Population structure of pelagic fishes in the Baltic

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An attempt is made to define principles of differentiation and to distinguish the main permanent groups of Baltic spring- and autumn-spawning herring and sprat that probably correspond by the level to populations. An important feature of the groups is that they belong to different ecological complexes. Five spring-spawning gulf herring, four spring-spawning sea herring, seven autumn herring and three sprat populations have been discerned. It is assumed that in differentiation of sprat groups the main role is played by bottom relief and circulation pattern in the Baltic Sea. At present, ICES assesses only four herring stock units by populations (the Western Baltic, Southern Baltic, Gulf of Riga, and Gulf of Finland populations), and all three sprat units.

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Introduction

The occurrence in commercial fishes of intraspecific groups differing by various features has long been known (Kessler, 1864). At present, in times of intense fishery, differentiation of these groups has become of great practical importance, because for rational exploitation of resources stocks considerably differing from others in abundance dynamics and other characteristics have to be managed separately.

Differentiation of Baltic herring and sprat groups, especially delimitation of their areas, has always been problematic. This has been caused by the gradualness of the change in features of the species from one sea area to another. It is connected with the hierarchic character of intraspecific groups, their mixing and adaptation to various environmental conditions. Even within the limits of a particular population the total reproductive mixing can occur irregularly and not necessarily in every reproduction season. Therefore, in various parts of the population area features of specimens can be somewhat different. Also, the relatively young age of the Baltic Sea (approximately 10 000 years) and substantial changes in environmental conditions during its existence have to be taken into consideration. On this account genetic differentiation of groups in the Baltic Sea fishes cannot be deep (cf. Aneer, 1985).

The principle of differentiation of herring and sprat populations

Attempts have been made to distinguish the main permanent Baltic spring and autumn herring and sprat groups that probably, by level, correspond to populations (i.e. between them a certain reproductive isolation occurs). In concrete groups, the mechanism of isolation is dependent on biological peculiarities of species as well as on biotic and abiotic environmental conditions in their area. Isolation of reproduction of groups of certain species in space and/or time reflects the fact that the groups belong to different ecological complexes. Therefore, in differentiation and delimitation of populations it is necessary to find their natural borders – the ecosystem gradients by which they are isolated.

Abiotic enviromental conditions and, depending on them, biota of the open part of the Baltic Sea differ from those of the Gulf of Riga, the Gulf of Finland, and the Gulf of Bothnia. The latter clearly falls into two basins – the Bothnian Sea and, north of the Quark, Bothnian Bay. In the open Baltic, on the basis of characteristic bottom relief (existence of a chain of deeps separated by thresholds) and the circulation system (induced by bottom relief and the multilayered water structure as well as the peculiar dynamics of water masses), areas permanently differing from one another have been established (Fig. 1). In abiotic environments, as well as in biota between the indicated areas, greater gradients occur. Since considerable gradients in oceanological conditions (salinity, temperature, oxygen content, currents, and so on), as well as the areas of low productivity of food organisms, represent obstacles for distribution in certain directions, they can turn out to be potential borders of population areas (Figs. 2, 3). In addition to the indirect influences described, the
circulation systems governing in certain regions can affect the fishes directly, causing passive migration of pelagic eggs, larvae, young fish, and adults, especially during the periods of their low activity in winter.

In the majority of populations (gulf herrings, coastal herring of the Southern Baltic, and sprat) a certain reproductive isolation is reinforced by location in the vicinity of spawning areas, rich feeding grounds, and wintering places. In other populations performing long migrations, the relative spawning isolation is based on relative constancy of alteration of climatic and environmental conditions governing migrations.

Obviously, some variability should be assumed in population areas. Variations in environment or in population abundance can cause the borders of the population areas to change.
Herring groups

The Baltic Sea is inhabited by spring-spawning and autumn-spawning herrings that have differentiated in the Atlantic Ocean long before the formation of the present Baltic Sea (Svärdson, 1961). They differ on the level of sibling species (Blaxter, 1958; Ojaveer, 1988). It can be estimated that the Baltic spring- and autumn-spawning herrings differ from corresponding sibling species in the Atlantic on the subspecies level. There are periodical fluctuations in relative abundance of Baltic spring and autumn herrings.

Between certain sea areas the features of Baltic spring herring differ considerably more than these of autumn herring.

Spring-spawning herrings

Populations of gulf and sea herrings should be distinguished. Compared to sea herrings, gulf herring populations: (1) are adapted to live in considerably more continental conditions; and (2) live their whole life at the salinities critical for biological processes (Khlebovich, 1974) or below, and generally do not undertake long migrations. Gulf herrings differ from sea herrings in morphological features, otolith types (Ojaveer et al., 1982), muscle esterases (Martinson et al., 1979), growth rate (Fig. 4), and other characteristics.

Gulf herrings of the Baltic Sea can be divided into five populations (Fig. 2) differing in abundance dynamics, morphological features and so on (Otterlind, 1962; Ojaveer et al., 1982; ICES, 1986). Their features are reminiscent of the White Sea herrings of Atlantic origin (the Dvina, Onega, and Ivanovsk populations) that show their likely common descent.

Despite the main reproduction periods of gulf and sea herrings being separated, in the contact zones between them intermediate groups have arisen. The most important of them populates the western part of the Gulf of Finland.

Living conditions of the sea herring during the ontogenesis and also those of its different populations vary considerably more than in the gulf herring. Sea herrings spawn in, and in their early stages inhabit, coastal areas of the Baltic Sea at relatively variable temperatures and salinities. The adults feed and winter at more constant temperatures and higher but more variable salinities (in the Baltic Sea from 7% to 16-20%, but the Rügen herring population up to the salinities in the Skagerrak) than gulf herring.

Sea herrings can be subdivided into the following populations (Fig. 2): (1) Swedish east coast herring; (2) herring of the eastern part of the Central and Northern Baltic; (3) coastal herring of the Southern Baltic; and (4) Western Baltic herring (mainly Rügen herring). They differ in abundance dynamics, growth rate, morphological and other features (Figs. 4, 5; Popiel, 1958; Otterlind, 1962; Biester, 1979; Ojaveer et al., 1982). As the transition area between the Swedish east coast herring population and the Eastern Central and Northern Baltic sea herring population, the zone running alongside the central part of the Gotland Deep (where herring commonly do not migrate to because of the unfavourable oxygen and temperature conditions and the scarcity of food) should be considered. The northern border of the Southern Baltic coastal herring is constituted by a zone poor in food, and where, in addition, considerable changes in the abiotic environmental conditions occur (Ojaveer and Kaleis, 1974; Järvekülg, 1979; Mälkki and Tamsalu, 1985). In the border area between the Southern Baltic and the Rügen herrings the gradient in abiotic and biotic environment is fairly substantial (Fig. 2; Kaleis, 1970; Biester, 1979; Mälkki and Tamsalu, 1985). Reproductive mixing between the populations is obviously limited (Popiel, 1958; Otterlind, 1962; Biester, 1979). Apparently all the populations include components that do not mix fully in every reproduction period.

**Figure 4.** Growth in weight of spring herrings in ICES Sd 22-24 = 1; Sd 25-27 (coastal) = 2; Sd 25-27 (sea) = 3; Sd 28-29S = 4; Sd 32W = 5; Sd 32E = 6; G. of Riga = 7; Sd 31E = 8; Sd 30E = 9; In parentheses Ws.

**Figure 5.** Dynamics of herring spawning stock biomass by assessment units of the ICES Working Group (ICES, 1987). Sd 22-24 + Sd IIIa = 1; Sd 25-27 (coastal) = 2; Sd 25-27 (sea) = 3; Sd 28-29S = 4; G. of Riga = 5; Sd 30E + 29NE = 6; Sd 31E = 7; Sd 32 = 8.
Hence at present throughout the Baltic Sea spring herring predominates herring stock; the herring stock assessment by the ICES Working Group on Pelagic Stock in the Baltic relates virtually completely to spring spawning stock (ICES, 1986). Comparing the Working Group assessment units scheme with that of the populations (Fig. 2) it becomes evident that at present the Working Group assesses the herring stocks of the Gulf of Riga, the Gulf of Finland, the Western Baltic, and the Southern Baltic by natural units only (in ICES Subdivisions 25–27 the coastal herring and the Swedish east coast herring are assessed separately).

Autumn-spawning herrings

On the basis of morphological features, growth pattern, abundance dynamics and other characters (Hessle, 1925; Ojaveer, 1988) in Baltic autumn herring, seven populations can be discerned - those of the Western Baltic, the Southern Baltic, the western part of the Central and Northern Baltic, the eastern part of the Central and Northern Baltic, the Gulf of Riga, the Gulf of Finland, and the Gulf of Bothnia.

Sprat groups

Sprat feeds and spawns chiefly in the areas of ridges and slopes of deeps and winters mainly in deep areas of the open Baltic and adjacent parts of gulfs. This is because of the biological peculiarities of sprat – it is generally sensitive to low temperatures in winter and has pelagic eggs that require a certain salinity for normal development. Sprat eggs have been found up to the Aland Sea. In the Gulf of Bothnia its eggs have been found, but no larvae (Hessle, 1927). Sprat reproduction decreases in the Gulf of Finland, especially in the eastern part. In the Gulf of Riga sprat is found principally in the western part.

Features of sprat of various regions of the Baltic Sea differ considerably less than those of herring (Hessle, 1927). However, growth zone dimensions in sprat otoliths (Aps and Ustinova, 1986), its morphological features (Veldre and Hell, 1961; Seletskaja, 1970), dynamics of stock size, growth and year-class abundance (Figs. 6, 7; Elwertowski, 1960; ICES, 1986) considerably differ by sea areas. These differences mean that the Baltic sprat stock cannot be considered as one unit. The low percentage of old sprat in the Western Baltic, compared with the Northern and Eastern Baltic, is probably due to the higher level of natural mortality in the western and southern parts of the sea caused by the higher abundance of cod.

Taking into consideration the attachment of sprat to deeps and its relatively limited tendency to actively migrate (Veldre and Hell, 1961; Aps and Ustinova, 1986), it can be assumed that in the differentiation of its groups, circulation pattern and bottom relief in the Baltic Sea have played the main roles (Fig. 1). On these grounds roughly three sprat groups can be distinguished.

1. The group inhabiting the area of the Gotland and Gdańsk Basins, with the characteristics of water masses and stratification typical of the Baltic Sea, can be regarded as the principal Baltic sprat population. It spawns from March–April to July (Elwertowski, 1960). At the beginning of the reproduction period spawning occurs in deep layers in the warm water of Kattegat origin. Later, spawning continues in the surface layers.

2. In the area of the Bornholm Basin and Western Baltic sprat, the characteristics of water masses are intermediate between the typical for the Baltic Sea and the Kattegat. At the beginning of the spawning season in February–March, the spawning zone is separated from that of the former population. Later, in pelagic layers the spawning areas of the populations associate (Grauman, 1983).

3. Sprat of the Northern Baltic lives in freshened surface water flowing out of the Gulfs of Finland and Bothnia, and in the gulfs mentioned. In its area, salinity is within the limits or below the critical values for biological processes (Khlebovich, 1974). It

![Figure 6. Growth in weight of sprat in ICES Subdivisions 22–25 = 1; Sd 26 + 28 = 2; Sd 27, 29–32 = 3. In parentheses W.](image)

![Figure 7. Dynamics of sprat spawning stock biomass by assessment units of the ICES Working Group (ICES, 1987). 1 = Sd 22–25; 2 = Sd 26 + 28; 3 = Sd 27, 29–32.](image)
spawns from June to August and only in the surface layers. It can be considered that one of the main factors responsible for the formation of the sprat population is the high abundance of its chief food organisms in the area of Gotska-Sanden–Saaremaa–Hiiumaa–south of the Gulf of Finland (Sergejev et al., 1970; Ojaveer and Kaleis, 1974). Temperature and salinity conditions in the areas of this population are more complicated, the vegetation season is shorter, and fluctuations in feeding conditions are sharper than in the areas of the other populations. However, in periods of favourable abiotic conditions for sprat and low abundance of cod in the Northern Baltic, the abundance of this population can be high and more stable than in other populations on account of lower natural mortality.

It can be concluded that the number of sprat assessment units of the ICES Working Group on Pelagic Stock in the Baltic corresponds to the situation in nature. Yet it seems that the transition area between the central and northern sprat populations is located somewhat south of the borderline between the ICES Subdivisions 28 and 29 (58°30'N) used at present as the formal border of the stocks.

References