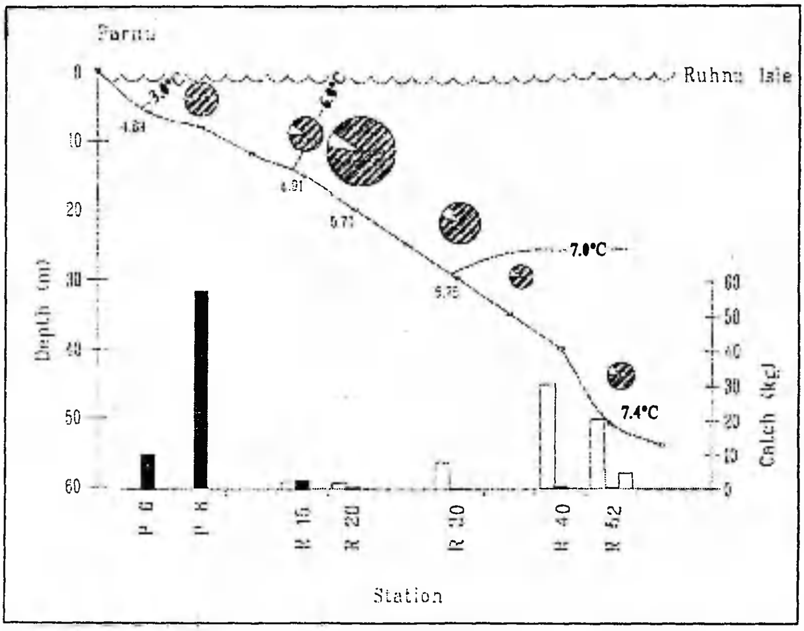

Figure 4. Water temperature (°C), salinity of the near-bottom water layer (‰), zooplankton biomass (g m^{-3}) and fish catches (kg) in the Gulf of Riga in autumn (November). Zooplankton biomass: 1 mm in diameter = 0.02 g m^{-3}. For other legend see Fig. 2.

In November (Fig. 4), water temperature gradually increased beginning from coastal areas (Pärnu Bay) towards deeper parts of the Gulf (from 3.0 to 7.4 °C). Warmer water masses were observed in Ruhnu Deep. Salinity of the near-bottom water layer tended to increase during the investigation period (May–November). Very low zooplankton biomass (0.01–0.14 g m^{-3}), in comparison with other cruises, was recorded. Like in September, copepods prevailed in the zooplankton biomass (in November 80.0–94.3%). Freshwater fish had migrated towards their wintering areas – the Pärnu River estuary – while marine pelagic and cold-water fish were mainly found around their wintering locations in deeper water layers (Stations R 40 and R 52).

Herring, pike-perch and smelt were taken as representatives of the groups of marine boreal, freshwater and cold-water species, respectively, as they were rather abundantly present in catches.

As a rule, pike-perch was found always above the seasonal thermocline. It performs feeding migrations in the warm surface water reaching the areas in the Gulf of Riga far from Pärnu Bay, and on the coastal slope above the thermocline, submerging from spring to autumn (Fig. 5, A).

Larger feeding aggregations of herring were usually situated on the coastal slope in the upper part of the mixing zone at the thermocline (Fig. 5, B) and in the thermocline (Ojaveer, 1988). However, older specimens of herring, although not abundant, were present in deep cold water layers during the feeding period. Their stomachs were found to contain more meiobenthic organisms (mysids) than in the herrings caught in or above the thermocline.

During the feeding period, the biggest concentrations of adult smelt occurred in the lower part of the mixing zone at the thermocline (Fig. 5, C). Juvenile smelt were also found in the upper part of the mixing zone and above it.

On the basis of the above data, a scheme was constructed showing the distribution of feeding fish aggregations on the coastal slope in the Gulf of Riga in relation to thermocline (Fig. 6).

Discussion

Previously, Elmgren (1984 and references therein) has classified the biota inhabiting the Baltic Sea according to their origin into four categories: marine boreal species, freshwater species and cold-water glacial relicts of freshwater and marine origin. On the basis of his extensive studies on fish distribution in relation to temperature, Neuman (1977, 1979) has grouped fishes according to their temperature preferences.

Frontal zones are considered to be the regions of elevated biological productivity (Mann and Lazier, 1991). Comparatively high fish catches were always obtained from the Irbe Sound area. This area has been thoroughly studied with regard to water exchange between the Baltic Proper and the Gulf of Riga. A quasipermanent but migrating salinity front of complicated horizontal and vertical

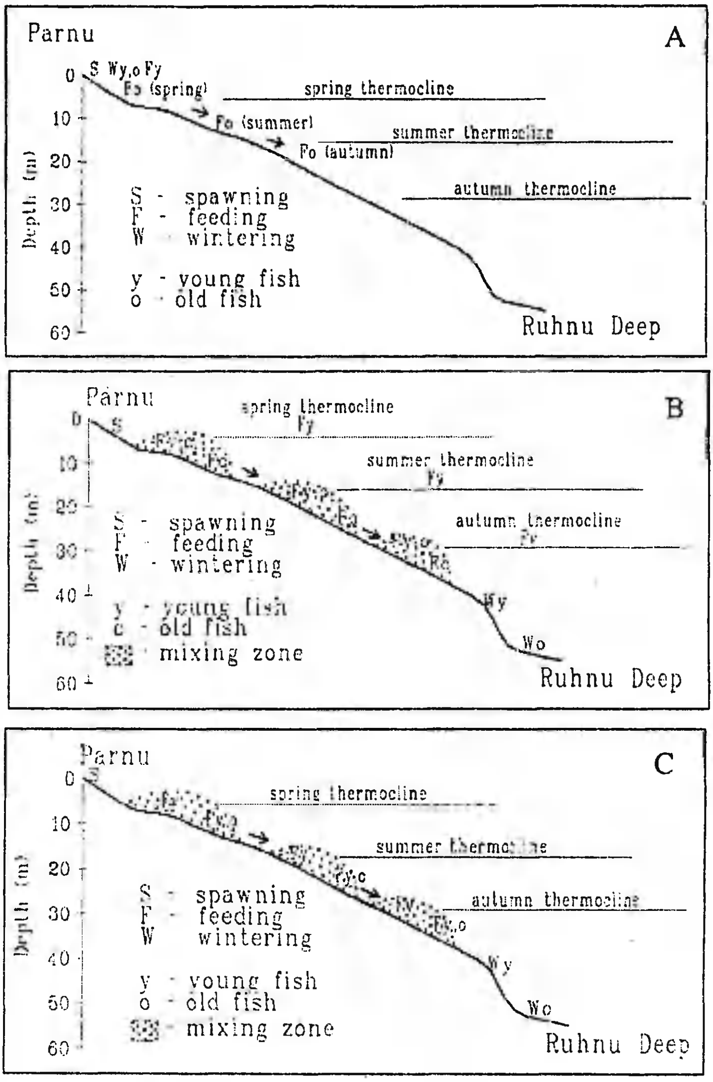

Figure 5. Spawning, feeding and wintering of pike-perch (A), herring (B) and smelt (C) on the coastal slope of the Gulf of Riga.

structure has been observed in this area (Lips, 1995; Lips *et al.*, 1995). This could serve as an explanation for high fish catches and zooplankton biomass values and their remarkable variability observed in this region. Berzinsh *et al.* (1994) documented the presence of hydrological fronts near the river estuaries in the Gulf of Riga, amongst others also in the Pärnu River estuary. They point out the importance of wind regime on the location and configuration of the fronts. As stated earlier, large fish aggregations occurred in Pärnu Bay and also close to the

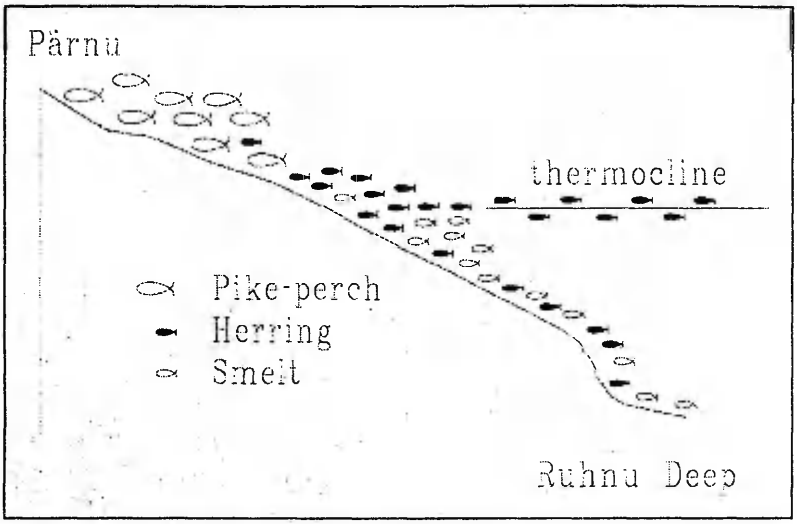

Figure 6. Location of feeding aggregations of adult fish of different origin (freshwater species of southern origin – pike-perch; marine boreal – herring and cold-water fish – smelt) in relation to thermocline on the coastal slope of the Gulf of Riga.

seasonal thermocline. These facts confirm the view of elevated secondary and tertiary productivity of frontal zones. Ojaveer and Kalejs (1974) reported higher biological productivity in the regions of the Baltic Sea where upmixing of phosphorus compounds from below the thermocline or halocline was intense. This coincided most pronouncedly with the 'mixing zones' at thermocline or halocline, respectively. Munk (1995) found a distinct concentration of cod larvae and the peak in the abundance of macroplankters and copepods in the vicinity of a hydrographic front at the shelf slope of the Norwegian Trench. He stated that there existed a tight coupling between the frontal zone formation and the biological productivity of the area.

During summer, zooplankton occurred in larger amounts in shallow areas (Pärnu Bay), where the share of copepods was relatively higher than elsewhere on the coastal slope at that time. In addition to high production, one of the possible reasons may be its moderate predation by plankton-eaters owing to a rather limited numbers of adult herring in this area in summer. This is probably due to too high water temperature for the feeding of herring (Ojaveer, 1988). In the feeding period, generally lower zooplankton biomass values were recorded in the Irbe Sound than in any other area. In comparison with other seasons (particularly with autumn), the share of copepods in the total zooplankton community was the lowest in summer. That could be due to higher production of other zooplankton groups (cladocerans) and elevated selective grazing pressure of pelagic fish on the zooplankton community. In autumn the share of copepods in the zooplankton community rose again but the total zooplankton biomass declined notably.

Some findings by Berzinsh *et al.* (1994), e.g. lower temperatures in the Gulf of Riga in summer usually occur in the Irbe Sound; the maximum vertical temperature gradient in summer is located in the eastern region; lower surface temperatures in autumn are observed near the river mouths, were confirmed by the present study.

As the cold-water fish are forced to inhabit near-bottom water layers in the relatively shallow Gulf of Riga, there might arise the question of oxygen deficiency that additionally could affect their distribution. However, during the observations, oxygen concentration, measured not higher than 20 cm above the bottom surface, did in no case fall below 3.1 mg $O_2\,l^{-1}$. Apparently, oxygen is not commonly a limiting factor for demersal organisms in the area studied.

The fact that juvenile smelt were found above the seasonal thermocline and older herring below it is obviously connected with their adaptation to the variations in feeding conditions. It is probable that compared to the behaviour of smelt and herring in the environment they have originated from, in the Gulf of Riga their feeding habits have changed. It could be considered as an adaptation to the local environmental conditions. Our observations –older specimens of herring, although not abundant, were present in deep cold water layers during the feeding period – are in a line with the results of the studies made by Neuman (1982).

Research on the response of fish aggregation to variations in environmental conditions and processes in the oceans has been scanty as shown by Laevastu (1993). The same author also pointed out that the emphasis in fisheries research has mainly been directed to resource assessment and to fisheries management and not to fish as a component of ecosystems. Solar radiation and surface winds are the most important weather elements affecting the thermal depth structure and stability of the water column. After its formation in spring, the seasonal thermocline gradually descends until disappears at the onset of homothermium in autumn. Feeding pelagic fish aggregations, the largest of which keep in the mixing zone of seasonal thermocline and in the thermocline generally follow this movement (Fig. 5). Wind direction can determine the catchability of some fish (Laevastu, 1993). This was also partly observed during the current study in the shallow Pärnu Bay. During prevailing northerly winds, freshwater fish catches were notably smaller in this region than those during southerly winds. This was especially evident in summer and early autumn.

Other factors affecting fish catchability by trawl are noise and vibration produced by the ship and trawl (for review see Laevastu *et al.*, 1996). Their influence upon fish catches is probably bigger in shallower areas. Thus, in comparison with fish catches from deeper parts of the Gulf, it might well be that those from Pärnu Bay and adjacent shallow areas are more affected by ship noises.

Pelagic fish availability for bottom trawl differs in different seasons. Wintering aggregations (from late autumn till early spring) of pelagic fish are less mobile and keep close to the bottom layers. Thus, they are then more available for bottom trawl than during the feeding period, when they are more dispersed and the younger fish inhabit pelagic water layers. Therefore, due to methodological reasons and fish distribution, the fish catches taken at different stations during one cruise are not always directly comparable with those obtained on cruises performed during other seasons.

Conclusions

- In general, main differences in spatio-temporal behaviour of the three groups of fish in the Baltic fish fauna could be outlined as follows:

fish group	spawning time	feeding	wintering
freshwater and estuarine fish	spring–summer	above thermocline	coastal zone
marine boreal fish	spring–summer	upper part of mixing zone	deep water layers
cold-water fish	winter–spring	lower part of mixing zone and below thermocline	deep water layers

Earlier studies, made by Neuman (1982), partly support these results.

- The feeding behaviour of smelt (a part of young fish feed in the upper part of the mixing zone and above the thermocline) and that of the local herring population (feeding area of old specimens encompasses also cold waters far below the thermocline) should be considered as an adaptation to the local conditions of the Gulf of Riga.
- During the feeding period, main fish aggregations occur in the Pärnu River estuary (mainly freshwater fish) and the Irbe Sound area (mainly marine pelagic fish), where a permanent salinity front occurs. Temporal – primary and secondary thermocline – hydrological fronts attract high pelagic fish concentrations, which move with descending thermocline from spring to autumn deeper towards the open part of the Gulf of Riga.

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II

Ojaveer, H. Application of experimental trawl data for estimation
of fish stock dynamics in the Gulf of Riga (Baltic Sea).
Submitted to ICES Journal of Marine Science.

Application of experimental trawl data for estimation of fish stock dynamics in the Gulf of Riga (Baltic Sea)

Henn Ojaveer

Abstract

Composition of ichthyofauna was monitored by experimental bottom trawl surveys in Pärnu Bay and the NE part of the Gulf of Riga during 1974–1986 and 1994–1996. Based on these data and applying the following GLM model: log (mean monthly catch + 1) = Year + Month + ε, long-term changes in abundance of 12 fish species were constructed. The method represents a possibility for estimation of stock dynamics of fish populations, including non-assessed and non-target species

Decrease in the abundance and extermination of some marine demersal and cold-water fishes has caused notable impoverishment of the fish community mostly in deeper parts of the basin from the end of the 1970's. Changes in the abundance of freshwater fish stocks were less pronounced and some of them have recently increased in size. Compared to that during the 1980's, the size of pelagic fish stocks has improved. These changes were probably induced by a complex of different factors incl. altered abiotic conditions, pollution of the marine environment, fishing and predation.

Key words: abundance, cold-water fish, experimental bottom trawlings, freshwater fish, glacial relicts, Gulf of Riga, long-term changes, marine species.

Introduction

Management of exploited fish populations and other marine living resources is developing towards management of marine ecosystems (Laevastu, 1996). This involves maintenance of their health and species diversity. In addition to exploited stocks, investigation and assessment of stock condition of other fishes, including non-assessed and non-target species, as well as the main links of food webs and the abiotic environmental parameters, will be necessary.

The Gulf of Riga represents an ecological subsystem of the Baltic Sea (Ojaveer and Elken, 1997) which is under strong anthropogenic impact both in terms of pollution of marine environment and exploitation of fish resources. Adaptation of fishes to the local unique environmental conditions has resulted in differentiation of populations in several species — e.g., herring and probably also smelt and eelpout. The abundance dynamics, growth rate and a number of other characteristics of these populations clearly differ from corresponding parameters of neighbouring populations (e.g., Ojaveer, 1991).

Presently the method of assessment and management of exploited stocks in the Baltic doesn't allow separate treatment of fish stocks in the Gulf of Riga because they are handled as components of much larger regions. Spring herring population of the Gulf of Riga is regarded as an element of the herring assessment unit in ICES Sub-divisions 25-29+32, sprat is taken as a fraction of a large unit covering the whole Baltic. Cod occurring periodically in the Gulf of Riga is treated as a component of the Eastern Baltic cod population (Sub-divisions 25-32).

Stock dynamics of non-assessed species of regional commercial importance (eg., pikeperch, perch, whitefish, eel) have been analysed mostly on the basis of commercial catch statistics (Lehtonen 1985; Winkler 1991; Svedäng 1996), which often is of questionable reliability and takes into account the recruited part of a stock only. Non-commercial fish stocks (e.g. sticklebacks, gobies, bleak) have gained almost no attention as there are no published data available on this matter for the Baltic. In the brackish Baltic Sea, where the species diversity is low and local food chain, therefore, imperfect with a number of empty niches (Elmgren, 1989), the importance of non-commercial and less abundant species in mediating energy flow between trophic levels in various niches is probably higher than in true marine or freshwater environments. In this respect, knowledge in the stock dynamics of the fish from these categories is of fundamental importance. As compartments of marine food webs, non-target species serve as an important diet for commercial fish, are their competitors for the same food resource and predators for their early life stages or act as intermediate hosts and transmitters of parasites (e.g., Tanasiichuk, *et al.*, 1966; Zander, 1991; Zander, 1993; Ojaveer *et al.*, 1997 (in press)).

Since the condition of fish stocks and the stable functioning of the ecosystem of the Gulf of Riga are extremely important for the communities populating its coasts, preconditions should be developed for separate management of this ecosystem in the future. As a transition stage from the present situation towards the separate management of the ecosystem of the Gulf of Riga, below the results of investigations on the dynamics of both exploited and non-target fish stocks are discussed and a possible method for corresponding assessment presented. The data from experimental bottom trawlings of similar survey design over the years 1974–1986 and 1994–1996 were used. Fluctuations in the abundance of twelve the most frequently occurring fish taxa were investigated by means of a multiplicative model on logarithmic transformed catch numbers. Changes in the abundance of less frequently occurred species were studied by comparing the mean catch numbers over the two periods 1974–1980 and 1994–1996.

Material and Methods

1. The data

Bottom trawl surveys were conducted on the transect from Pärnu Bay (Pärnu River estuary) to Ruhnu Deep (Fig. 1) by means of a small sterntrawler (length 12.5 m, 90 HP) in 1974–1986 and 1994–1996. During the first period, the cruises were performed in the Laboratory of Commercial Fish Resources in the Tallinn Department of the Baltic Fisheries Research Institute (BaltNIIRH). In 1974–1980 and 1994–1996, monthly surveys were carried out from April to November–December whereas only 1–3 surveys per year (in autumn) were conducted in 1981–1986.

The trawlings were carried out at daylight with a mean trawling speed of 2.5 knots, the towing time was of 30 minutes duration, estimated trawl opening area was 40 m^2 and mesh size in the codend 8 mm (from May to July 1994 20 mm). The hauls were performed at fixed depths. There were however minor changes in selection of sampling stations over the two periods studied. In 1974–1986, the deepest station hauled was at 40 m whereas during 1994–1996, additional trawlings were performed in Ruhnu Deep (Stations 52 m and 54 m; Figure 1). In shallower region (in depth range from 5 m to 12 m), more stations were fished during 1974–1986 as compared to the recent period of study.

Abundance of all species in a catch was determined through direct counts or through sub-sampling if the catch was too large. Due to possible inaccuracy in identification of two stickleback species (*Gasterosteus aculeatus* and *Pungitius pungitius*) in the first period of study, sticklebacks were not analysed at species level. Also gobies (*Pomatoschistus* spp.) were not identified to species.

2. Analysis of spatial distribution of different fishes

Distribution of twelve the most abundant fish taxa over the whole study area was analysed using mean abundance values per haul by stations (depths). To account for the different depth coverage over the periods 1974–1986 and 1994–1996, some corrections in the original survey data were inevitable. For the shallower part, additional hauls in stations at 5 m, 7 m and 10–11 m depth in 1974–1986 were treated as replicates for the stations at 6 m, 8 m and 12 m, respectively. The stations deeper than 40 m fished during 1994–1996 were interpreted as replicates of the Station 40 m. Such aggregation of the data was also followed in further analysis.

3. Analysis of dynamics of species abundance and species richness

At the first step, the catch per effort data was analysed by the following GLM model:

$$\log(\text{catch}+1) = \text{Year} + \text{Month} + \text{Depth} + \text{Year*Month} + \text{Year*Depth} + \text{Month*Depth} + \varepsilon, \qquad (1)$$

where: catch — the number of a certain fish caught per 30 min haul; 1 was added to all catches to allow to calculate logarithms from zero values,
Year, Month and Depth — the year-effect, month-effect and depth-effect, respectively;
ε — the error term;
Year*Month, Year*Depth and Month*Depth are interaction terms.

Results of this model suggested that the year*depth interactions were, in general, not statistically significant at 5% level. The year*month effect appeared to be significant in case of the most of fish species. However, in most cases, this was caused by a few number of the year*month interaction terms. Therefore the year*month effect, except that of sticklebacks and gobies, was considered to be at 5% level insignificant in the model whereas the month*depth interaction was found statistically different for all species. The existence of statistically significant interactions hinders clear interpretation of the main effects.

A second problem with this model was a high number of zero catches for the majority of species. The reason was that most species were restricted to a limited distribution areas within the survey area (Figure 2). A possible solution to avoid the 0-catch problem would be to analyse each species within its main distribution area only. This approach, however, was not applicable for pelagic species and also for some fresh-water species, due to their seasonal migrations on the coastal slope (Ojaveer, 1997).

In order to circumvent these problems, the monthly survey was chosen as one observation. This implies that for data analysis the following model was applied:

$$\log(\text{mean catch}+1) = \text{Year} + \text{Month} + \varepsilon, \qquad (2)$$

where mean catch is the monthly average catch by number of a species.

The year-effect in the model (2) was used as an index describing dynamics of fish stock abundance. Index values were calculated for twelve most important species (the species having yielded the total catch more than 500 individuals over the all years studied).

To characterise long-term dynamics of the number of fish species present in experimental hauls (species richness) in two different areas — shallow Pärnu Bay (Stations P6-P8) and deeper parts of the Gulf of Riga situating usually below the seasonal thermocline (Stations R25-R40), the following model was applied:

$$\log(\text{mean number of fish species}) = \text{Year} + \text{Month} + \varepsilon, \qquad (3)$$

where mean number of fish species is monthly average number of fish species in a catch per area. The results of this model were later log-retransformed.

Results

The list of cyclostome and fish species with the total numbers caught during the whole study period are given in Table 1. The fish were grouped according to their origin and with regards of their ecology and distribution pattern in the Gulf of Riga (Ojaveer, 1997).

The survey area covered most of the coastal slope in the Gulf of Riga — from the shallow near-coastal zone to the deepermost areas in Ruhnu Deep. The spatial distribution of the most abundant species are shown on Figure 2. It clearly demonstrates the shift from freshwater fish dominated part of the ecosystem in shallower areas to cold-water and marine demersal fish predominated community in deeper regions of the survey area, whereas intermediate depths were, in general, occupied by marine euryhaline species. However, the distribution of some fish of marine origin (gobies and straight-nosed pipefish) were chiefly found in the near-coastal stations (P6-R12) of the study area.

For the marine pelagic (herring, sprat) and, cold-water and marine demersal species (eg., smelt, eelpout, cod) the year-effect was found to be statistically significant in the model whereas the month-effect was often insignificant. The model explained between 50 to 77% of the variability in the data (Table 2). Generally higher abundance of these fish species in the 1970's was followed by a marked decline in the 1980's. Recently, the stock condition of clupeoids has considerably improved whereas smelt and eelpout have showed only a slight increase in numbers and cod has been exterminated from the Gulf of Riga. In general, the year-effect of sticklebacks exhibited, with certain deviations, an increasing trend over the study period (Figure 3).

Changes in the stock abundance of freshwater fish (except pikeperch) were less pronounced as compared to that of the fish analyzed above. In contrast to the month-effect, the year-effect appeared to be insignificant in the model that explained less than 50% variability in the data (Table 2). As compared to the first study period the abundance of pikeperch and bleak tended to be higher in 1994–1996 whereas no clear changes in the catch rates of other species — white bream, vimba bream and perch, were detected (Figure 3).

Dynamics in the abundance of less numerous species were estimated by means of comparing their average values of the two periods with the full-year survey coverage: 1974–1986 and 1994–1996, respectively. It appeared that the fish inhabiting shallower areas showed, in general, opposite or smaller changes in the mean abundance values as compared to that of glacial relicts or marine demersal fish. For instance, the abundance of bream and straight-nosed pipefish has increased recently whereas sea snail, sea scorpion and lumpsucker were caught in 1994–1966 as a single specimen and fourhorned sculpin and sandeel were not met with in the hauls during the latter period (Table 3).

Dynamics of the mean number of fish species present in experimental hauls in Pärnu Bay (Stations P6-P8) and deeper parts of the Gulf of Riga (generally below the seasonal thermocline, Stations R25-R40) during 1974-1986 and 1994–1996 is shown on Figure 4. In Pärnu Bay, the number of fish species exhibited, with certain exceptions in 1983–1985, slight increase. Decline in this characteristic in deeper parts of the Gulf of Riga during 1978–1985 (from 5.1 to 2.3, respectively) and following increase in 1994–1996 (mean 4.3) was obvious. Recent increase in the mean number of fish species per haul was caused by elevated frequency of occurrence of pelagic euryhaline (sprat, sticklebacks) and some cold-water species (smelt, eelpout) while other demersal and cold-water fishes were only occasionally present in experimental catches.

Discussion

During the recent two decades, certain trends in the main environmental parameters in the Gulf of Riga have been documented. After low riverine freshwater discharge during 1963–1977, generally higher runoff values were observed from 1978 to 1991. This, together with absence of big saline water inflows into the Baltic during the period 1977–1993 (Matthäus, 1993), caused gradual decline of water salinity beginning from the late 1970's (Berzinsh, 1995). Also, decreasing tendency of oxygen content and increase of the mean temperature in deeper water layers from the 1960's to the 1990's was observed by Berzinsh (1995) and Sidrevics *et al.* (1993). When analysing nutrient data set from 1975–1988, Suursaar (1995) concluded that the trophic level of the Gulf of Riga had generally increased. It was evidenced by elevated nitrate and phosphate concentrations and concomitant increase in chlorophyll '*a*' content (Jansone, 1995). Above-mentioned changes have led to worsening of living conditions for glacial relicts and the fish of marine origin being, therefore, partly responsible for the decline of these fish stocks in the basin. In contrast, freshwater fish stocks have probably benefited from decreased salinity conditions, especially those which are tolerant to moderate eutrophication — e.g., percids and bream (Leach *et al.*, 1977; Rundberg, 1977; Lehtonen and Hilden, 1980), but in exploited species the clear effect was obviously overshadowed by other factors (e.g., fishery).

Clupeoids, being the main exploitable fish resources in the Baltic, have been well studied for their stock dynamics (for review see Parmanne *et al.*, 1994) and will, therefore, be only briefly discussed here. The dynamics of the year-effect of herring correlated well ($r^2=0.90$) with the dynamics of herring total biomass estimated from the single-species VPA during the 1974–1980 period, but, in contrast showed different patterns afterwards (Figure 3; ICES, 1996). As compared to the period 1974–1980, the recent very high Gulf of Riga herring total biomass (below 95 000 and over 191 000 tons per year, respectively; ICES, 1996), was not confirmed by the results of the current study: the year-effect in 1994–1996 demonstrated similar values to those in the 1970's. General periodicity observed in the stock abundance of sprat — higher values during the second half of the 1970's, low stock size during the first half of the 1980's, and the highest-ever values in the mid 1990's — agreed relatively well (r^2=0.55) with the VPA estimated total biomass of the fish for the whole Baltic Sea (Sub-divisions 22-32; ICES, 1996). However, variability in sprat stock size in the Gulf of Riga, estimated by the year-effect, is much larger than the mean for Sub-divisions 22-32. This phenomenon is likely a more pronounced predation effect of cod as generally lower sprat abundance in the Gulf of Riga was registered during high cod stock size and vice versa.

Rich year-classes of the eastern Baltic cod population, hatched in 1976, 1979 and 1980, during or after strong saline water inflows into the Baltic Sea, caused increase in its spawning stock biomass (SSB) above 700 000 tons (Sub-divisions 25-32) during 1979–1984 (ICES, 1996) and further the invasion into the Gulf of Riga since 1978 (Figure 3). Dynamics of annual commercial catches of cod in the Gulf of Riga showed similar pattern to that of the year-effect: after peaking two years later (in 1980) with 4 249 tons per year, they declined continuously afterwards and remained below 500 tons during the second half of the 1980's. Disappearance of cod from the Gulf of Riga in the late 1980's was mainly governed by a decline in the SSB due to unfavourable hydrological conditions for reproduction and constantly high fishing effort since the beginning of the 1980's (ICES, 1996). Results from cod stomach analysis have revealed that clupeoids had major importance in cod diet. The share of other fish in cod diet did generally not exceed 10% by weight (Uzars, 1975; Uzars, 1985). Amongst them smelt, eelpout, sandeel, gobies, lumpsucker and butterfish were presented (Bagge, 1981; Uzars, 1994). Therefore, notable decline in abundance or disappearance of these fish species from experimental catches during the 1980's could partly be attributed to the impact of cod predation.

Besides predation by cod, other factors were probably responsible for changes in the abundance of cold-water preferring smelt and eelpout stocks. High exploitation level of smelt in the late 1960's and first half of the 1970's (mean catch over 1000 tons per year), coupled later with unsuccessful reproduction due to increasing pollution of the areas of drift of its embryos and larvae in the rivers discharging into Pärnu Bay have probably contributed to the decrease of smelt stock. As a consequence, sharp decline in the abundance of smelt larvae in Pärnu Bay area in the mid 1970's was evident: average abundance of the larvae above 10 mm size class per 10 min trawling with Hensen net dropped from 56.3 in the 1964–1969 period to 3.3 during 1977–1986 (Ojaveer and Gaumiga, 1995). Recently, after removal of the main pollution source and in the conditions of generally decreased eutrophication processes in Pärnu Bay (Suursaar, 1995) the abundance of smelt larvae have demonstrated insignificant increase recently (H. Špilev, pers. comm.), but commercial catches have continued to decline and reached the lowest values in record during the mid 1990's (mean for 1994–1996 3.0 tons per year). The decrease in eelpout stock size in the beginning of the 1980's was likely governed also by too heavy fishing pressure; the average annual catches (incl. by-catch) amounted to 14.5 thousand tons during 1971–1975 and 6 thousand tons in 1976–1980, after which directed eelpout fishery was closed in the basin up to the mid 1990's.

In Pärnu Bay, commercially exploited freshwater fishes exhibited statistically insignificant changes in the year-effect over the two periods studied. The decrease in perch stock size during the 1990's was much more evident in the official catch statistics from this region than from the results of experimental surveys. Generally higher catches were taken during 1974–1986 (mean 940 tons per year) as compared to the 1994–1996 period (mean 208 tons per year) which is to some extent controversial to the current results. Increase of pikeperch abundance in experimental hauls during 1994–1996, compared to the 1974–1986 period, was much less obvious than respective changes in official commercial catch records (annual means for the periods 238 and 106 tons, respectively). However, pikeperch length distribution in experimental catches during recent years indicates clear overexploitation signals and insignificantly higher abundance during 1994–1996 is to be taken as an effect of recently hatched good year classes.

Of non-commercial species, gobies, that are adapted to estuarine conditions in the research area, populating mostly shallower regions (Figure 2), exhibited general decreasing tendency in stock abundance during 1974–1986. This is in a good agreement with changes in the mean number of goby larvae in Pärnu Bay: obvious decline in their abundance from the 1960's (over 1300 individuals per 10 min haul with Hensen net in 1960–1963) to the 1980's (ca. 200 larvae in 1985–1989) was observed by Ojaveer and Gaumiga (1995). Improved food resource is one possible explanation for recent increase in the stock size of bleak. Our recent investigations confirm that the new cladoceran species — *Cercopagis pengoi* — that invaded into the NE Gulf of Riga in 1992 and reaches very high biomass values during warm season, is at this time the most important prey item for this species, making up to 100% of stomach contents of the fish (A. Lankov, pers. comm.). The same consideration applies also for sticklebacks (Ojaveer *et al.*, 1977 (in press)), whose year effect shows, with some deviations in 1983–1985, an increase over the years. Although there existed specialised stickleback fishery until 1981 (maximum catch over 800 tons in 1979), there are no clear evidence to suggest that this has affected the abundance of these fish.

It is believed that the catch method applied — bottom trawl — samples adequately all marine and cold-water species as the survey transect covers their main distribution areas. However, in difference, freshwater species (e.g., white bream and bleak) are probably sampled to some extent less representatively, compared to previous fish categories, as these species are distributed also in more shallow regions than covered by stations of our trawl surveys (Figure 2). Therefore, due to long-term changes in environmental conditions (mainly salinity fluctuations), abundance dynamics of freshwater fish stocks could include ‘noise information’, caused by expansion or shrinkage of their distribution area. Mismatch of dynamics of commercial catches and the year-effects recorded within the current study for some species (e.g., perch and vimba bream) and poorer statistics values of GLM models could be attributed to the above-mentioned problems. Therefore, in order to get better results for the fish which are abundantly distributed in coastal areas, comparative experimental studies with relevant catch methods (e.g., by means of different trapnets and gillnets or using small coastal trawl) would be necessary.

Due to constraints of the data, connected to the recording system applied during the 1974–1986 period, evaluation of the fish stock dynamics was abundance-based in the present study. However, the current method allows also to obtain other numerical data necessary for assessment of various fish stocks, where more detailed information (e.g., catch rates in biomass, length and age distribution of a fish species in a catch) is required.

Conclusions

1. Based on experimental survey data, the first attempt has been made to evaluate long-term changes in the ichthyofauna in the Gulf of Riga. It appeared, that fishes of different ecological groups exhibited, in general, different patterns of stock abundance dynamics over the years studied.
2. A complex of different factors — fluctuations of the main abiotic parameters and pollution of the marine environment, resource exploitation and species interactions — were probably behind the fish stock size dynamics in the Gulf of Riga. They appeared to affect fishes at various ontogenetic stages of their life history and the relative impact by these have varied by years and over periods.
3. The method applied (monitoring of species abundance based on long-term data, regularly sampled on a transect through the main feeding and wintering areas of an ecological subsystem) provides a possibility for estimation of stock size and condition of fish populations. Data of present estimate are generally in a good agreement with the results of assessments of important commercial species (herring, sprat and cod) by the methods presently applied in the ICES Baltic Fisheries Assessment Working Group (ICES, 1996). Also, it represents a realistic possibility for evaluation of stock condition of non-assessed commercial fish and non-target species, which is important for estimation of the state of an exploited ecosystem.

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Table 1. List of cyclostome and fish species, together with the total numbers caught, in the Gulf of Riga during the survey period.

Common name	Scientific name	Total catch (numbers)
Cyclostomes		
River lamprey	*Lampetra fluviatilis*	97
Fish		
Marine boreal fish		
Baltic herring	*Clupea harengus membras*	538 583
Sprat	*Sprattus sprattus balticus*	30 285
Gobies	*Pomatoschistus* spp.	4 837
Cod	*Gadus morhua callarias*	1 274
Sandeel	*Ammodytes tobianus*	215
Straight-nosed pipefish	*Nerophis ophidion*	105
Flounder	*Platichthys flesus*	48
Black goby	*Gobius niger*	2
Broad-nosed pipefish	*Syngnathus typhle*	2
Garpike	*Belone belone*	1
Turbot	*Psetta maxima*	1
Freshwater fish		
Sticklebacks	*Gasterosteus aculeatus*, *Pungitius pungitius*	82 504
Pikeperch	*Stizostedion lucioperca*	11 776
Perch	*Perca fluviatilis*	2 026
White bream	*Blicca bjoerkna*	1 137
Bleak	*Alburnus alburnus*	756
Vimba bream	*Vimba vimba*	527
Bream	*Abramis brama*	306
Ruffe	*Acerina cernua*	196
Roach	*Rutilus rutilus*	38
European whitefish	*Coregonus lavaretus*	6
Dace	*Leuciscus leuciscus*	2
Ide	*Leuciscus idus*	1
Knifefish	*Pelecus cultratus*	1
Cold-water fish and ice-age relicts		
Smelt	*Osmerus eperlanus eperlanus*	156 127
Eelpout	*Zoarces viviparus*	5 304
Sea snail	*Liparis liparis barbatus*	168
Four-horned sculpin	*Triglopsis quadricornis*	94
Sea scorpion	*Cottus scorpius*	10
Lumpsucker	*Cyclopterus lumpus*	8
Butterfish	*Pholis gunnellus*	1
Eel	*Anguilla anguilla*	43

Table 2. The descriptive statistics of the GLM's (type I).

Fish	Error source	d.f.	s. of sq.	F	Probability	r^2
Herring	Model	21	43	2.73	<0.01	0.55
	Year	15	30	2.66	<0.01	
	Month	6	13	2.90	0.02	
	Error	47	35			
	Corrected total	68	78			
Cod	Model	21	29	5.67	<0.001	0.72
	Year	15	28	7.62	<0.001	
	Month	6	1	0.78	ns*	
	Error	47	12			
	Corrected total	68	41			
Sprat	Model	21	100	2.23	0.01	0.50
	Year	15	73	2.27	0.02	
	Month	6	27	2.13	ns	
	Error	47	100			
	Corrected total	68	200			
Sticklebacks	Model	21	130	7.39	<0.001	0.77
	Year	15	46	3.65	<0.001	
	Month	6	84	16.75	<0.001	
	Error	47	40			
	Corrected total	68	170			
Smelt	Model	21	88	2.36	<0.01	0.51
	Year	15	69	2.59	<0.01	
	Month	6	19	1.78	ns	
	Error	47	84			
	Corrected total	68	172			
Eelpout	Model	21	46	2.20	0.01	0.50
	Year	15	39	2.62	<0.01	
	Month	6	7	1.15	ns	
	Error	47	47			
	Corrected total	68	93			
Pikeperch	Model	21	41	2.06	0.02	0.48
	Year	15	26	1.82	ns	
	Month	6	15	2.65	0.03	
	Error	47	44			
	Corrected total	68	85			
Perch	Model	21	19	1.66	ns	0.43
	Year	15	11	1.38	ns	
	Month	6	8	2.37	0.04	
	Error	47	26			
	Corrected total	68	45			
Vimba bream	Model	21	4	1.06	ns	0.32
	Year	15	1	0.42	ns	
	Month	6	3	2.64	0.03	
	Error	47	10			
	Corrected total	68	14			
Whitebream	Model	21	11	1.54	ns	0.41
	Year	15	7	1.32	ns	
	Month	6	4	2.11	ns	
	Error	47	16			
	Corrected total	68	27			
Gobies	Model	21	36	1.76	ns	0.44
	Year	15	24	1.66	ns	
	Month	6	12	2.01	ns	
	Error	47	45			
	Corrected total	68	81			
Bleak	Model	21	12	1.94	0.03	0.46
	Year	15	5	1.17	ns	
	Month	6	7	3.87	<0.01	
	Error	47	14			
	Corrected total	68	28			

* non-significant at 95% level (p>0.05).

Table 3. Average abundance (number of individuals per 30 min of trawling) of some less frequently occurred fish species for the two periods of full-year survey coverage.

Fish species	Abundance	
	1974–1980	1994–1996
Bream	< 0.1	1.8
Straight-nosed pipefish	0.1	0.5
Ruffe	0.4	0.3
Seasnail	0.4	< 0.1
Sandeel	0.4	not found
Fourhorned sculpin	0.2	not found

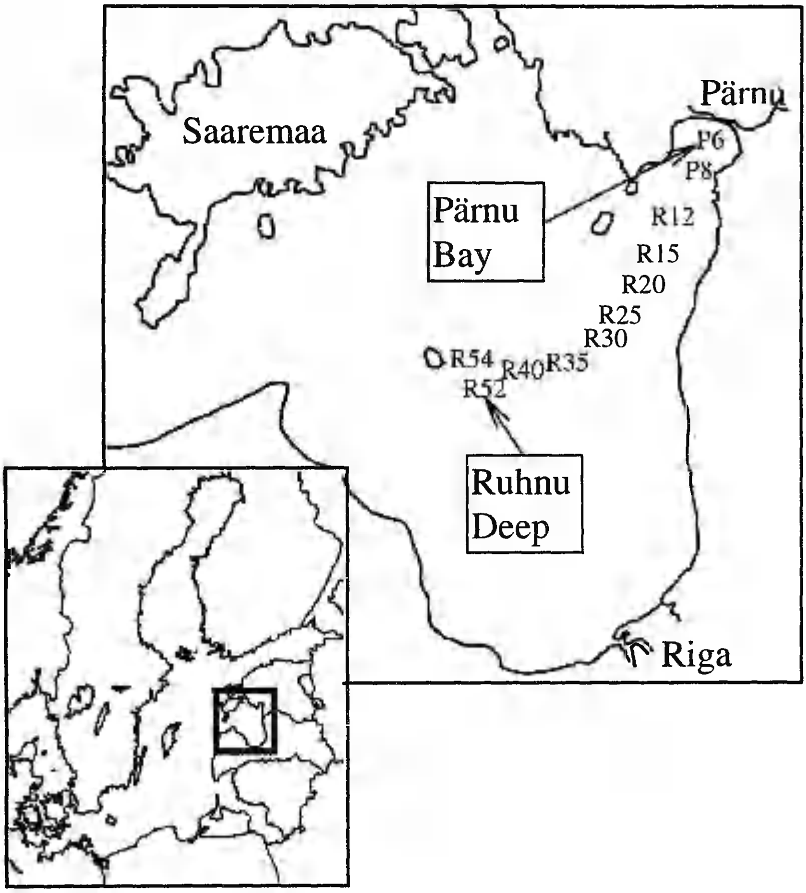

Figure 1. Location of trawling stations in the Gulf of Riga. The number indicate depth of a given station.

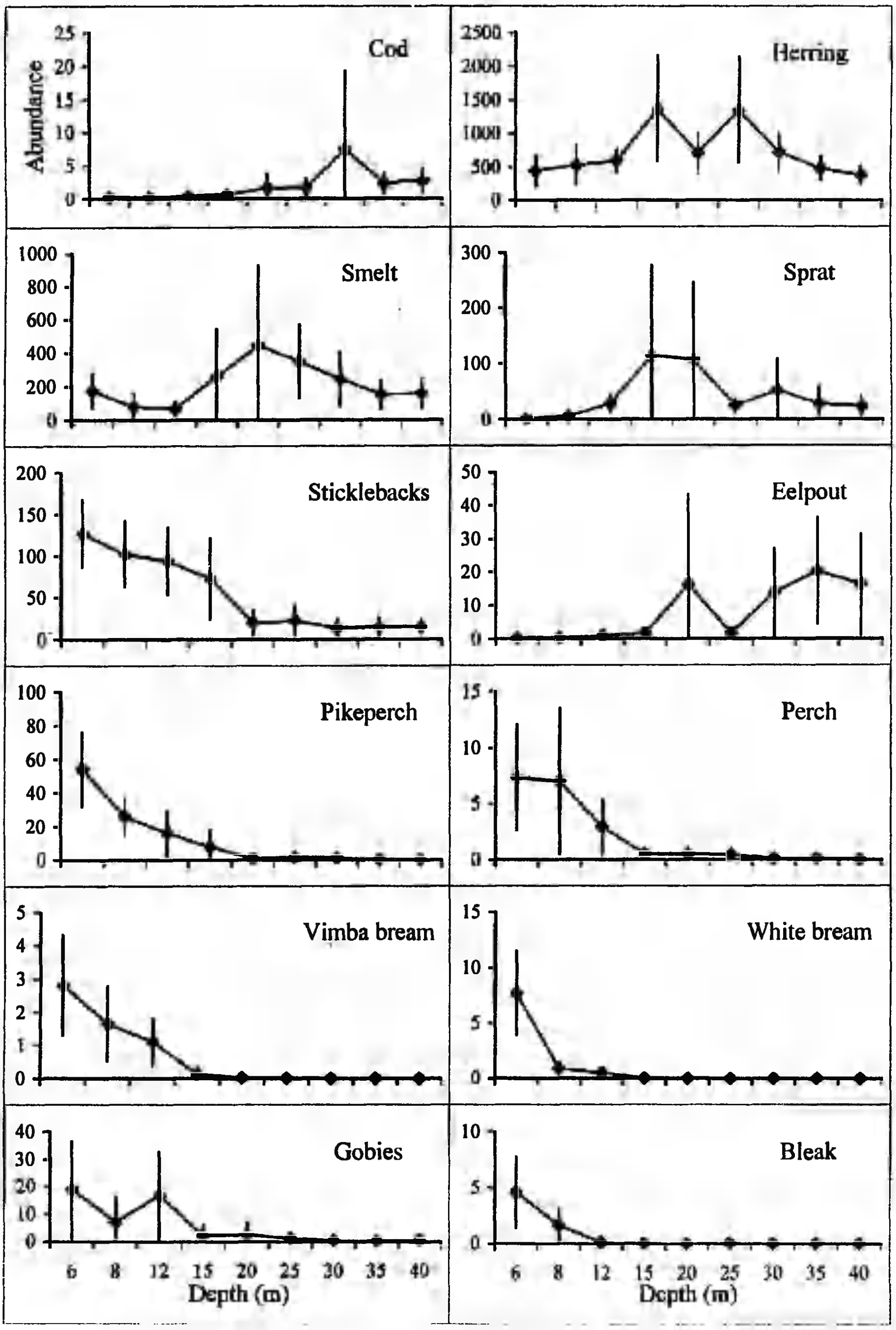

Figure 2. Depth distribution of twelve the most abundant fish taxa on the coastal slope of the Gulf of Riga. Fish abundance is expressed as a mean number of individuals (with 2xS.E. bars) per 30 min of trawling. For calculations, survey data from the years 1974–1986 and 1994–1996 were used.

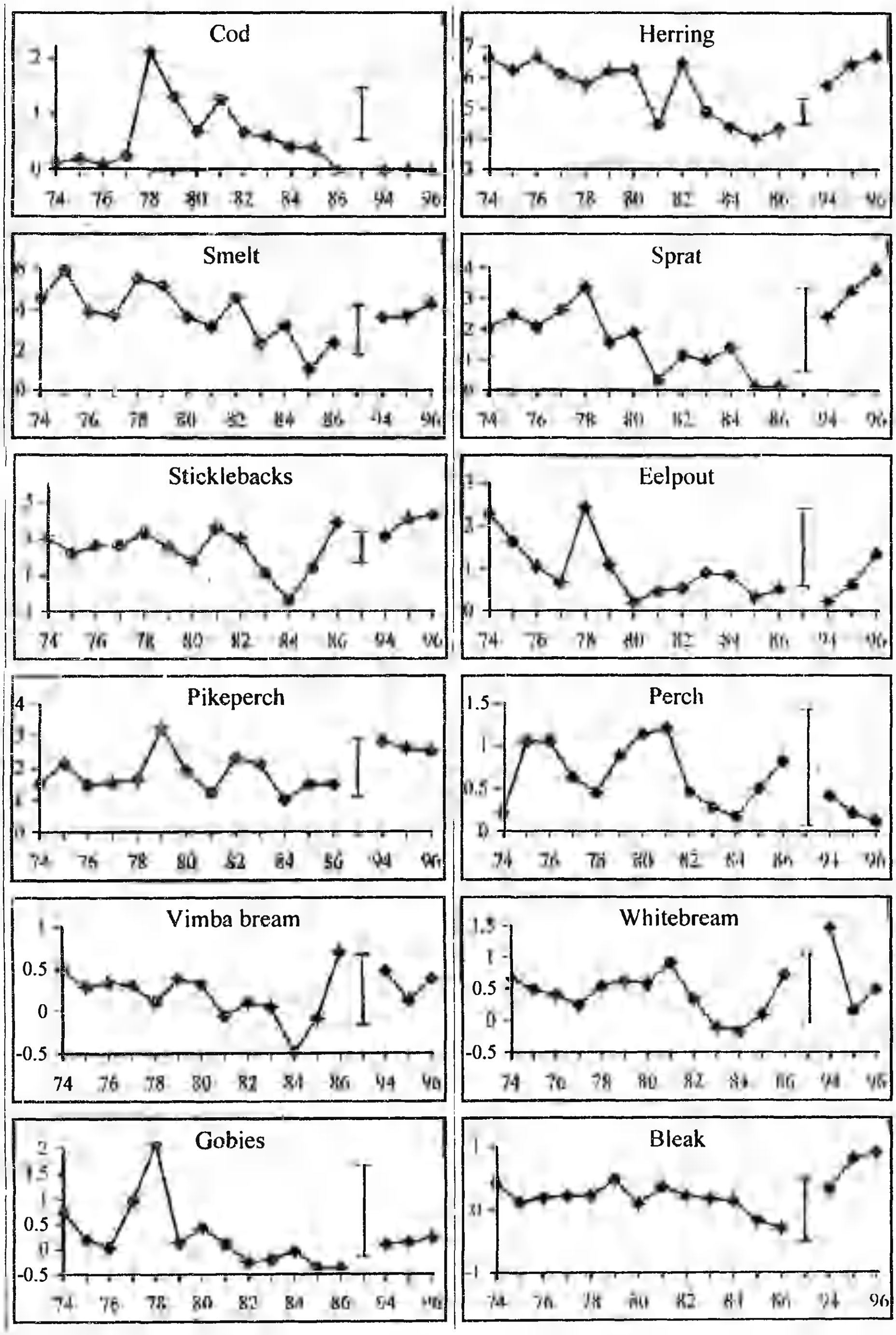

Figure 3. Dynamics of the abundance-based year-effect with the least significant difference (LSD) bar for twelve of the most abundant fish in the NE Gulf of Riga over the years 1974–1986 and 1994–1996.

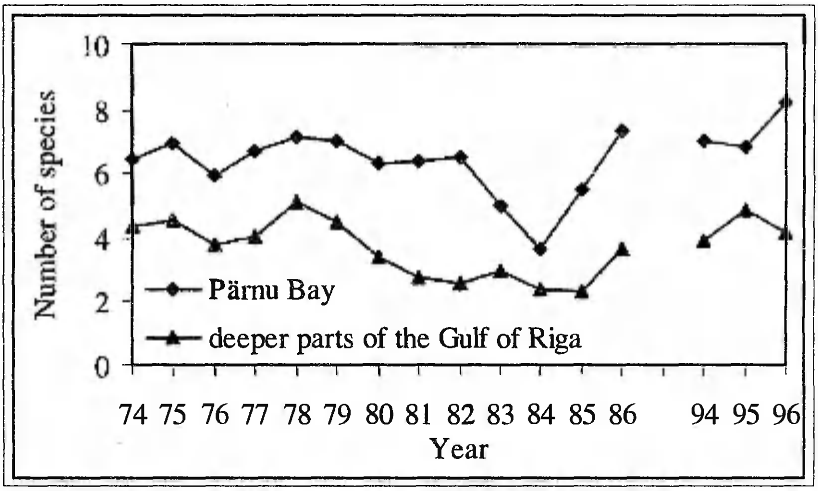

Figure 4. Dynamics of the mean number of fish species present in experimental bottom trawl catches in Pärnu Bay (≤8 m) and deeper parts of the Gulf of Riga (≥25 m) during 1974–1986 and 1994–1996.

III

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Adaptation of eelpout, *Zoarces viviparus* (L.), to spatially changing environment on the coastal slope of the Gulf of Riga (Baltic Sea)

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ABSTRACT

Eelpout were caught in the region from Pärnu River estuary (Pärnu Bay) to the Ruhnu Deep in the middle of the Gulf of Riga. Shallow Pärnu Bay is characterised by permanent hydrological front that separates it from other areas of the Gulf of Riga, remarkably higher water temperature during the feeding period, higher species diversity and enhanced biological production. In the Gulf of Riga, during warm season, sharp seasonal thermocline effectively separates warmer surface water from cooler layers below it, where species composition of the biota is poorer (constitutes mainly of cold-water preferring species) and productivity lower as compared to that in Pärnu River estuary.

Investigations on eelpout growth parameters, appearance of sagittal otoliths with the size of annual increments, number of vertebrae, reproduction pattern and feeding habits allow to conclude that adaptation of eelpout, originally probably stenothermic glacial relict, to different environments in the Gulf of Riga has lead to development into two phenotypically distinct and spatially separated ecological groups (stocks): one of them distributes in cold deep water layers below the seasonal thermocline and the other in much variable conditions in shallow coastal zone (the Pärnu River estuary).

Due to fluctuations of location of seasonal thermocline, the fish inhabiting transitional zone between the main distribution areas of these two stocks face highly variable hydrological conditions and display intermediate or mixed pattern of the parameters measured. Obviously, adaptation processes are the most intense in this group.

Introduction

Glacial relicts constitute an important component of the Baltic fauna. They invaded the Baltic Sea after the last glaciation that finished approximately 10,000 years ago. Due to existence or absence of broad connections with neighbouring waterbodies during different historical time periods of development of the Baltic Sea, their invasions have probably taken place in several waves (Järvekülg 1973). In their migration routes as well as during various historical developmental stages of the Baltic basin they have faced widely changing salinity conditions (e.g. Segerstråle 1966).

However, the relicts have shown less adaptability towards higher temperatures. Therefore, presently they occupy in the Baltic Sea mainly the areas where low temperature along with high oxygen concentration up to the bottom layer are simultaneously retained all the year round. Such conditions can be found mainly in the Gulf of Riga, Gulf of Finland and Gulf of Bothnia.

Some characteristics of eelpout clearly indicate its belonging to the category of ‘glacial relicts’: reproduction of the fish takes place during cold season, it is very sensitive to changes in water oxygen concentration (Fisher *et al.* 1992), the fish prefers generally low water temperature in shallower areas (Neuman 1982, Jacobsson *et al.* 1993) also occurring abundantly in cold water layers in deep areas (Gaumiga 1981) and exhibiting fairly high growth rate at low temperatures (Fonds *et al.* 1989). However, Fisher *et al.* (1992) state that the species is well-adapted to environmental hypoxia being able to survive over short anoxic periods. This points to wide adaptability range of the species to various or changing environmental conditions.

Eelpout is a sedentary species showing considerable geographical variations both in meristic and genotypic indices (Frydenberg *et al.* 1973, Christiansen *et al.* 1976, Hjorth and Simonsen 1976, Schmidt 1917). However, most of the studies published up to now deal with eelpout from very limited depth range (e.g., Aneer 1975, Kristoffersson and Oikari 1975). Only some of authors (Netzel and Kuczynski 1995, Urtans 1990) have studied the species on considerably wider depth scale. As the fish occurs both in shallow (Jacobsson *et al.* 1993) and deep water layers (Netzel and Kuczynski 1995, Aneer 1975) facing thus highly variable environmental conditions (temperature, oxygen, salinity etc.), comparative investigations (e.g., on meristic characteristics, migration patterns, stock structure and growth rate) of the species from different depth ranges in the same region are necessary.

The current study investigates response of eelpout to spatially variable environmental conditions in the Gulf of Riga. Discrimination of eelpout groups was done on the basis of structure and appearance of sagittal otoliths, accompanied by studies in fish growth rate, mean number of vertebrae and reproduction pattern. To indicate dependence of different eelpout groups on complexes of prey animals of different origin, food composition of the fish was examined.

Material and Methods

For the current study, the fish were obtained from monthly performed experimental bottom trawl surveys on the transect Pärnu Bay- Ruhnu Deep during May–November, 1994–1997 and as by-catch from commercial fishery (Figure 1, see also Ojaveer 1997). Taking into account the governing factor for distribution of the main fish aggregations on the coastal slope of the research area — the seasonal thermocline, the research area was divided for further investigations into the following three sections:

1. The Pärnu River estuary — the region under direct influence of inflowing river waters situating above the seasonal thermocline. It is characterised by elevated biological productivity and higher species diversity.
2. Intermediate depths — the region of fluctuation of location of the seasonal thermocline on the coastal slope in the Gulf of Riga.
3. Deeper areas in the Gulf of Riga that situate permanently below the seasonal thermocline (generally ≥25 m). These water layers are mainly populated by organisms preferring cold-water environment, incl. glacial relicts. Also, species diversity and biological productivity is lower in these layers as compared to that in the river estuary.

For investigations of eelpout growth rate, data of 237, 423 and 328 eelpouts caught in the above mentioned areas 1, 2 and 3, respectively, in April–May, 1994–1996 were used. The fish were aged from sagittal otoliths. Otoliths of the fish from the first two regions were aged in ethanol, without preliminary preparations, in a light microscope at magnification of 32 × with side illumination on dark background. Otoliths of the fish from the deepest area were considerably smaller and had numerous irregular hyaline structures. Therefore, their ageing was comparatively difficult. Before age reading they were embedded into paraffine and the surface of the otolith was ground to enable good visibility of otolith structures.

For otolith investigations, eelpouts were caught in April–May, 1996. The right sagitta of 43 fish from each sub-area investigated was prepared for further measurements by repeatedly performed grinding of the surface producing good transparency and contrast of the otolith structures. The following otolith measurements were taken:

1. Otolith length — distance from the tip of *rostrum* to *postrostrum*;
2. Otolith width at focus — perpendicular to the length measurement from ventral to dorsal edge;
3. Diameter of the birth ring along the line of the otolith length measurement;
4. Width of yearly increments — distance from focus to the end of respective winter ring on rostrum (Figure 2).

To avoid influence by different growth conditions in various years to otolith yearly increments, as the first step, otolith measurements of the fish born in the same year (5-year-old) were compared. As there were relatively few specimen from the deepest area, and in order to reach a more general conclusion irrespective to the 'birth year', as the second step, the five first otolith annual rings of the 5–8-year-old fish were subjected to analysis.

For vertebrae counts, eelpouts were caught in the shallowest and deepest regions in May, 1997. As a characteristic feature, the corpus of the first vertebra, that linked to the interface of the occipital bone, was notably shorter than the following. The last vertebra counted started from the last vertebral interface and reached to the end of the skeleton.

For feeding investigations, food-containing stomachs of 56 and 53 eelpouts, caught in May, 1997 from the deepest and shallowest areas, respectively, were analysed. In order to estimate uniformity of occurrence of different food taxons identified in eelpout stomachs, Levin's measure of standardised niche breadth (B_A) for those regions were calculated (Krebs, 1989):

$$B_A = [(1/\Sigma p_j^2)-1]/(n-1), \text{ where}$$

p_j — is the fraction of j-th food item in eelpout stomachs,
n — is the total number of food taxons identified in stomachs of the fish.

Results and Discussion

1. Otolith differentiation and distribution of eelpout ecological groups

All respective otolith measurements, except diameter of the birth ring, showed statistically significant differences ($p<0.01$) between the three different regions studied. Mean otolith dimensions of the fish of similar age (5-years-old) and width of otolith annual increments, irrespective of the 'birth year' of the individuals, caught in shallower regions were larger compared to those in deeper areas (Table 1).

In addition to above-given regularity, notable differences in otolith shape of the fish caught in the deepest and shallowest region were evident. Otoliths of the fish exhibiting most rapid growth ('coastal type') have well-developed *excisura major* between the clearly protruding *rostrum* and *anterostrum* (Figure 2). It should also be noted that otolith shape of this type slightly changes with the age of fish: as compared to that of younger individuals, in otoliths of older fish the *rostrum* is more protrusive. Otoliths of the fish from deeper areas ('deep type') are more ellipsoid-like in shape with less fragmented dorsal edge, compared to that of 'coastal type'. *Excisura major* is almost absent (Figure 2). Otoliths of the fish from the transitional region ('intermediate type') displayed commonly intermediate visual shape characteristics or represented a mixture of the two main otolith types.

According to the above-given differences in otolith appearance of the fish, distribution areas of different eelpout groups were mapped on Figure 1. Two spatially separated eelpout stocks, one populating the Pärnu River estuary and the other deeper parts of the Gulf of Riga, can clearly be distinguished. Eelpout, inhabiting the transitional area (the region of migration of the seasonal thermocline; depth range ca. 8–20 m) between those distinct stocks face highly variable hydrological conditions and display intermediate or mixed otolith characteristics. Overlapping of the areas 1 and 2, that is rather limited, is due to widening of the distribution area of the 'coastal type' fish toward deeper parts of the Gulf of Riga in summer, as compared to the situation in spring. This is apparently caused by an increase of the water temperature in this region at this time. Probably, in the transitional area the eelpout adaptation process to new (higher and more changeable) temperature conditions as well as more variable prey animals, are the most intense and the natural selection should be the strongest within the research area.

Previous studies have indicated that fish otolith growth is under dual control: overall shape is regulated genetically whereas otolith size is influenced by environmental conditions — temperature (e.g. Lombarte and Lleonart 1993). Thus, there should exist at least two genetically differentiated eelpout groups (populations) in the Gulf of Riga: in Pärnu Bay (Area 1) and deeper regions (Area 3), when judged on the basis of otolith appearance. Remarkably lower otolith growth in deeper regions as compared to that in shallower areas, observed also in our study is, according to the theory, mainly caused by lower water temperature during growth period.

2. Number of vertebrae

Meristic characters, especially vertebrae numbers, have been used for investigations in stock structure of fishes (e.g. Parsons 1972, Templeman 1981, Ojaveer 1988).

The number of vertebrae are determined during embryonal and larval development (Hempel and Blaxter 1961, Parsons 1972). In this respect, critical period for eelpout is after fertilization of the fish in July–September (Tanasijchuk 1970). At this time, strong seasonal thermocline separates shallower warm water from cooler water layers below it, populated by the 'shallow and deep type' of eelpout, respectively. The mean number of vertebrae of the 'deep type' eelpout is significantly different from that of the 'shallow type' fish (116.5±0.2 n=87 and 115.0±0.3 n=68, respectively, $p<0.001$). Thus, higher mean number of vertebrae develops at colder temperature and *vice versa*.

In other fish, similar inverse relationship between the number of vertebrae and spawning temperature has been reported by Clark and Vladykov (1960) and Garside (1966). Field studies on eelpout (Frydenberg *et al.* 1973) and experiments with other species (e.g., Hempel and Blaxter 1961, Lindsey 1962) suggest that the vertebrae number is to a high degree genetically controlled. Løken and Pedersen (1996) concluded in their study, that in cod the differences in vertebrae counts between coastal and Northeast Arctic cod are, at least partly, genetically determined. The possibility on the genetical control on eelpout vertebrae number in the Gulf of Riga should be clarified in further studies.

3. Fish growth

The general rule, observed for otoliths, was also valid for fish growth: the individuals displayed considerably higher length-at-age and weight-at-age values and generally remarkably higher von Bertalanffy growth characteristics in all age-groups in shallower regions compared to those in deeper areas (Figure 3).

Eelpout lenth-at-age values observed within the current study in the deepest area were considerably lower than those recorded in similar depth range off Tvärminne area in the Gulf of Finland by Kristoffersson and Oikari (1975). Our values are more close to the numbers found by Lehtonen and Valtia (1973, cited in Kristoffersson and Oikari 1975).

Differences in growth rate of the fish and their otolith size between the eelpouts caught in the shallowest and deepest area seem to be rather exceptionless. We failed to find any specimen with the features characteristic to the 'deep type' in the coastal strip in Pärnu Bay and *vice versa*. However, the intraovarian growth of fry (both in length and weight) and that of its otoliths seems to be independent of sampling area, or environmental conditions, and is, apparently, species-specific conservative feature of eelpout.

4. Feeding

Despite of rather limited number of food-containing stomachs analysed, still some quite obvious tendencies with respect to feeding habits of the fish could be made. The number of food items identified in eelpout stomachs in Pärnu Bay exceeded that in deeper areas. Similar narrowing of eelpout food spectrum in relation to depth gradient in the Gulf of Riga has previously been observed by Urtans (1990). By abundance, typical shallow-water inhabitants — bivalves and *Corophium volutator* — were in a large majority in eelpout diet in shallower areas whilst cold-water preferring *Pontoporeia* spp. solely dominated in deeper parts of the Gulf of Riga (Table 1). This pattern can also be seen from the Levin's measure of standardised niche breadth, showing strong dominance of a few taxons in the diet of the fish in both regions (0.124 and 0.065, respectively). However, this dominance was ca. 2 times stronger in the cold-water environment. Although a glacial relict *Saduria entomon* occurred, by abundance, in eelpout stomachs in rather low proportions (Table 1), appr. 25% of the fish had preyed upon this organism in both areas sampled indicating, thus, considerable importance of this cold-water species for the fish as a food resource, probably on the whole coastal slope in the Gulf of Riga.

5. Reproduction

Spatially separated reproduction areas or temporally isolated spawning periods (e.g. Ojaveer 1988) have been considered as one of the most important preconditions for existence of separate fish stocks. Besides to otolith appearance and different growth rates, another strong evidence suggesting the existence of separated eelpout stocks in the Gulf of Riga is reproduction pattern of the species. From previous studies performed by Jacobsson *et al.* (1993) it is known that eelpout reproduces in shallow areas. Our investigations revealed that the fish very likely gives birth to youngs also in the deepest area sampled: we found abundant occurrence of pregnant females at 30–40 m depth both in the beginning and at the end of its reproduction period. It is extremely unlikely that the fish in a late stage of pregnancy will undertake for it quite long migration from the Ruhnu Deep to shallower coastal areas for giving birth to youngs. Another strong evidence for the above suggested reproduction pattern of the species is occurrence of 0-group individuals in experimental bottom trawl catches in Ruhnu Deep during all the years (1994–1997) sampled.

Contrary, Jacobsson *et al.* (1993) concluded that females migrate in autumn to shallower areas in order to give birth to youngs. However, their investigation area reached to depths of about 20 m not including, in our terms, distribution area of the ‘deep type’ eelpout. Their results should, in our context, be interpreted in a way that, in addition to the ‘coastal type’ fish, reproduction of eelpout of the ‘intermediate type’ takes also place in shallow coastal zone. However, we have not studied this possibility yet. Therefore, at the stage of current knowledge, there is no controversy between their and our results.

Fourhorned sculpin (*Myoxocephalus quadricornis*), generally accepted as a glacial relict, prefers cold water and is usually distributed below the seasonal thermocline in summer. However, Hansson (1980) reported its occurrence in Luleå area in shallow water, above the seasonal thermocline at this time. He explained this phenomenon as due to food limitation in deeper areas. Kostrichkina (1968) draws the line between two different complexes of bottom invertebrates at 20–25 m in the Gulf of Riga: the shallower part is populated mainly by organisms of boreal origin with contribution of warm-water animals whilst crustaceans of arctic origin dominate in the deep part. This zonation corresponds relatively well with our results on the existence of the ‘deep type’ stock below 20 meters. Also, biomass of benthic invertebrates in shallower areas considerably exceeds that in deeper parts providing thus much better feeding conditions for the fish in this region, as compared to that in deeper areas. Probably, richer food supply is the reason for development of separate ecological group of this sedentary cold-water preferring species in warm-water environment above the seasonal thermocline. Thus, feeding conditions exert probably powerful influence upon distribution of glacial relicts having started step by step breaking of the stenothermic nature of the species in the Gulf of Riga. As the result, comparatively eurytherm group of eelpout, adapted to its present area, has originated. However, presence of the spatially separated group below the seasonal thermocline points to the originally stenotherm character of eelpout at the species level. This group has still retained its stenotherm nature and possesses good perspectives for survival as long as necessary abiotic (temperature, oxygen content) and biotic (complex of glacial relicts as prey animals) conditions will persist in the Gulf of Riga.

Besides the consideration that different phenotypically and/or genotypically distinct groups / populations of eelpout have been formed as a result of adaptations to the local conditions, there remains possibility that natural immigrants, which migrated into the Baltic, have already been genetically and ecologically differentiated. This possibility has been stated for some benthic invertebrates (*Pontoporeia affinis*, *Heterocyprideis* and probably also *Saduria entomon*) by Järvekülg (1973) and herring (Ojaveer 1988) forming a number of local populations in the Baltic Sea. Therefore, this possibility should also be considered as a probable factor for existence of regionally separated eelpout populations or groups in the Baltic Sea.

In conclusion, there are several indications to support the hypothesis of the existence of different phenotypically distinct ecological groups, or spatially separated eelpout stocks in the Gulf of Riga. The suggested mechanism for formation of a separate group of this originally stenotherm cold-water fish in shallower areas with very variable temperature regime lies on better feeding conditions in those regions whereas adaptational success of the fish to new conditions is probably determined to a high degree in the transition area between the different environments.

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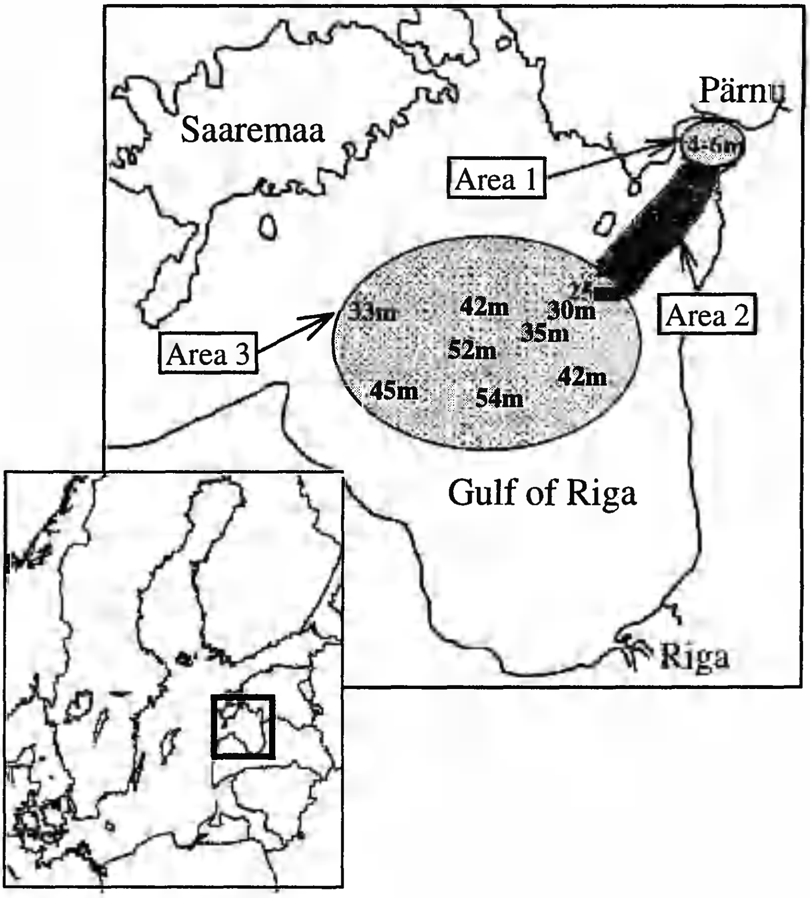

Figure 1. Sampling locations with the map showing the spatial distribution of different eelpout (*Zoarces viviparus*) ecological groups in the Gulf of Riga. Numbers in the shadowed areas indicate sampling depths. For details on the distribution areas see the text.

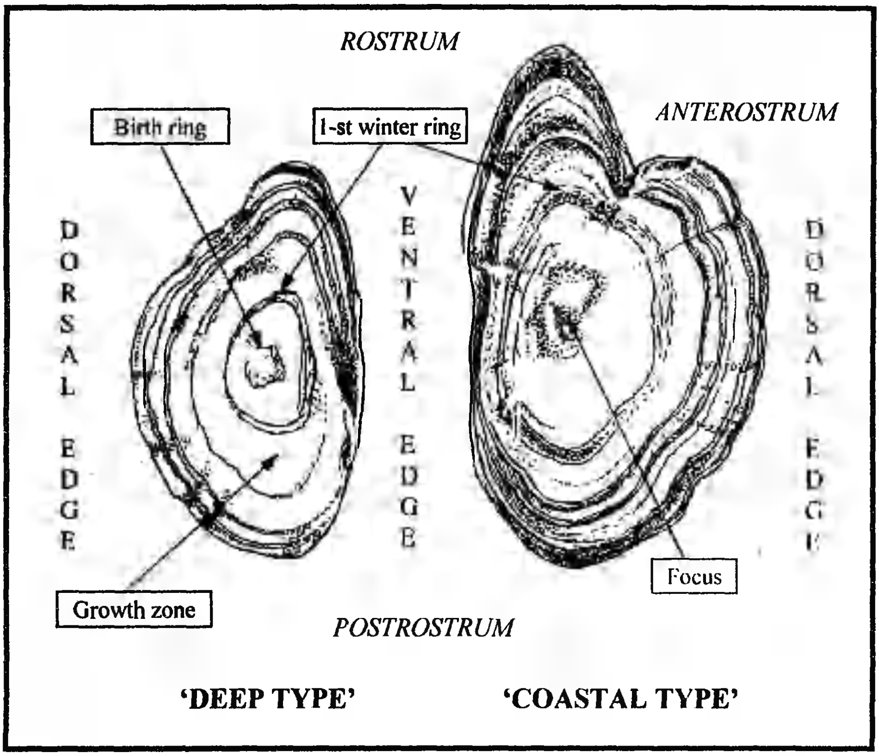

Figure 2. Lateral views of typical (untreated) sagittal otoliths of eelpout (*Zoarces viviparus*) from deeper parts (≥25 m) of the Gulf of Riga ('deep type', 4 winter rings) and the coastal strip in the Pärnu River estuary ('coastal type', 2 winter rings).

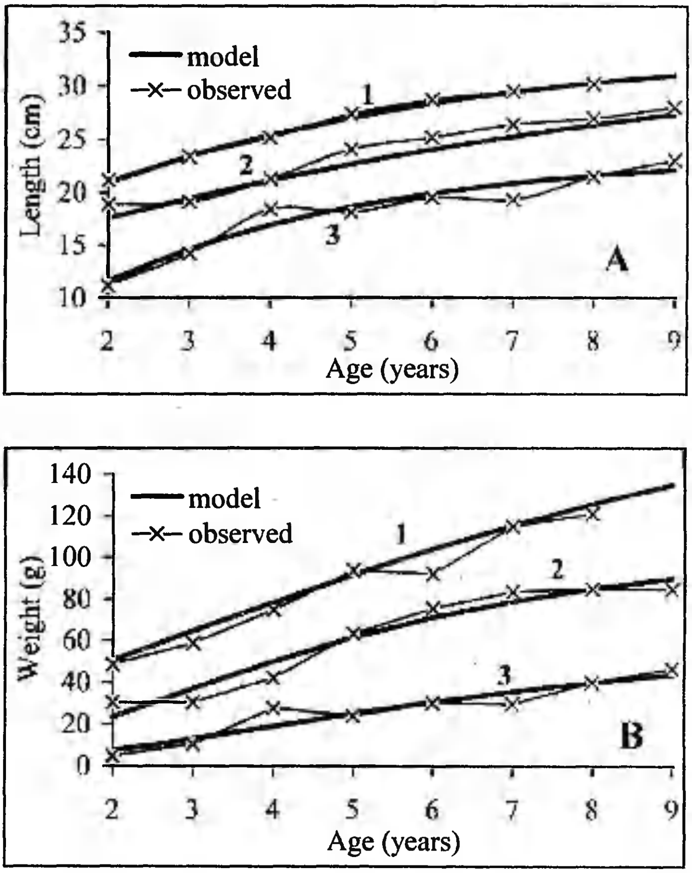

Figure 3. On the von Bertalanffy growth model based computed length-at-age (A) and weight-at-age curves (B), together with graphs of observed mean numbers, for different eelpout (*Zoarces viviparus*) ecological groups in Pärnu Bay and the Gulf of Riga.

1 — ‘Coastal type’ (L_{inf} = 34.0 cm, W_{inf} = 197.3 g);
2 — ‘Intermediate type’ (L_{inf} = 35.8 cm, W_{inf} = 105.4 g);
3 — ‘Deep type’ (L_{inf} = 23.7 cm, W_{inf} = 59.7 g).

Table 1. Otolith dimensions, birth ring diameter and width (mm) of the first five yearly increments of the right sagitta of eelpout, *Zoarces viviparus*, (mean±S.E.) for the three ecological groups identified in the Gulf of Riga. Otolith length and width were determined for 5-year-old fish. Other measurements were performed on otoliths of 5–8-year-old eelpout (n=43). Width of an annual growth zone was determined as the distance from the otolith focus to the end of respective winter zone on rostrum. Except the diameter of the birth ring, in all the otolith measurements the difference was significant (p<0.01) between the three eelpout groups studied.

Parameter	'Coastal type'	'Intermediate type'	'Deep type'
Otolith length	2.94 ± 0.03 (n=20)	2.62 ± 0.04 (n=28)	2.23 ± 0.11 (n=8)
Otolith width	1.60 ± 0.02 (n=20)	1.49 ± 0.03 (n=28)	1.32 ± 0.05 (n=8)
Birth ring diam.	0.59 ± 0.01	0.59 ± 0.01	0.58 ± 0.01
1-st annual ring	0.61 ±0.01	0.58 ± 0.01	0.53 ± 0.01
2-nd annual ring	0.92 ± 0.01	0.81 ± 0.01	0.68 ± 0.01
3-rd annual ring	1.16 ± 0.02	1.01 ± 0.02	0.82 ± 0.01
4-th annual ring	1.34 ± 0.02	1.17 ± 0.02	0.94 ± 0.02
5-th annual ring	1.47 ± 0.02	1.28 ± 0.02	1.04 ± 0.02

Table 2. Composition and importance of different food taxons identified in eelpout (*Zoarces viviparus*) stomachs.

Area / food item	Share of the taxon in eelpout diet (%, by abundance)	% of eelpout stomachs, where the food item was present
Pärnu Bay		
Macoma baltica	64.4	52.8
Corophium volutator	21.4	5.7
Cardium edule	10.5	11.3
Saduria entomon	1.9	24.5
Clupea harengus juv.	0.7	15.1
Gammarus spp.	0.4	1.9
Pungitius pungitius	0.3	3.8
Osmerus eperlanus juv.	0.2	3.8
Gasterosteus aculeatus	0.1	1.9
Cyprinidae juv.	0.1	1.9
≥25 m in the Gulf of Riga		
Pontoporeia spp.	86.6	69.6
Macoma baltica	5.9	1.8
Saduria entomon	3.8	25.0
Corophium volutator	3.2	3.6
Clupea harengus juv.	0.3	1.8
Osmerus eperlanus juv.	0.3	1.8

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Forage Fishes in the Brackish Gulf of Riga Ecosystem

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Abstract

The number of fish species inhabiting the Gulf of Riga is relatively low, but exceeds 50. Baltic herring constitute around 90% of the commercial catches, while the other major commercial species, sprat and smelt, are less abundant. Stocks of demersal fishes, including cod, sculpins, seasnail, and lumpsucker, are currently greatly depressed. However, the abundance of eelpouts and gobies is increasing. Among noncommercial fishes, the proportion of sticklebacks (three-spined stickleback and nine-spined stickleback) is the highest. Other species were met only occasionally. Predators, e.g., pikeperch, dominate in the coastal areas.

The largest concentrations of feeding fish occur in the mixing zone at the seasonal thermocline and around it, because the best feeding conditions are found there. Clupeoids are predominantly specialized for feeding on zooplankton (copepods and, to a lesser extent, cladocerans), whereas the diet of smelt is more diverse and consists mainly of mysids, zooplankton, and fishes. Abundant sticklebacks are important food competitors for other zooplankton-feeders, mainly in coastal areas. Fish diets show remarkable spatio-temporal variability, depending also on prey community structure and fish size. Probably, mainly due to seasonal changes in hydrological conditions, temporal differences in the zooplankton community were observed.

Over 100 parasite species belonging to 12 classes of invertebrates were identified. The most important parasites of forage fishes were determined with regard to their prevalence rate. Of the most abundant forage fishes, herring, smelt, and sticklebacks can be considered as the main supplementary/paratenic hosts for the main helminths in the parasitofauna of the Gulf of Riga.

Introduction

Dynamics of species composition and the structure of fish and zooplankton communities in the Gulf of Riga are mainly influenced by changes in abiotic conditions. This depends essentially on water exchange between the North and Baltic seas, determined mostly by large-scale meteorological changes over the North Atlantic. As the last saline water inflow into the Baltic Sea in 1993 was moderate and took place after the longest stagnation period recorded since 1976 (Matthäus 1993), the present hydrological situation in the Gulf of Riga could be characterized as low in salinity—a mean of 5.1 ppt was measured within the current study—but satisfactory in oxygen regime: oxygen concentration in the near-bottom water layer did not fall below 3.1 mg per liter. The Gulf of Riga (maximum depth 62 m) lacks a halocline, but a sharp seasonal thermocline exists during the warm season. Another factor having major effect on the fish community is anthropogenic pollution, to which deterioration of the condition of some fish stocks could partly be attributed (e.g., Gaumiga 1981, Ojaveer 1996). Composition and abundance of fish species in the Gulf of Riga are also influenced by fisheries and the presence or absence of cod as the main large marine predator (Ojaveer 1996). Changes in these main governing factors trigger alterations in species composition, and abundance and distribution of the organisms, which, in turn, lead to variations in predator-prey and parasite-host interaction patterns in the basin.

The present study was undertaken in order to investigate distribution of fish aggregations on the coastal slope; species composition and seasonal dynamics of the zooplankton as the main food resource of pelagic fishes; and spatio-temporal dynamics of the diet composition of the most abundant forage fishes in the Gulf of Riga: herring (*Clupea harengus membras*), sprat (*Sprattus sprattus balticus*), smelt (*Osmerus eperlanus eperlanus*), three-spined stickleback (*Gasterosteus aculeatus*) and nine-spined stickleback (*Pungitius pungitius*) in 1994-1996. Infestation of the fish with parasites was studied during the 1982-1996 period.

Materials and Methods

Bottom trawl surveys were performed at stationary stations in the Gulf of Riga (Figure 1) by means of a small stern trawler (length 12.5 m, 90 hp) from May to November in 1994-1996. Altogether 21 cruises with 201 samplings were carried out. The stations were towed during the daylight for 30 minutes each tow, at a mean trawling speed of 2 knots. Estimated trawl opening area was 40 m^2 and mesh size in the codend 8 mm (except 20 mm from May to July 1994). From the Irbe Sound area, samples were taken from May to August only. In each catch, fish were identified to species, counted, and the total weight of each species calculated. In total catch calculations, non forage fishes were excluded;

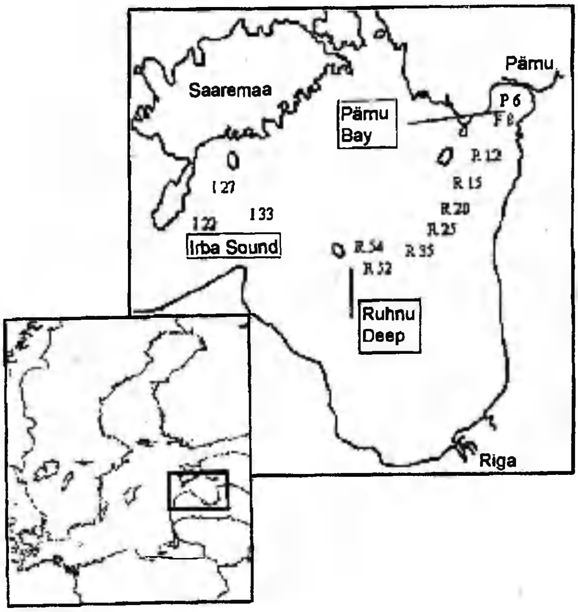

Figure 1. Location of trawling and sampling stations in the Gulf of Riga. The numbers indicate station depth.

these were mainly warm-water fishes of freshwater origin, e.g., pike-perch (*Stizostedion lucioperca*), bream (*Abramis brama*), and white bream (*Blicca bjoerckna*) populating mainly the Pärnu River estuary. Location of the seasonal thermocline was determined using a portable thermo-oxymeter (MJ 94, Elke Sensor, Estonia). Salinity of the near-bottom water layer was determined according to the method of Koroleff (1979).

In each station, zooplankton was sampled from bottom to surface (large Juday net, mesh size 90 µm). The samples were preserved and analyzed according to Lumberg (1976) and Ojaveer (1997). Data used in this paper cover the years 1994-1995 and May-August 1996.

For fish stomach analysis, routine hydrobiological methods (VNIRO 1971) were applied. Altogether 1,284 herrings, 547 sticklebacks, 397 smelts, and 271 sprats, caught during 1994-1995, were used for stomach content investigations. The simplified Morisita index of dietary overlap and electivity index, based on biomass and abundance values, respectively, were determined (Krebs 1989). In electivity index calculations, fish stomachs containing prey items other than zooplankton were excluded. Data on pikeperch food composition are based on qualitative investigations of 701 fish stomachs containing food in 1995-1996.

For further data analysis, the study area was divided into four subregions: stations P6 and P8—Pärnu Bay, inhabited predominantly by organisms of fresh- and warm-water origin; R12-R35—the northeastern part of the Gulf of Riga migration area of the seasonal thermocline from late spring to autumn; R52 and R54—Ruhnu Deep, representing conditions that favor distribution of glacial relicts and other cold-water-preferring organisms; and I22-I33—Irbe Sound area, the transition region between open sea and the Gulf of Riga.

A total of more than 3,000 sticklebacks, in excess of 1,200 herrings, over 1,000 sprats, about 700 smelts, and over 6,000 specimens of different predatory fish species (e.g., pikeperch, perch, trout, cod, turbot) were analyzed for parasites according to the standard method of total parasitological autopsy. Fishes were collected from various sources in different locations in the Gulf of Riga during 1982-1996. Ascaroid nematodes were determined and identified according to Fagerholm (1991).

Results and Discussion

Distribution and abundance of fish aggregations on the coastal slope

During the main feeding period in summer, fishes inhabiting the coastal slope from Pärnu Bay to Ruhnu Deep were mainly concentrated in the mixing zone at the seasonal thermocline. There the fish catches were significantly higher than those in adjacent stations (Mann-Whitney U-test, $p < 0.01$); an average 68% of fish catches were taken from this specific region. The term "mixing zone" was first introduced by Ojaveer and Kalejs (1974). Feeding aggregations of fish around the seasonal thermocline moved from spring to autumn with descending thermocline deeper toward the open part of the Gulf of Riga (Ojaveer, 1997).

Adult sprat (2-4 years old) were mainly within the uppermost part of the mixing zone at thermocline (Figure 2) and in the Irbe Sound area, whereas juvenile specimens were found mostly in the Irbe Sound region. Abundance of sprat was frequently on the same order of magnitude as that of herring, the mean value being in the range of about 70 specimens per haul.

Smaller and younger herring (mainly 1-4 years old) were concentrated in the upper part of the mixing zone and in the Irbe Sound area. Larger and older specimens were found in the lower part of the mixing zone and less abundantly also far below the thermocline (Figure 2). Herring clearly dominated in catches, the mean abundance falling into the range of about 500 specimens per haul.

Smelt, a glacial relict, inhabits mostly cold-water regions below the seasonal temperature front being more abundantly aggregated in the

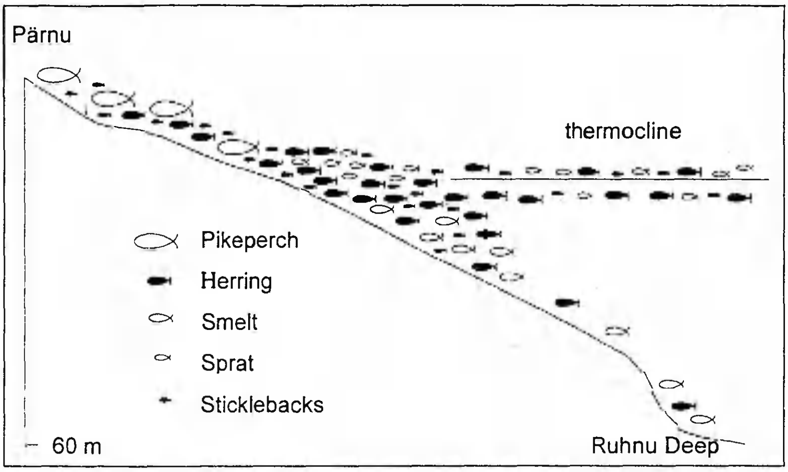

Figure 2. Schematic picture showing distribution of the main feeding concentrations of the most abundant adult forage fishes and their main predator, in relation to seasonal temperature front during the periods of absence of large marine predators, in the Gulf of Riga.

lower part of the mixing zone (Figure 2). Juvenile and younger smelt (young of the year) were also found above the thermocline. Moderate (in the range of nearly 50 specimens per trawl) mean abundance of smelt was recorded.

Sticklebacks, which generally prefer coastal and estuarine areas, were found in high numbers (mean value exceeding 100 fish per catch) all over the study area, showing higher abundance values in autumn.

Distribution of the largest feeding pelagic fish aggregations is generally determined by location of the mixing zone. Due to higher biological productivity (Ojaveer and Kalejs 1974), these regions are characterized, in general, by higher zooplankton biomasses and, consequently, improved feeding conditions for planktivorous fish. Also, environmental conditions (temperature) seem to favor aggregation of fish species with different temperature preferences (e.g., sprat, herring, and smelt) in the mixing zone. Within the current study, significantly lower numbers of empty stomachs of adult clupeoids was observed in the mixing zone at the seasonal thermocline than above and below it (Mann-Whitney U-test, $p < 0.05$). However, this regularity was generally not observed for smelt and sticklebacks. Another numerical value used in evaluation of the feeding intensity of fish in the current study is the stomach fullness index. This index of herring and smelt, caught in the mixing zone, tended to be higher in this region when compared to that of adjacent areas.

Thus, aggregation of pelagic fish shoals in the mixing zone at the seasonal thermocline is probably due to richer food supply, results generally in elevated feeding activity of fish.

There are probably two different biological groups of eelpout (*Zoarces viviparus*) (mean abundance <5 fish per trawl) in the Gulf of Riga: one inhabits deep and cold water regions and another is adapted to warm water conditions in shallow coastal areas (Ojaveer et al. 1996). Therefore, their abundance does not seem to be related to the location of the mixing zone of the seasonal thermocline. Other fish species were met only rarely; e.g., gobies (*Pomatoschistus spp.*), seasnail (*Liparis liparis barbatus*), lumpsucker (*Cyclopterus lumpus*), and straight-nosed pipefish (*Nerophis ophidion*) were met by bottom trawl less frequently.

In autumn, fishes of marine origin gradually gather in the Ruhnu Deep for wintering whereas freshwater species overwinter mainly in the Pärnu River estuary.

Zooplankton biomass and species composition

Seasonal dynamics of the biomass of copepods and that of the total zooplankton are shown in Figure 3. Of rotifers, *Keratella cochlearis, K. quadrata,* and *Synchaeta* spp. (mostly *S. baltica*) clearly dominated. *Bosmina coregoni maritima* and *Podon* spp. prevailed from cladocerans. Recently a new cladoceran, *Cercopagis pengoi,* invaded the Gulf of Riga (Ojaveer and Lumberg 1995). It occurred very abundantly mainly in coastal areas in summer. Of copepods, the highest biomass values were recorded from July until October, with prevalence of *Eurytemora hirundoides* and *Acartia* spp. (mainly *A. bifilosa*) which constituted an average 75% of biomass. The proportion of copepods in the zooplankton community clearly increased from June to October (Figure 3) with concomitant growth in the importance of *Acartia* spp. over *E. hirundoides.* Thus, freshwater and marine euryhaline species clearly predominated in the zooplankton community. The glacial relict *Limnocalanus grimaldii* (*L. macrurus*) and marine species *Pseudocalanus elongatus* and *Temora longicornis* were present in samples from deeper regions (R35-R54) but in small numbers only. These results correspond well with the recent situation in the Gulf of Riga (Sidrevics et al. 1993) and the Gulf of Finland (Lumberg and Ojaveer 1997).

Fish feeding

Dietary overlap

In Pärnu Bay, the diets of adult herring, smelt, and sticklebacks were rather similar and consisted mainly of *E. hirundoides* (Figure 4). In the northeastern part of the Gulf of Riga, sticklebacks were also important competitors for food of pelagic commercial fishes: the main prey item for them was *E. hirundoides.* Due to the elevated share of *Neomysis integer* and small fishes in the food of smelt in this region, the simplified

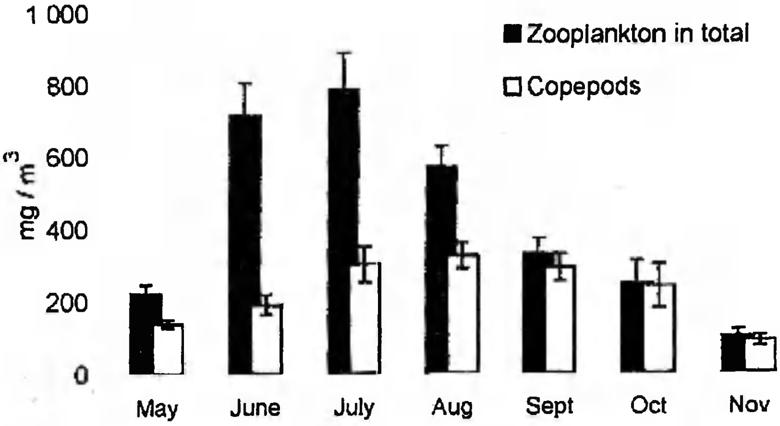

Figure 3. Seasonal differences in total zooplankton and copepod biomass (mean values, with standard error bars) in the Gulf of Riga in 1994-1996.

Morisita index of overlap between smelt and other pelagic fishes was rather low. In the Ruhnu Deep, the food spectrum of herring consisted mainly of *E. hirundoides* and *Mysis relicta*, causing the highest food similarity values with sprat and smelt, respectively. Other values were very low, indicating weak diet overlap and decreased competition for food as compared to other areas (Figure 4). In the Irbe Sound area, herring and sprat exhibited the highest dietary overlap, mainly due to *E. hirundoides* and *B. c. maritima*. Besides these zooplankters, sticklebacks were found to prefer other cladocerans and also insects. Therefore, the Morisita similarity indices between clupeoids and sticklebacks were moderate. In contrast, the diet of smelt consisted with rare exceptions of small fishes and nektobenthic organisms in this area (Figure 4). The spatial and species-dependent feeding dynamics of the above-mentioned fishes were probably mainly connected with their different food preferences (*E. hirundoides, B. c. maritima*, mysids) and distribution of suitable food (*C. pengoi, N. integer, M. relicta*).

Electivity

The average electivity indexes of herring, sprat, and sticklebacks for the most frequently occurring zooplankters in fish stomachs are given in Figure 5. *Eurytemora hirundoides* seems to be the most preferred food item, having relatively high values of the index that are generally based on rather low spatio-temporal variability of their availability. In contrast, *Acartia* spp. and *Podon* spp. exhibited great variation in availability

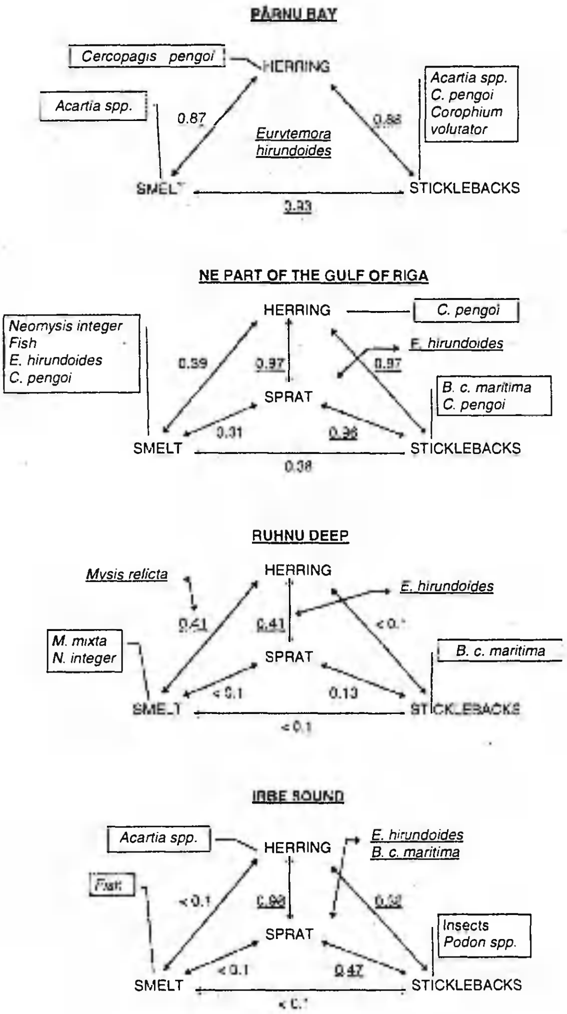

Figure 4. ***Spatial dynamics of the simplified Morisita index for the most abundant forage fishes in the Gulf of Riga during 1994-1995. Common prey items having the strongest influence on higher similarity indices are underlined. Similarity indices are also underlined. Other important prey taxa are boxed.***

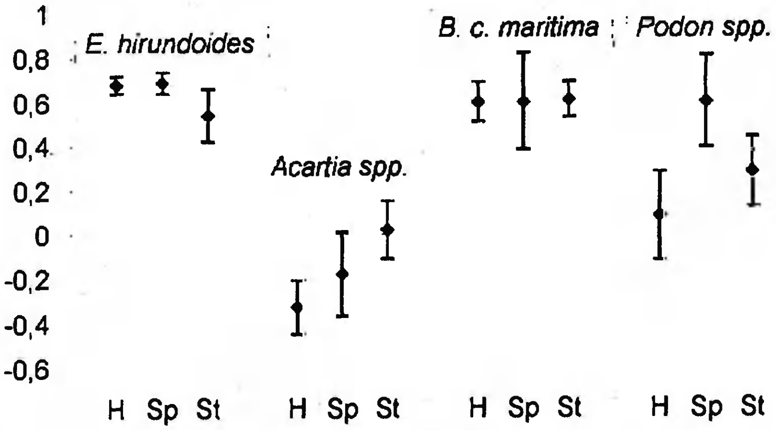

Figure 5. Mean electivity indices (with standard error bars) of herring (H), sprat (Sp), and sticklebacks (St) for different zooplankton taxa in the Gulf of Riga during 1994-1995.

which generally caused relatively low mean values of the index with one exception: a surprisingly high electivity index of sprat for *Podon* spp. was recorded in the northeastern part of the Gulf of Riga. Although high mean electivity indices of clupeoids for *B. c. maritima* and of sprat for *Podon* spp. were observed, according to our results, they occurred in the diet of these fishes generally in rather low amounts (Table 1). However, according to Lankov (1988) and Starodub et al. (1992), *Bosmina* and *Podon* could be more important in the diet of this species in the northern and eastern Baltic than indicated by the results of present investigations.

Seasonal dynamics of food composition

Characteristic seasonal changes in food composition of fishes were observed in Pärnu Bay and the northeastern Gulf of Riga. For herring, the share of zooplankton decreased and that of nektobenthos gradually increased from spring to autumn. A decline in the importance of *E. hirundoides* for herring and sticklebacks with concomitant increase of the role of *Acartia* spp. was also evident (Figure 6). This is in good agreement with respective changes in the copepod community: from spring to autumn, the proportion of *Acartia* spp. gradually rose and that of *E. hirundoides* dropped. In summer, increased variability in the diet of herring and sticklebacks was mostly due to elevated consumption of cladocerans, mainly *C. pengoi* and *B. c. maritima*. In addition to that, in the food

Table 1. Diet composition of different size classes of herring, smelt, sprat, and sticklebacks (% by wet weight), and pikeperch (% by abundance).

Baltic herring

Food/fish length (cm)	<10.0	10.0-11.9	12.0-13.9	14.0-15.9	16.0-17.9	>18.0
Eurytemora hirundoides	57.0	88.4	77.0	65.8	51.0	92.2
Acartia spp.	35.3	3.3	7.7	5.3	6.4	3.9
Limnocalanus grimaldii	00.4	0.3	1.8	6.0	0.3	
Total copepods	93.8	92.1	85.2	73.0	63.0	96.4
Cercopagis pengoi	0	0.7	7.7	16.4	6.4	0
Total cladocerans	4.9	2.4	11.8	19.4	6.4	0.2
Zooplankton	98.8	94.6	97.0	92.4	70.4	96.6
Mysids	0	0.5	1.6	6.3	29.1	3.5
Nektobenthos	0	1.9	1.6	6.6	29.6	3.5
Fish larvae	1.2	3.5	1.4	1.0	0	0

Smelt

Food/fish length (cm)	<8.0	8.0-9.9	10.0-11.9	12.0-13.9	14.0-15.9	>16.0
Eurytemora hirundoides	18.7	31.6	22.5	2.1	0	0
Total copepods	20.1	37.0	22.5	2.1	0	0
Cercopagis pengoi	3.4	0.3	3.2	14.8	0	0
Total cladocerans	12.9	1.6	7.0	16.9	1.3	0
Zooplankton	33.0	28.6	29.5	19.0	1.3	0
Neomysis integer	66.5	47.0	33.0	22.8	18.1	0
Mysis mixta, M. relicta	0.5	13.1	15.2	42.2	55.4	3.3
Nektobenthos	67.0	61.1	48.2	65.6	77.6	4.4
Other fishes	0	0.3	22.3	15.4	21.1	95.6

Sprat

Food/fish length (cm)	<9.0	9.0-9.9	10.0-10.9	11.0-11.9	>12.0
Eurytemora hirundoides	58.3	94.3	79.6	76.8	67.6
Acartia spp.	25.2	1.2	8.7	10.2	18.2
Total copepods	83.5	97.8	90.5	87.2	87.2
Bosmina coregoni maritima	4.2	1.5	4.9	8.4	8.3
Podon spp.	9.9	0.7	4.6	4.5	4.5
Total cladocerans	14.8	2.2	9.5	12.8	12.8
Zooplankton	100	100	100	100	100

Sticklebacks

Food/fish length (cm)	4.0-4.9	5.0-5.9	6.0-6.9	>7.0
Eurytemora hirundoides	59.7	32.4	64.4	77.2
Acartia spp.	3.4	4.7	6.0	4.3
Total copepods	63.4	44.0	72.1	81.5
Bosmina coregoni maritima	12.9	2.8	3.8	5.4
Podon spp.	19.2	2.8	3.8	5.4
Cercopagis pengoi	0	4.2	1.1	0
Total cladocerans	32.4	47.7	7.3	7.6
Zooplankton	96.0	91.9	80.4	89.1
Nektobenthos *(Corophium)*	0	5.5	11.7	8.7
Insects	4.0	2.6	7.9	2.2

Table 1. (Cont'd.)

Pikeperch Food/fish length (cm)	<10.0	10.0-19.9	20.0-29.9	30.0-39.9	>40.0
Neomysis integer	35.4	35.3	8.8	0	0
Corophium volutator	28.0	17.6	7.4	2.7	0
Nektobenthos	64.1	52.9	17.6	3.0	0
Baltic herring	12.2	11.8	69.1	74.7	78.1
Smelt	3.0	0	1.5	7.6	2.4
Sticklebacks	0	3.0	5.9	8.5	4.9
Gobies	20.7	17.6	4.4	1.9	0
Other fishes	35.9	47.1	82.4	97.0	100.0

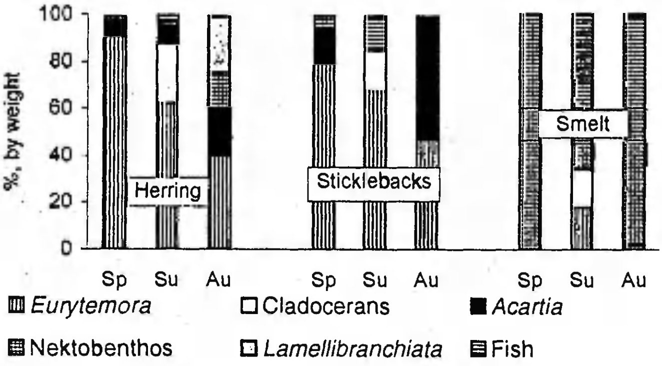

Figure 6. Seasonal changes in the main dietary items of herring, smelt, and sticklebacks in Pärnu Bay and the northeastern Gulf of Riga (Sp, Spring; Su, Summer; Au, Autumn).

of smelt the importance of zooplankters (*E. hirundoides*) together with smaller fishes markedly increased (Figure 6). Additional qualitative stomach content analysis of herrings and three-spined sticklebacks, caught from stations P8-R15, revealed their strong preference for *C. pengoi*: up to 100% of analyzed fish stomachs contained this animal. Thus, this cladoceran seems to be an important food item in the diet of pelagic and benthopelagic fishes during summer. The increased proportion of small fishes in the diet of smelt during summer is obviously connected with gradual offshore migration of 0-group herring and smelt. Also, the abundance of *E. hirundoides* considerably increased during the warm season, which could partly explain their augmented role in the diet of smaller smelt, occupying partly the mixing zone at thermocline.

Changes in food composition related to fish size

The proportion of *E. hirundoides* gradually decreased and that of *L. grimaldii* and nektobenthos increased in the food of herring belonging to medium size classes (10.0 <L (cm) <17.9; Table 1). The importance of *Acartia* spp. was very high in the diet for the smaller fish (L <10 cm, mainly 0-age). These fish were predominantly caught during the second half of summer and in autumn, when *Acartia* spp. clearly dominated over *E. hirundoides* among copepods. Thus, changes in prey community structure could partly explain this phenomenon. *Centropagis pengoi* was mainly consumed by fish of medium sizes. Obviously, this cladoceran is too large a prey item for small herring. Bigger fishes occur mainly in deeper (and colder) parts of the Gulf of Riga and, therefore, these zooplankters are probably not available for them, as they prefer warm (surface and coastal) waters (Ojaveer and Lumberg 1995). Obviously due to shortage of their common prey items (nektobenthos, *Limnocalanus*), herring of the biggest size class (L >18 cm) preyed mostly on zooplankton, *E. hirundoides* (Figure 6).

The most important food items for smelt were mysids: stomachs of smaller individuals (L <11.9 cm), also inhabiting warmer water layers, contained mainly *N. integer*, which is abundantly distributed in warmer coastal waters in the northeastern Gulf of Riga (Kotta 1980). Larger smelt (L >12.0 cm), living predominantly below the seasonal temperature front, consumed mainly glacial relicts *M. mixta* and *M. relicta* which inhabit deeper regions of the gulf (Kotta 1980). Mainly due to the increased amount of *E. hirundoides*, the share of zooplankters was rather high in the diet of smaller smelt. The species composition of the diet of the biggest individuals was notably narrower than that of other size groups and consisted mainly of fishes (Table 1).

The importance of *E. hirundoides* in sprat diet continuously decreased and that of *Acartia* spp. and *B. c. maritima* increased with increasing fish length (L >9.0 cm). No clear tendency could be observed for *Podon* spp. content in fish stomachs (Table 1).

Stomachs of smaller sticklebacks (4.0 < L (cm) < 5.9) contained generally more cladocerans (*B. c. maritima* and *Podon* spp.) than bigger fishes whereas longer individuals (L >6.0 cm) tended to consume more nektobenthic organisms (*C. volutator*). The most important food item for sticklebacks was generally *E. hirundoides* (Table 1).

Mainly due to a long-lasting stagnation period, the Gulf of Riga currently lacks large marine predatory fishes. The largest abundant predator in the study area is pikeperch, inhabiting mostly Pärnu Bay. However, larger individuals (l >20 cm) migrate during feeding deeper toward the open part of the Gulf of Riga, occurring always above the seasonal thermocline (Figure 2). This determines to a great extent the diet of this species: smaller individuals consumed mainly *N. integer*, *C. volutator*, and gobies; the most suitable and preferred prey for bigger fishes being herring (Table 1).

Parasite infestation

Over 100 parasite species, belonging to 12 classes of invertebrates, were identified. Due to this large number, specific attention was paid, at first, to parasites causing mass infestation of fishes and second, to those parasites for which forage fishes (clupeoids, smelt, and sticklebacks) serve as supplementary and/or paratenic hosts. Parasites of freshwater origin dominated in the parasitofauna of these species (Table 2). The most important marine euryhaline parasites were the protozoan *Eimeria sardinea* and nematodes *Contracaecum osculatum* and *Hysterothylacium* spp., and also acanthocephalans, *Corynosoma* spp. Herring, smelt, and both stickleback species were obviously the main supplementary-paratenic hosts for the main helminths of fish-eating birds (Laridae), seals (mainly grey seal, *Halichoerus grypus*), and predatory fishes. It is commonly accepted that the parasite fauna of clupeoids, especially that of herring, is very specific. However, in the brackish-water environment in the Gulf of Riga, of those specific parasites occurring with reasonably high prevalence rate, we only found *E. sardinea*. Mass infestation of herrings with this parasite began in the early 1990s and continuously increased. Infestation of herring by representatives of the family Anisakidae (except *Raphidascaris acus*) has increased since the end of the 1980s.

Certain size-dependent dynamics of parasitic infestation of smelt were recorded: the infestation rate with Anisakidae larvae of fishes belonging to the 0-1 year classes was about 3 times higher than that of larger specimens. In contrast, *Cystidicola farionis* occurred in 55-70% of smaller smelts but close to 100% of larger individuals.

Conclusions

1. Zooplankton and forage fish community of the Gulf of Riga is at present strongly dominated by estuarine and marine euryhaline components.

Table 2. **Most important parasites of forage fish in the Gulf of Riga. Numbers in brackets indicate the annual infestation rate of the respective parasite (%).**

Parasite	Fish as a host	Location in fish	Intermediate host	Definitive host
Protozoa				
Eimeria sardinea	Herring, sprat (36-91)	Testicles	—	—
Glugea hertwigi	Herring (1-12), smelt (1-3)	Parenchyma tissue, gonads etc.	—	—
G. anomala	Sticklebacks (1-23)	Connective tissue, muscles, skin	—	—
Cillophora (Urceolaridae)	Clupeoids (1-35), sticklebacks (1-80)	Gills, skin, nostrils	—	—
Helminthes				
Cestoda				
Schistocephalus solidus (pl.)	Three-spined stickleback (6-75)	Body cavity	Copepods	Birds (mainly *Larus*)
S. pungitii (pl.)	Nine-spined stickleback (1-12)	Body cavity	Copepods	Birds (mainly *Larus*)
Diphyllobothrium dendriticum (pl.)	Three-spined stickleback (<6)	Body cavity	Copepods	Birds, mammals (incl. humans)
Bothriocephalus scorpii (pl.) (?)	Sticklebacks (3-47)	Gastrointestinal system	Copepods	Turbot, salmonids, sculpins, flounder
Triaenophorus nodulosus (pl.)	Smelt (1-5), sticklebacks (1-23)	Mainly liver, also kidney and spleen	Copepods	Pike, salmonids
T. crassus (pl.)	Smelt (1-3)	Mainly liver, also kidney and spleen	Copepods	Pike
Proteocephalus filicollis (pl.) and (i.)	Sticklebacks (<70)	Intestine	Copepods	Pike

Table 2. (Cont'd.)

Parasite	Fish as a host	Location in fish	Intermediate host	Definitive host
P. percae (pl.)	Smelt (1-6), sticklebacks (<40)	Gastrointestinal system	Copepods	Perch, pike
P. neglectus (pl.)	Sticklebacks (<20)	Gastrointestinal system	Copepods	Trout, (other salmonids?)
Trematoda				
Diplostomum sp. *metacercariae* (m.)	Herring (<30), smelt (<70), sticklebacks (<100)	Eye (*corpus vitreus*)	Mollusks (Limnaeidae)	Birds (*Larus*, *Ardea*, *Mergus*)
Cryptocotyle concava (m.)	Smelt (<11)	Fins, gills	Mollusks (*Hydrobia*)	Birds (mainly *Larus*)
Nematoda				
Raphidascaris acus larvae (l.)	Clupeoids, mainly herring (<44), smelt (<60), sticklebacks (<99)	Parenchyma tissue, mesentery	Crustaceans, amphipods, insects, *Oligochaeta*	Pike, pike—perch, salmonids
Contracaecum osculatum (l.)	Clupeoids, mainly herring (<37), smelt (<78), sticklebacks (<65)	Liver, mesentery, gonads, etc.	(Crustaceans, mysids, isopods, *Polychaeta*)?	Seals
Hysterothylacium auctum (l.)	Clupeoids (<26), smelt (<46), sticklebacks (<60)	Liver, mesentery, gonads, etc.	(Crustaceans, mysids, isopods, *Polychaeta*)?	Eelpout, cod, flounder, sculpins
H. aduncum (l.)	Clupeoids (<7), smelt (<23)	Liver, mesentery, gonads, etc.	(Crustaceans, mysids, isopods, *Polychaeta*)?	Salmonids, cod
Acanthocephala				
Cystidicola farionis (i.)	Smelt (<99)	Swimbladder	*Pontoporeia affinis*	—
Corynosoma semerme (l.) and *C. strumosum* (l.)	Herring (<15), smelt (1-38)	Mesentery	*Pontoporeia affinis*	Seals
Pomphorhynchus laevis (l.)	Herring (<3), smelt (<47), sticklebacks (<25)	Mesentery	Gammarids	Cyprinids, flatfish, pike, salmonids etc.

i = imagos, l = larvae, m = metacercariae, pl. = plerocercoid

2. During the main feeding period, the largest fish aggregations occurred in the mixing zone of seasonal thermocline (clupeoids and smelt) and also around it (clupeoids). Sticklebacks were distributed rather abundantly all over the study area.
3. Spatio-temporal and size-dependent dynamics in the diets of fishes are connected with different food preferences and availability of prey groups.
4. Sticklebacks are important food competitors for pelagic commercial fishes mainly in shallower areas.
5. The majority of the parasites identified in 1982-1996 belonged to the freshwater complex. Herring, smelt, and sticklebacks were the most important supplementary/paratenic hosts for the main helminths in the parasitofauna of predatory fishes, sea gulls, and seals in the Gulf of Riga.

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ON THE ROLE OF *CERCOPAGIS (CERCOPAGIS) PENGOI* (OSTROUMOV) IN PÄRNU BAY AND THE NE PART OF THE GULF OF RIGA ECOSYSTEM

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Abstract. The invasion of a new Cladocera species, *Cercopagis (Cercopagis) pengoi* (Ostroumov), into Pärnu Bay and the NE part of the Gulf of Riga ecosystem is reported. A brief description of its geographic origin and distribution, morphology, and systematics is also presented. Our investigations show that the distribution of *C. pengoi* is patchy in the Gulf of Riga. The main predator of *C. pengoi* is Baltic herring in the Gulf of Riga. Despite of the abundant presence of copepods, the herring diet (0-group excluded) consists mainly of the cladoceran *C. pengoi.* In several stations up to 100% of herring stomachs contained this species.

C. pengoi plays a minor role in the diet of the three-spined stickleback, nine-spined stickleback, and smelt. The stomachs of the 0-group Baltic herring, sprat, white bream, and bleak did not contain this cladoceran species.

Key words: Gulf of Riga ecosystem, *Cercopagis pengoi.*

INTRODUCTION

Investigations in the Gulf of Riga ecosystem were started by K. Frisch and H. Riikoja in the 1920s. During the past 40 years several changes in the Gulf of Riga ecosystem structure have been reported, including changes in the phytoplankton species composition and an increase in primary production; decrease and disappearance of a considerable number of zooplankton, zoobenthos, and fish species that require unpolluted water; rapid development of heterotrophic microbiological communities; decrease in the catches of several fish species, etc. (Ojaveer, in press). These changes are mainly caused by periodical local and global climate fluctuations and by human activities (high pollution load and resource exploitation). On the other hand, these changes indicate a labile character of the Gulf of Riga ecosystem. The lability is also evidenced by a sharp outbreak of a new cladoceran species, never before found in the Gulf of Riga. The presence of *Cercopagis (Cercopagis) pengoi* in the Gulf of Riga was for the first time stated in July and August 1992 (Lumberg, unpubl. data). However, the ecological role of that species remained unknown.

Another outburst of *C. pengoi* was observed in July and August 1994. In 1994 some ecological investigations were performed in order to assess the role of this cladoceran species in the local marine food web.

MATERIAL AND METHODS

Bottom trawlings (mesh size 10 mm) were performed in Pärnu Bay and the NE part of the Gulf of Riga (Fig. 1) on 18 August (stations 1—3) and 23 August (stations 4—6 and a control trawling at station 1) 1994. The temperature of water layers and the oxygen concentration in the near-bottom water were measured with the thermo-oximeter MAR-VET JUNIOR, model MJ94. Zooplankton was sampled at each station (large Juday net with a mesh size of 100 μm). The fish stomach fullness and the fat content in its intestines were estimated on a scale from 0 (empty) to 3 (full).

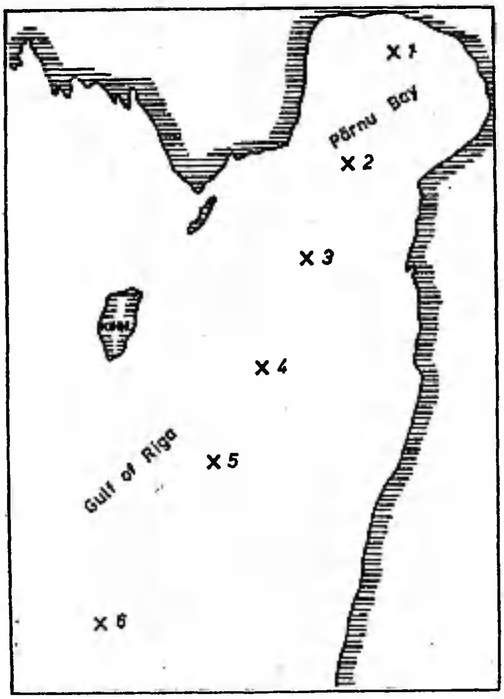

Fig. 1. Location of the sampling stations (*1—6*) in Pärnu Bay and the NE part of the Gulf of Riga.

CHARACTERISTICS OF *CERCOPAGIS (CERCOPAGIS) PENGOI* (OSTROUMOV, 1981)

The species belongs to the order Cladocera, genus *Cercopagis* (Sars, 1897).

The body of the animal is clearly divided into head, pectoral limbs, and tail spine. The anterior part of the head consists of a round eye, in which the amount of dark pigment is considerably smaller than the eye diameter (Fig. 2). The length of the female is 1.2—2.0 mm, that of the male 1.1—1.4 mm.

Fig. 2. *Cercopagis (Cercopagis) pengoi* (Ostroumov, 1891).
a parthenogenetic female; *b* gamogenetic female; *c* male (Мордухай-Волтовской & Ривьер, 1987).

Earlier *C. pengoi* was known from the Caspian, Azov, and Aral seas (Fig. 3). The species is also widespread in the Danube, Dnieper, and Bug rivers. It occurs in coastal lakes in Bulgaria. It has also been found in the Tsimlyansk and Kakhovka reservoirs. *C. pengoi* occurs usually in the areas of low salinity and it can also dwell in fresh water.

In the northern Caspian Sea a specific form of the species occurs. Probably due to higher salinity of the environment, the *C. pengoi* of the Aral Sea differs from the Caspian and Ponto-Azov forms (Мордухай-Болтовской & Ривьер, 1987).

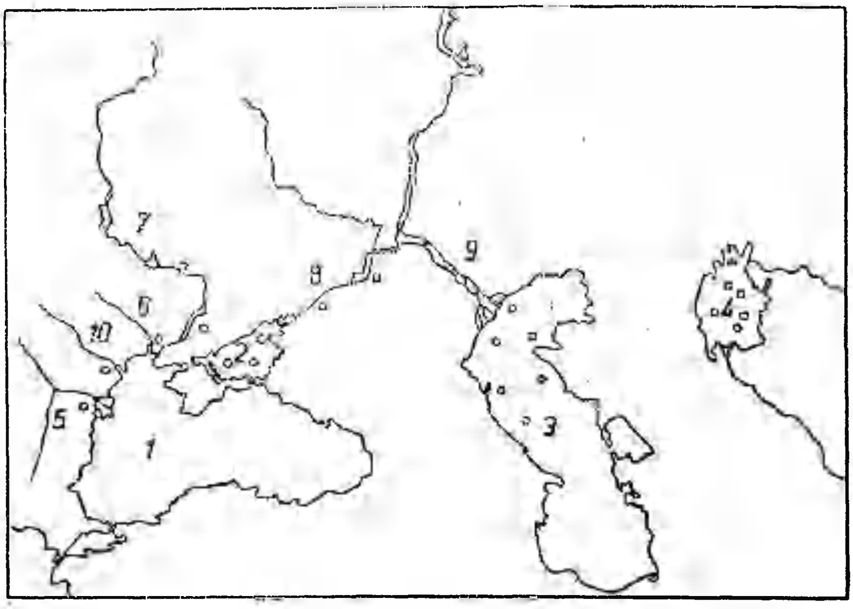

Fig. 3. Occurrence of *Cercopagis (Cercopagis) pengoi* (Мордухай-Волтовской & Ривьер, 1987).
1 Black Sea, *2* Sea of Azov, *3* Caspian Sea, *4* Aral Sea, *5* Danube, *6* Bug, *7* Dnieper, *8* Don. *9* Volga, *10* Dniester.

RESULTS AND DISCUSSION

C. pengoi was first discovered in Pärnu Bay and the NE part of the Gulf of Riga on 9 July 1992 (2 ind$\cdot$m^{-3}). In late July and August massive occurrence of that species was observed. Some individuals (2 ind$\cdot$m^{-3}) were found as late as on 5 October 1992. The surface water temperature was 12.7 °C at that time.

In July—August 1994 massive occurrence of *C. pengoi* in the NE Gulf of Riga repeated.

Results of Baltic herring (*Clupea harengus membras* L.) stomach analysis in 1994 revealed that *C. pengoi* plays an important role in the diet of this fish species. The studied stomachs (0-group fish excluded) contained both half-digested and fresh *C. pengoi*, indicating that the cladoceran is a suitable, energetically profitable, and freely consumable prey of Baltic herring in the area investigated. During our investigations in 1994 the average stomach fullness of Baltic herring was two units. The fatness of the investigated herrings varied between 1 and 3 (mean 1.5). This relatively high fatness index was unusual among the commonly lean herring in the Gulf of Riga. It is well known that since the early 1980s the Baltic herring growth in the NE Baltic has considerably reduced (Lumberg & Ojaveer, 1991).

On an average, 83.1% of herrings (142 specimens analysed, those with an empty stomach excluded) fed on *C. pengoi*. The percentage of individuals with empty stomachs reached 18%. This indicator for stations 1—5, situated in the zone of warm surface water (surface temperature over 16 °C, thermocline absent), equalled 10% (Tables 1, 2). Thus, despite of an abundant presence of copepods (Table 3), herring fed on the recently invaded cladoceran species very actively, especially above thermocline. Therefore, there is some basis to believe that further presence of *C. pengoi* could contribute to an improvement of Baltic herring's feeding conditions and growth rate.

Our catches indicated that herring was not very abundant in the studied area in summer (July—August). The main reason was probably high water temperature, over 16 °C in the 15 m surface layer. It is known that the main herring feeding aggregations occur at 2—14 °C with a smaller fraction feeding at 16—17 °C (Оявеер, 1988). However, high temperature promotes rapid reproduction of cladocerans. Unfortunately, we have no numerical data on *C. pengoi* abundance during its reproduction maximum in late July and early August 1994, when its mass development occurred and the animals choked fishing gears. During our field work in late August the *C. pengoi* community was already declining (surface water temperature varied from 17.8 °C at station 1 to 16.3 °C at station 5). No adhesion of *C. pengoi* to trawl was observed. Herring abundance in the warm surface layer during the *C. pengoi* abundance maximum is rather low. Therefore, despite of its high stomach fullness, herring can utilize only a minor part of the *C. pengoi* biomass production. Probably the bulk of the *C. pengoi* biomass is mineralized and transferred into the biogeochemical matter and energy cycle via sedimentation and subsequent heterotrophic destruction. At station 5, only 18% of the feeding herring consumed *C. pengoi*, whereas at station 4 this percentage reached 100% and at station 6 was 67%. These facts could point to an unequal and mosaic distribution of the *C. pengoi* community over the studied area.

We did not find any *C. pengoi* specimens in the stomachs of the 0-group herring. The juvenile herring feeds only on copepod nauplii occurring abundantly in plankton (Table 3). Consequently, the presence of *C. pengoi* has no direct impact upon the survival and abundance of

Table 1

Some results of the Baltic herring stomach analyses

Station	Number of individuals analysed	Percentage of individuals (with empty stomachs excluded) feeding on *Cercopagis pengoi*	Percentage of individuals with empty stomachs
1	8	100	0
1*	20	100	0
2	15	93	7
3	20	100	0
4	20	100	10
5	20	18	45
6	39	67	62
TOTAL	142	MEAN 83	18

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* control trawling.

Table 2

Characteristics of the sampling stations

Station	Depth, m	Thermocline	Near-bottom water layer temperature, °C	Near-bottom water layer oxygen concentr., ppm
1	6	absent	17.8	9.3
2	8	absent	17.7	9.6
3	12	absent	15.2	3.9
4	15	absent	16.4	3.8
5	20	absent	13.9	4.3
6	29	at 18—20 m	4.5	4.7

Table 3

Zooplankton abundance (individuals per m^3) in stations 1, 2, and 3 on 18 August and at control sampling in station 1 (1*) on 23 August

Zooplankton groups	Station			
	1	2	3	1*
Rotatoria	18 200	47 100	38 640	22 920
Cercopagis pengoi	280	100	40	300
Cladocera	360	200	40	300
Copepoda nauplii	5 760	16 400	7 800	29 940
Copepoda	10 120	29 550	13 120	39 360
Mollusca larvae	40	150	200	180
Cirripedia larvae	400	700	120	3 420
TOTAL	29 120	77 700	52 120	66 180

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* control trawling.

the 0-group herring and the strength of the forming herring year-class depends mainly on the abundance of copepod nauplii. Obviously, *C. pengoi* is too big for the 0-group herring.

Other important commercial fish species — sprat (that is not abundant in the Gulf of Riga), white bream, and bleak — did not feed on that cladoceran species. Three-spined stickleback, nine-spined stickleback, and smelt stomach contained among other food half-digested *C. pengoi* specimens. Consequently, the cladoceran *C. pengoi*, which has recently invaded into the Gulf of Riga, has become an important constituent of the local food web and is directly grazed by fishes.

However, in connection with the *C. pengoi* invasion into the Gulf of Riga, a number of questions should be clarified with further studies, e. g. what the diet of *C. pengoi* in the Gulf of Riga is, which advantages this species has in competition with other zooplankton species traditionally occurring in the Gulf of Riga, and how its abundant presence will influence the functioning of the ecosystem of the Gulf of Riga.

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VI

Ojaveer, H. Exploitation of biological resources of the Baltic Sea
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Exploitation of biological resources of the Baltic Sea by Estonia in 1928–1995

Henn Ojaveer

Summary

The main exploitable biological resources in the Estonian zone of the Baltic Sea are fish stocks. Fishes of marine origin constitute the main bulk (on the average 91%) of catches. Some freshwater and migratory fishes, having usually only marginal role in the total weight of fish landings, are of special importance for local fishermen in certain regions. Other living resources — red algae and seals — have been exploited in rather small amounts.

The main factors having controlled changes in the condition of fish stocks and catches are natural conditions, marine pollution, eutrophication and exploitation rate.

Key words: Baltic Sea, Estonia, marine living resources, exploitation.

Fisheries

Baltic herring (*Clupea harengus membras*) has been the most important fish in Estonian fisheries for a long time (Figure 1). A sharp increase in herring landings from the late 1940s was mainly caused by the development of trapnet fishery. During the early 1950s, herring bottom trawl fishery was started. Due to overfishing on spawning grounds in the early 1950s, the landings decreased. Implementation of restrictions on the number of trapnets and some other measures of stock conservation, accompanied by strong year-classes, resulted in continuation of the increase in landings in the 1960s. This was also favoured by a high demand for herring at these times. Since the early 1960s, in Estonian waters pelagic species are mainly fished with pelagic pair trawls. Deterioration of stock condition in the late 1970s and early 1980s as well as changes in the exploitation pattern and fishing policy in the USSR, caused a gradual decrease in catches from the late 1970s until the early 1990s. Exploitable spring-spawning herring stocks consist of open sea and gulf herring populations, responding differently to changes in the ecosystem. Good sea herring year-classes were formed in periods of high advection of the Kattegat waters whereas rich year-classes of the gulf herring have been hatched in the periods of high wind activity and rich river inflow. Drastic drop in the share of autumn spawning herring in the total herring catches could be attributed to a integrated effect of overexploitation, marine pollution and unfavourable natural reproduction conditions (Ojaveer, in press). Changes in socio-economical situation in the 1990s, triggered mainly by political changes, have increased the demand for at present generally underexploited herring resources.

Sprat (*Sprattus sprattus balticus*) landings have exhibited growth tendency from the late 1950s with the peak in the first half of the 1970s (Figure 1). The catches based on rich sprat year-classes hatched in 1955, 1957, 1959, 1967, 1969, 1972 and 1975 (Veldre, 1986). As in the case of herring, the most important reason for the increase in sprat catches was development of catching technics. Due to an improvement of cod stock condition, sprat spawning stock biomass and landings reached a very low level in the early 1980s (IBSFC, 1992). In the first half of the 1990s, when cod fall into deep depression, both sprat biomass (IBSFC, 1992) and the catches started to increase. Fluctuations in sprat stock conditions mostly depend on the strength of year-classes and the abundance of its predator — cod. Formation of good sprat year-classes is governed by several factors: high temperature of upper water layers, rich feeding conditions, abundant spawning stock size and low natural mortality (Kruger, 1972, Veldre, 1986).

Cod (*Gadus morhua callarias*) stock condition depends mainly on its year-class strength, determined to a high degree by the inflow of saline water. Hatching of good recruit in the Eastern Baltic cod stimulates its migration into Estonian waters. Following an improvement in stock condition and inccrease in fishing effort (Dementjeva *et al.,* 1951), cod catches considerably augmented during the late 1930s and the first half of the 1940s (Figure 1). The decline in cod stock abundance in the 1950s, resulted in negligible landings until the late 1970s. Cod fishery started to intensify again after considerable improvement of cod stock condition in the late 1970s (IBSFC, 1992). Recently the Eastern Baltic cod was in deep depression due to unfavourable environmental conditions for reproduction and very low number of cod spawning stock (Baranova, 1995).

Flounder (*Platichthys flesus*) is mostly caught with trawls and danish seines. The maximum catch in Estonia was taken in 1965 (2 731 tons). Decrease in flounder catches in the late 1980s and early 1990s reflect concomitant decline in the stock size.

From the fishes of freshwater origin, perch (*Perca fluviatilis*) is fairly widely distributed in Estonian coastal waters and should be considered as the most important fish in the near-coast zone. An increase in perch catches, observed during the 1970s (Figure 2), was due to strong year-classes which entered into fishery during that period, favourable market price and implementation of improved catch recording method (Pihu *ET AL.,* in press). According to them, the decrease in perch landings during the 1990s was partly a consequence of worsening of perch stock condition. At present, small perch (including juvenile stages) suffer under high fishing pressure, due to their elevated need for export. Contrarily to several other fishes, perch seems to be less vulnerable to the consequences of eutrophication; the fish even can gain profit from it due to the improved food amount (Ojaveer & Gaumiga, 1995).

Pike-perch (*Stizostedion lucioperca*) inhabits mostly Pärnu Bay (NE Gulf of Riga) and is one of the most important export fishes. After-war official pike-perch landings have only rarely reached the pre-war level (Figure 2). However, there remains serious suspect as to the reliability of recent catch records. Pikeperch stock has suffered under heavy fishing pressure during recent years, evidenced by almost a lack of bigger specimen in experimental trawl catches. Fortunately, the recruitment seems to be fairly strong and sufficient. It can be, at least partly, attributed to the artificial spawning substrates, that have been put on the pike-perch spawning grounds by local fishermen every year since 1980. Other factors, that have negatively affected pike-perch abundance are dredging works close to the fairly restricted spawning area, eutrophication of the marine environment, strong winds and low water temperature during spawning period and severe winters (Erm, in press).

The main smelt (*Osmerus eperlanus eperlanus*) fishing grounds in Estonian waters are situated in the lower reaches and estuary of the Pärnu River (NE Gulf of Riga). During the 1960s, overfishing was the most probable cause for decrease in stock size and landings (Figure 2). Later on, pollution from a soviet military base likely hindered formation of strong recruitment. Recent removal of the pollution source has resulted in some increase of the abundance of smelt larvae in Pärnu River estuary (Spilev, pers. comm.) and possibly could support higher landings in future.

Like in eel (*Anguilla anguilla*), the decline in landings of whitefish (*Coregonus lavaretus lavaretus*) (Figure 3) reflects fairly well the stock dynamics, except during the immediate post-war years. Starting from the 1950s, over-exploitation caused high landings. Catch restrictions, that were implemented from the second half of the 1970s appeared to be too late. Later on, the main factors in the continuing decrease of the stock abundance and landings have been marine pollution and eutrophication, often accompanied by unfavourable temperature conditions during the embryonic development. Unfortunately, artificial incubation of fry has not lead to the expected results (Sõrmus, 1992).

Sticklebacks (*Gasterostus aculeatus* and *Pungitius pungitius*) occur abundantly in shallow coastal waters and have highly negative impact upon some commercially valuable fish stocks (Tanasiichuk *et al.*, 1966). The main obstacle for rapid increase in stickleback fishery (that started in 1947) was insufficient number of proper gears. Intensified stickleback exploitation started in the 1960s (Figure 3), mostly due to the abovementioned reason coupled with direct socio-economical interest (the fish was used for animal fodder and fish meal) and financial stimuli for the fishermen. At present, fishermen lack of financial interest for stickleback fishery.

Sharp reduction in pike (*Esox lucius*) landings, from an average of 462 tons during the pre-war years (1928–1940) to 42 tons in the 1990s, is probably caused by eutrophication of the marine environment.

Catches of other target fishes, mostly of local importance — garpike (*Belone belone*), vimba bream (*Vimba vimba*), white bream (*Blicca bjoerkna*) and ide (*Leuciscus idus*) have commonly been low and rather variable. Four-horned sculpin (*Triglopsis quadricornis*), sea scorpion (*Myoxocephalus scorpius scorpius*) and eelpout (*Zoarces viviparus*) have mainly been landed as by-catch.

Mean share of marine fish in the total Estonian landings from the Baltic Sea has increased from 80% during pre-war times (1928–1940) to 92% during 1945–1959 and to 95% in 1969–1995. These changes are mostly connected with mismanagement of coastal fish resources, including overfishing that resulted in deterioration and collapse of certain fish stocks, modernisation of the open-sea fishing technique, including procurement of more powerful trawlers, application of fish detection devices and implementation of efficient trawling methods. Constant and growing pollution pressure on the marine environment during the Soviet times had its detrimental effects, especially upon the coastal ecosystems, as these regions are exposed to the highest concentrations of land-based pollutants and in-flowing nutrients. Long-term climatic changes that have mirrored in concomitant changes of natural conditions of the Baltic Sea, have been another great source of variation in fish stocks and landings.

Other stocks

Commercial exploitation of the unique loose lying *Furcellaria lumbricalis-Coccoctylus truncatus* community in the West-Estonian Archipelago Sea for agar production started in 1966 and has been very strictly limited: catch quotas have varied from 800–1200 tons in wet weight per year; the highest trawl catch, 1 675 tons, was taken in 1977. This has allowed an increase in the total and specific (g/m^2) biomass of the stock and expansion of the area of distribution (Martin *et al.*, 1996).

Grey seal (*Halichoerus grypus*) and ringed seal (*Pusa hispida*) are the two seal species having been of interest for local seal hunters. Until 1968, seal catch was commonly not limited in the Baltic Sea, sporadically available Estonian catches reaching to over 1800 individuals in 1934. A bounty system for killed seals was introduced in 1937 (Anon, 1937). In 1969, a law regulating seal catch in the former Soviet Union zone of the Baltic Sea was implemented. Mostly due to organisational problems, lack of interest and shortage of efficient catch equipment, only one fifth of the quotas for ringed seals was officially used at these times. A sharp decline in seal population, caused mainly by unfavourable climatic conditions, growing pollution of marine environment and too intense hunting resulted in the total seal catch ban since 1980 (Genina, 1973, 1980).

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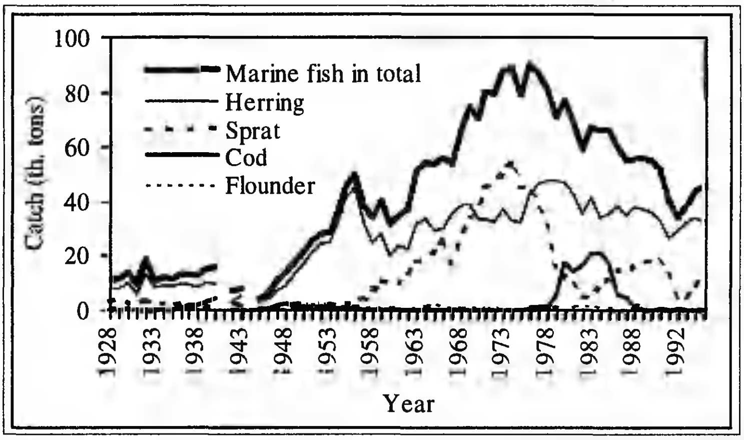

Figure 1. Estonian marine fish landings from the Baltic in 1928–1995.

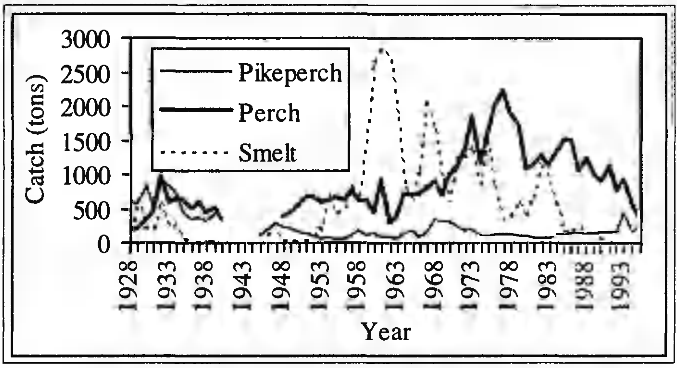

Figure 2. Estonian pike-perch, perch and smelt catches in the Baltic Sea during 1928–1995.

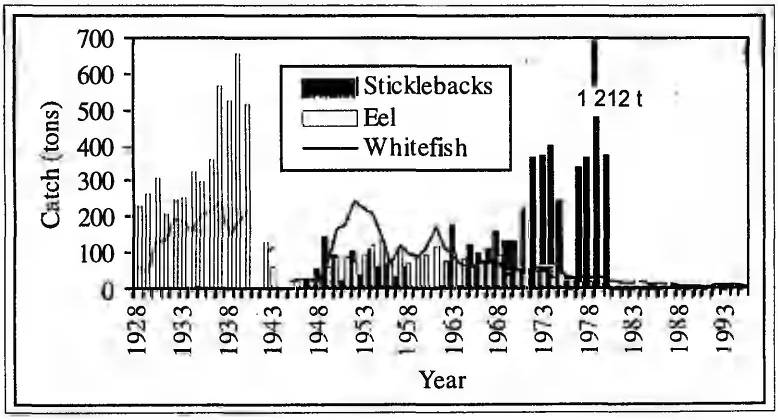

Figure 3. Estonian catch statistics of eel, whitefish and sticklebacks from the Baltic Sea in 1928–1995.

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Interpretation of the otolith structures in viviparous blenny *Zoarces viviparus*

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Summary

The otolith structure in viviparous blenny (*Zoarces viviparus*) was studied in fish of varying age and sizes collected in the Kattegat and in the Baltic Sea. We concluded that two major events in the early development of blenny were reflected in their otolith structure. Close to the core of the otolith, a thin hyaline ring structure forms at hatching in September-October. An additional, much broader, hyaline zone is formed during the period after birth in midwinter. In older fish, so-called 'growth zones', consisting of opaque material, were found to form in spring and summer. In August, the deposed otolith material changed to a hyaline character, resulting in a hyaline, 'winter zone' growth during autumn and winter. No effect of age or sex on the annual formation pattern could be detected.

Introduction

The viviparous blenny (*Zoarces viviparus* (L.)) has been selected as a suitable species by the Oslo and Paris Commission (OSPARCUM) and the Helsinki Commission (HELCOM) for monitoring toxic effects on reproduction. It is common in marine and brackish environments in Northwestern Europe, spends all its life in narrowly restricted areas, and its fry develop within the mother for 4–6 months, thus allowing controlled-effect studies during the most sensitive part of the life-cycle (Jacobsson et al. 1986; Jacobsson and Neuman 1991; Jacobsson et al. 1993). To elucidate reproductive responses and their ultimate effects on recruitment and year-class strength, ageing of fish is essential. Thus, there is a need for a good understanding of the otolith formation patterns in this species.

The viviparous mode of reproduction, however, complicates the interpretation of the otolith annual structures. In many fish species, both hatching and birth can be expected to cause hyaline (transparent, i.e., appears dark in reflected light) ring structures, because they are known to be connected with periods of stress, such as high or low temperatures or food shortage (e.g., Mosegaard 1986; Mosegaard et al. 1988). The viviparous blenny usually spawns in August in Swedish coastal waters, and the fry hatch about a month later (Kristoffersson et al. 1973; M. Vetemaa, pers. comm.). Within the ovary cavity, the fry probably do not encounter any dramatic food deficits, due to the secretion of amino acids and cell fragments of the female (Kristoffersson et al. 1973). However, birth takes place between December and February, i.e., during that part of the year when food is scarce and temperatures are low, both of which are factors leading to formation of hyaline otolith material.

In the relevant literature, otolith formation patterns in viviparous blenny have only been briefly discussed by Kristoffersson and Oikari (1975). It was suggested that this species has a hyaline otolith growth in summer and opaque (appears white or grey in reflected light) in winter, in contrast to most other temperate fishes (Bagenal and Tesch 1978). Kristoffersson and Oikari (1975) assumed that the otolith structure in 0 + fry from the Gulf of Finland was characterized by two opaque zones and two hyaline zones (Fig. 1). The second hyaline zone at the edge of the otolith was believed to have been deposited at the time of capture, i.e., in its first summer. The inner hyaline zone appeared to have been formed at birth. Consequently, the inner opaque zone is formed before birth and the outer opaque zone after birth in midwinter and before summer.

However, it is possible that the age of the fish was underestimated by 1 year in the study by Kristoffersson and Oikari (1975). The first hyaline zone could certainly have been formed in connection with birth in midwinter. However, the second opaque zone may equally well have been deposited during the first summer and the second hyaline zone at the edge during the following winter. In other words, the fish could have been 1 year older than assumed. A third opaque zone, corresponding to summer otolith growth, had not yet been formed, because the fish were caught early in the summer. As a consequence, there is cause for concern about the accuracy of age determinations in this species, which is a serious problem in the interpretation of monitoring data. The otolith formation patterns in viviparous blenny were studied by extensive field sampling, covering different habitats, in different seasons as well as fish of varying sizes and age, including newly born fry.

Material and methods

All the viviparous blennies, apart from free-living fry, were collected in fyke nets (i.e., framed hoop nets with a leader at

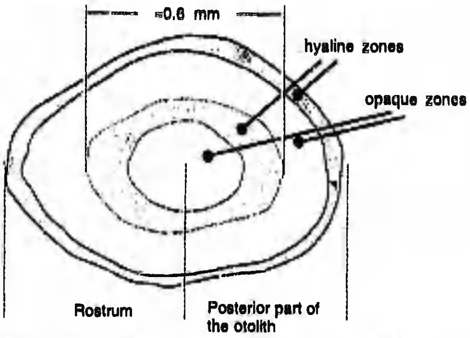

Fig. 1. The otolith structure of viviparous blenny (*Zoarces viviparus*) assumed by Kristoffersson and Oikari (1975) to be one-summer-old, caught on 8 June 1973 in the Gulf of Finland. (Fish length = 78 mm. Drawings made from a photograph in Kristoffersson and Oikari (1975))

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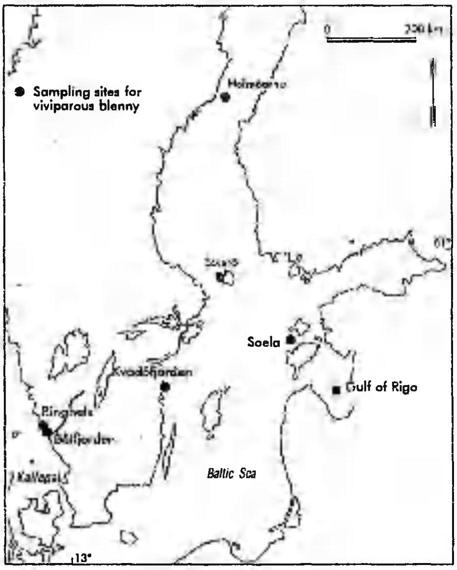

Fig. 2. Map showing sampling sites of viviparous blenny (*Zources viviparus*) on the Swedish west coast and in the Baltic Sea

the front hoop (e.g., Lagler 1978)) in the Kattegat and in the Baltic Sea between 1993 and 1995 (Fig. 2). Fish collected in the Gulf of Riga comprise specimen from the Irbe Sound, deeper parts of the Gulf of Riga and Pärnu Bay. The total length (in mm) and sex of every fish were noted. Sagittal otoliths were dissected, measured and analysed under a light microscope. Occasionally, the otoliths had to be ground on one or both sides to achieve a better sagittal view of the ring structures. Usually, both sagittal otoliths could be successfully prepared, and consequently, almost all measurements recorded are means of two otolith estimates.

Some specimens collected in spring at Ringhals and at Eckerö on Åland (Fig. 2) were considered to be 0 + fry, i.e., born during the preceding winter, due to their similarity in size relative to unborn fry (about 40–50 mm, Jacobsson et al. 1993). At the inlet to the once-through cooling system at the Ringhals nuclear power plant, fry were caught in a stationary mounted Isaacs-Kidd midwater trawl, modified for larvae sampling (Lindquist 1972). The fry were caught between 25 January and 30 March 1995 and measured 40–67 mm in length ($n = 62$). At Eckerö on Åland on 18 May 1994, fry were collected using a small-mesh trawl net. The fry ranged from 40 to 58 mm in length ($n = 8$). In addition, unborn fry were sampled from pregnant females collected at Båtfjorden in the Kattegat, and at Kvädöfjärden, Holmöarna and Soela in the Baltic Sea during November and December 1995.

Results and discussion

Hatching ring

In addition to the otolith structures identified by Kristoffersson and Oikari (1975), it was also possible to observe a thin hyaline ring structure around the core (Fig. 3). The mean diameter of this hyaline ring structure was 0.28 ± 0.06 mm (±SD) in fry (i.e., 0 + fish) from Ringhals ($n = 18$) and 0.21 ± 0.04 mm (±SD) from Eckerö ($n = 8$). Because this diameter is smaller than the total otolith diameter in unborn fry dissected from pregnant females in November and December (Table 1), it is reasonable to assume that it was formed close to hatching in September.

Birth ring

The otolith structure of the fry collected at Ringhals and at Eckerö on Åland was characterized by opaque growth from the core almost to the edge, interrupted by only a thin hyaline zone – the suggested hatching ring (Fig. 3). At the edge of the otolith, there was a hyaline zone. At Eckerö the mean diameter (the length of the axis between the rostrum and the posterior) was 0.58 ± 0.07 mm (±SD) ($n = 8$) and at Ringhals 0.74 ± 0.05 mm (±SD) ($n = 62$), which means they are somewhat

Fig. 3. The otolith of a viviparous blenny (*Zoarces viviparus*) fry (fish length = 55 mm), caught on 23 March 1995 at Ringhals. The otolith diameter = 0.82 mm from the rostrum to the posterior part. (Hatching ring is indicated by an arrow. 50 × magnification)

Table 1
The otolith size in unborn fry taken from females caught in November–December 1995. Otolith length (in mm) refers to the total length of the axis between the rostrum and the posterior, otolith breadth (in mm) refers to the largest breadth at right angles to the axis between the rostrum and the posterior

		Otolith length			Otolith breadth		
Area	Female number	Mean	S.D.	N	Mean	S.D.	N
Ringhals	1	0.60	0.01	5	0.45	0.01	5
	2	0.64	0.02	5	0.44	0.02	5
	3	0.65	0.01	5	0.44	0.01	5
	4	0.62	0.03	5	0.45	0.02	5
Kvädöfjärden	1	0.45	0.02	5	0.37	0.02	5
	2	0.49	0.02	5	0.35	0.01	5
	3	0.54	0.02	5	0.39	0.02	5
	4	0.53	0.01	5	0.40	0.01	5
Holmöarna	1	0.60	0.01	5	0.44	0.0	5
	2	0.59	0.02	5	0.42	0.01	5
	3	0.49	0.02	5	0.40	0.01	5
	4	0.55	0.06	5	0.43	0.03	5
Soela	1	0.54	0.01	5	0.41	0.01	5
	2	0.55	0.01	4	0.42	0.01	4
	3	0.53	0.02	5	0.40	0.01	5
	4	0.55	0.02	5	0.41	0.01	5

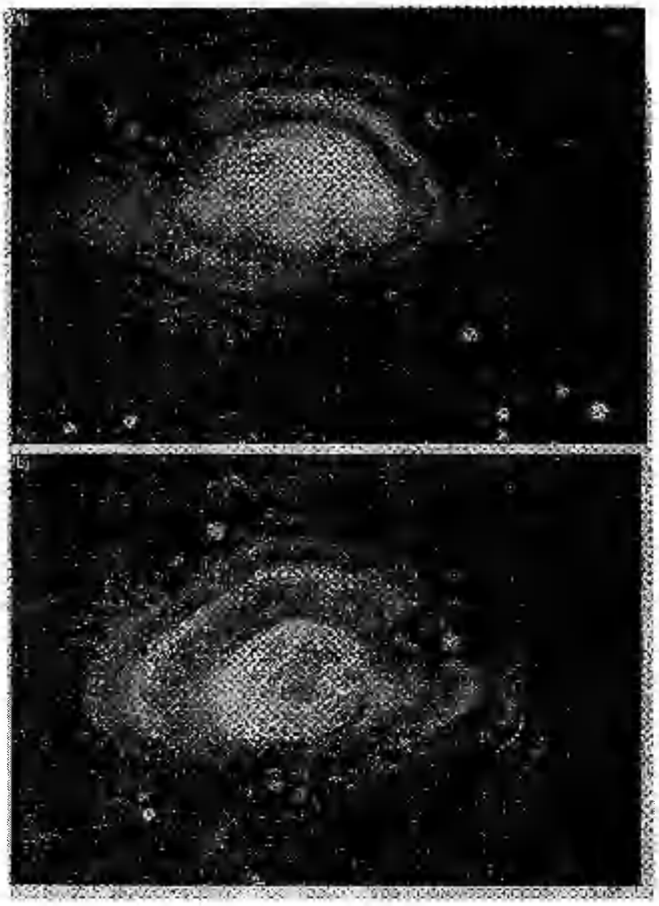

Fig. 4. The otoliths of 2-year-old viviparous blennies (*Zoarces viviparus*) caught in Båtfjorden from July 1994 to January 1995. (a) Female caught on 8 July 1994, fish length = 200 mm (b) Female caught on 23 November 1994, fish length = 262 mm (c) Female caught on 19 January 1995, fish length = 200 mm (d) Female caught on 5 April 1995, fish length = 248 mm (25 × magnification)

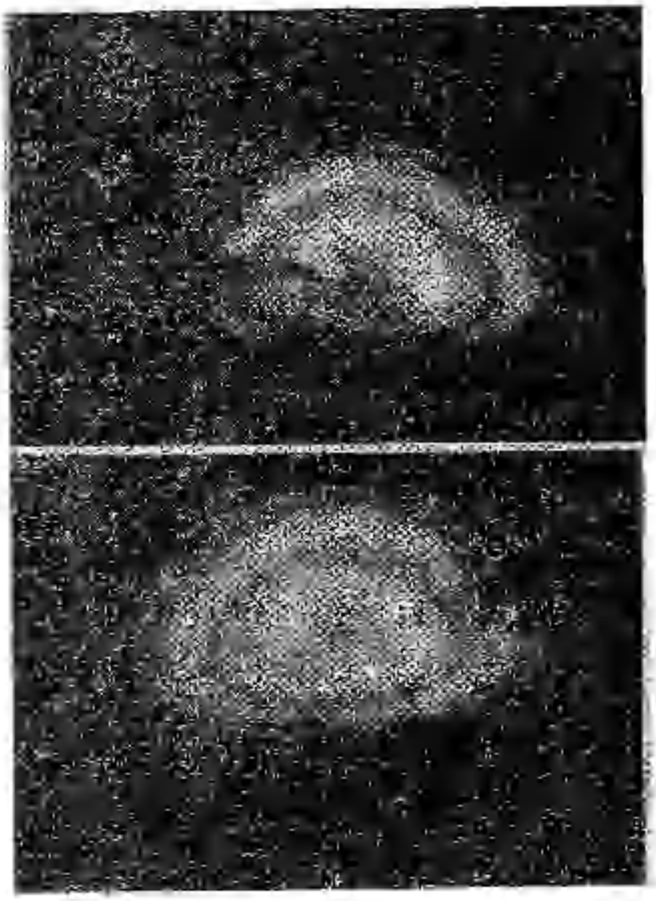

Fig. 4 (Continued)

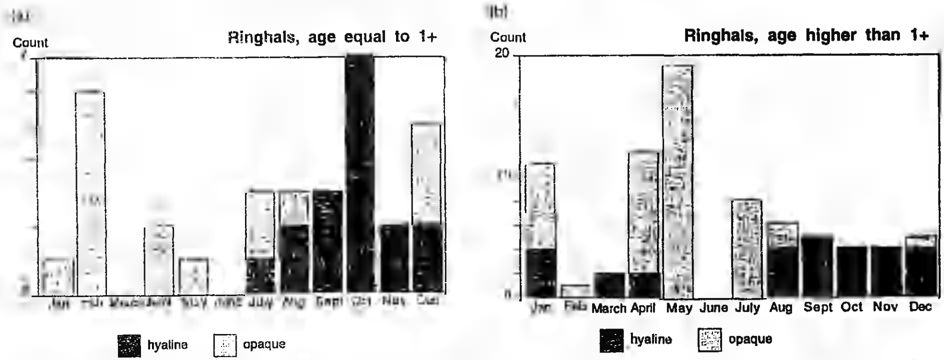

Fig. 5. The number of viviparous blennies (*Zoarces viviparus*) with opaque or hyaline structure at the edge of the otolith for various months at Båtfjorden from July 1994 to April 1995. (a) 1-year-old fish (1+) (b) Fish older than 1 year (≥2+)

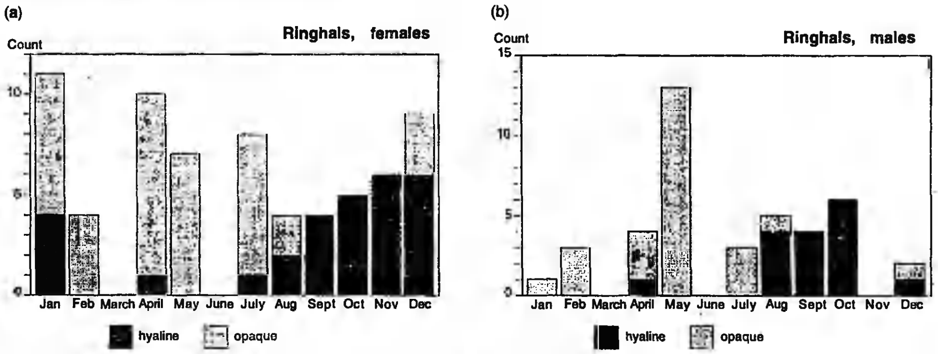

Fig. 6. The number of viviparous blennies (*Zoarces viviparus*) with opaque or hyaline structure at the edge of the otolith for various months at Båtfjorden from July 1994 to April 1995. (a) Females (b) males

larger than the otolith diameter in the unborn fry (Table 1). The only hyaline zone, apart from the thin hatching ring, was found at the edge, indicating that the formation of this zone probably coincides with birth in midwinter. These observations thus clearly show that one-summer-old fish do not have two hyaline and two opaque zones in their first spring/summer as suggested by Kristoffersson and Oikari (1975; Fig. 1).

It is worth noting that the size of the 'birth ring' can help in determining the age of viviparous blenny. By measuring the diameter of the first visible hyaline zone, it is possible to decide whether the structure probably belongs to a 'birth ring' or to an annulus, when the size range of the birth ring diameter is known.

Formation of hyaline and opaque zones after birth

The outermost zone of the otolith, the last zone deposited before capture, was studied in fish collected at monthly intervals at Ringhals. It was found that the deposition of opaque material occurred in spring and summer (Figs 4 and 5). In August, formation of a hyaline ring surrounding the opaque material was clearly visible. This hyaline ring continued to grow until December, when deposition of opaque material resumed in some specimens. The annual formation pattern was similar in both 1 + fish and older (Fig. 5), nor did it differ between sexes (Fig. 6). In the Baltic Sea areas, Kvädöfjärden and Gulf of Riga, the otolith formation pattern in adult fish was similar to that observed on the Swedish west coast (Figs 7 and 8). Thus, the viviparous blenny has an annulus formation pattern similar to most temperate fishes (Bagenal and Tesch 1978): hyaline (transparent) zones, 'winter-rings', are formed mainly during autumn and winter, with some starting already in summer. Opaque zones, also denoted as growth zones, are formed during early spring and summer; in the Kattegat the start is already in December–January.

The otolith structures in the Baltic fish were not as well demarcated as in the fish from the west coast. The opaque zones especially were less distinct, due to the presence of thin hyaline rings in the opaque material. These hyaline structures could often be characterised as irregularly occurring non-continuous formations, being comparatively less distinct than 'true' winter rings. This may reduce the reliability of age determinations, because such hyaline structures could sometimes be interpreted as winter zones.

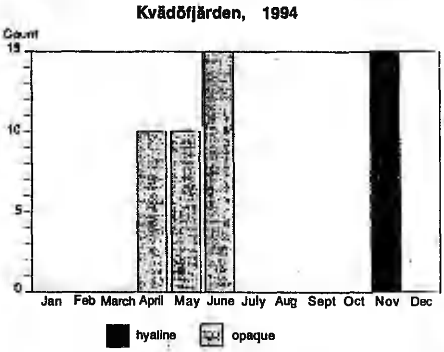

Fig. 7. The number of viviparous blennies (*Zoarces viviparus*) with opaque or hyaline structure at the edge of the otolith for various months at Kvädöfjärden in 1994

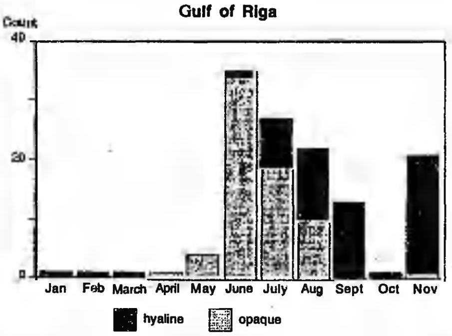

Fig. 8. The number of viviparous blennies (*Zoarces viviparus*) with opaque or hyaline structure at the edge of the otolith for various months in the Gulf of Riga in 1994–1995. The blennies were collected at various sites within the Gulf of Riga, from Irbe Sound to Pärnu Bay

Conclusions

Close to the core of the otolith, a thin hyaline ring with a diameter of about 0.2–0.3 mm can be identified. This ring formation is probably related to hatching within the ovary.

The first, and relatively broad, hyaline ring formation is deposited during the period after birth in midwinter. The ring diameter varies between 0.50 and 0.80 mm.

Opaque material is deposited in spring and summer. In July/August, the deposition of opaque material starts to be replaced by hyaline material. This hyaline zone continues to grow throughout the autumn at least until December. These results indicate that the annulus formation in the otoliths of viviparous blenny is not different from the common pattern in temperate fishes.

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Introductions and Transfers of Marine Organisms
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