The distribution of Baltic Sea fish species throughout their life history may be random or patterned, and these changes have been estimated by tagging programmes since the early years of ICES. The adaptive value of fish migration is strongly coupled with the optimization of the surrounding environment. The hydrographic conditions in the Baltic form an uneven continuity from southwest to northeast, and the physiological selection of fish species, their distribution, and their capability to migrate has taken place in varying environmental temperatures and salinities. In the life history of fish species in the Baltic Sea, the eurythermic and euryhaline species have had more adaptive value than those species which prefer constant salinities and temperatures. The euryhaline and eurythermic species are usually able to migrate more intensively than stenothermic and stenohaline species. Marine species have both rather local and more migratory stocks. Freshwater species are, in general, more stationary than marine species. The advantage of migrations in a patchy environment is that the impact of environmental variability on reproduction, survival, foraging, and growth decreases. ICES, as a coordinating organization, has played an important role in migration studies during the last 100 years and has been significant as a forum for developing new ideas and hypotheses on fish migration in the Baltic Sea.

Keywords: Baltic herring, Baltic salmon, cod, flounder, freshwater species, ICES, migration, plaice, sea trout, tagging.
The special report by Trybom (1907b) gave detailed results of Baltic salmon and sea trout tagging and migration studies conducted by various Member Countries in the Baltic area during 1902–1906. Among the recaptures was one salmon originally tagged off Bornholm in April 1906 and recaptured four months later in Bothnian Bay. This is believed to be the first documented Baltic salmon homing record in the scientific literature. Another salmon tagged in September 1905 in the eastern part of the Gulf of Finland outside the mouth of the Kymijoki River was recaptured in May 1907 in the neighbourhood of Memel (Klaipėda) showing, as a first record, the possible extent of the feeding migration of Baltic salmon (Figure 1). These early taggings of Baltic
salmon and sea trout were aimed mainly at estimating the distribution area and proportion removed by open-sea fisheries and coastal fisheries (Trybom, 1907b), and although the number of tagged fish each year was rather low, tagging provided new information on migration patterns of Baltic salmon and sea trout.

The state of the eel stock in the Baltic also received attention (Trybom and Schneider, 1907) in Committee C at the beginning of 1900. O. Nordqvist and J. A. Palmén started tagging eels in 1903 at the Tvärminne Zoological Station founded by Palmén in 1902 on Hanko Peninsula, Finland, the westernmost part of the Gulf of Finland (Nordqvist, 1903). Eel taggings were expanded further in 1904–1907. These first silver eel taggings and the subsequent recaptures in the Atlantic Ocean (Figure 1) contributed to the development of Johannes Schmidt’s famous hypothesis on eel life history (Schmidt, 1906).

Priorities during the 1920s–1940s

Fish migration studies in the Baltic in the 1920s–1940s concentrated mainly on commercially important marine, anadromous, and catadromous species such as Baltic herring, sprat, cod, plaice, flounder, eel, and salmon. The freshwater species in the Baltic did not receive any special attention from ICES, although many laboratories tagged freshwater fish in coastal areas (Ekman, 1916; Henking, 1923).

The main aims of all tagging studies during this period were to estimate the spatial and temporal distribution patterns and their annual changes. In the 1920s and 1930s, scientists began the practice of categorizing the recapture information according to distance travelled and to the typical fishing grounds in the Baltic Sea (Figure 2).

In the 1920s, special attention was paid to the most abundant species in the pelagic system, Baltic herring and sprat, and to their predator, Baltic cod (Heidrich, 1925; Hessle, 1923, 1925, 1927). Hessle (1925) showed that the slow-growing, long-lived, open-sea herring spawn mainly along the Swedish east coast from Hanö Bay to the Åland Sea in deeper water than the coastal spring-spawning herring in other locations. Hessle (1925) also showed that Baltic herring along the Swedish coast undertook long migrations extending from the Åland Sea to the southern part of the Baltic.

In the 1920s, sprat were shown to inhabit the Baltic from the Belt Seas and Western Baltic (ICES Subdivisions 22 and 24), to the Quark area in the north (Subdivision 30), and to the northeastern part of the Gulf of Finland (Subdivision 32) (Hessle, 1927). Three different sprat stock components were considered at that...
time, with a low rate of mixing with the Kattegat and Skagerrak stocks due to the salinity gradient and differences in many abiotic factors between the Western Baltic and the Kattegat (Hessle, 1927).

Hessle (1923) and his colleagues reported on the distribution, spawning, growth, and periodicity of Baltic cod year classes along the Swedish coast. Although these studies included only areas in the vicinity of the Swedish coast, they indicated great fluctuation caused by changes in the distribution patterns of cod year classes. Kändler (1944), in his classical work in which small numbers of cod were tagged, showed differences between cod stocks in the Baltic in the Transition Area around Bornholm (14°E).

In the case of Baltic salmon, Järvi (1938) reported that they nearly all fed in the Baltic Main Basin (Subdivisions 24–29) and that the most important feeding grounds were the Gotland Deep, the waters around Bornholm, and the Gdansk Basin. This important work summarized 15 years of information (1921–1935) on the basic biology, the fisheries, and obvious reasons for fluctuations in the Baltic salmon.

Decades of tagging and migration studies during 1950–1980

Fish migration studies using tagging were intensified considerably in ICES circles in the 1950s. An initial stimulus came when a Danish cutter accidentally discovered dense concentrations of young herring on the Bløden Grounds in July 1950 about 60–100 miles west of Esbjerg, Denmark, in the North Sea. This discovery and the fishery which subsequently developed stimulated discussion about the role and effect of the Bløden fishery on the North Sea herring fishery and led to an extensive tagging programme for herring in the North Sea and the Baltic Sea. The establishment of the International Baltic Sea Fishery Commission (IBSFC), and two ICES stock assessment working groups necessary for IBSFC activities served to elevate the need for tagging studies in the early 1970s.

Thus, the present knowledge of fish migration in the Baltic is based mainly on taggings made from the early 1950s to the 1980s, except in the case of Baltic salmon and sea trout, large numbers of which have been tagged each year up to the present. Between 1950 and 1980, several hundred thousand fish were tagged throughout the entire Baltic area (Aro, 1989) including Baltic herring, sprat, cod, plaice, flounder, Baltic salmon, sea trout, and freshwater species such as whitefish, pike, pikeperch, perch, bream, and burbot.

A common feature of all the tagging work has been to estimate annual migration patterns and their changes, the home range of various species, site fidelity for spawning, distribution of stock components and their mixing, and the effects of fishing at stock level, and also to evaluate the timing of annual migration patterns.

Main results from tagging and migration studies during 1950–1980

Herring

Tagging and migration studies have shown that in some areas Baltic herring can be divided into two or three components by their different migration patterns, such as spring-spawning coastal herring, spring-spawning open-sea herring, and autumn-spawning herring. Baltic herring in the southwestern Baltic, Kattegat, and Skagerrak have both spring-spawning and autumn-spawning components (Anwand, 1963a, 1963b), with spring-spawning stocks having a very clear migration pattern. The majority of the fish migrate from the feeding and wintering areas in the Skagerrak and Kattegat through the Öresund and the Belts into the Baltic in autumn and early winter, with a minority coming from other feeding areas around Bornholm, off the Polish coast, and Hanö Bay to the spawning grounds (Biester, 1979; Otterlind, 1985). The migration pattern of adult herring from the Baltic to the Kattegat and Skagerrak has also been confirmed by the occurrence of Anisakis nematode larvae in the adult herring from the Southwestern Baltic (Strzyzewskia and Popiel, 1974; Friess, 1977; Kühlmorgen-Hille, 1983). Herring in the Southwestern Baltic seem to have a clear homing ability (Jönsson and Biester, 1979) despite some controversy. In the Central Baltic, there are assumed to be three different stocks: spring-spawning coastal herring, spring-spawning open-sea herring, and autumn-spawning herring (Pepiel, 1984). These stock components have different migration patterns in the Southeastern and Central Baltic. In the Bothnian Sea, there are two spring-spawning coastal herring components (Hannerz, 1955, 1956; Otterlind, 1957; Parmannen and Sjöblom, 1982, 1986), one along the west coast and one on the east coast, both of which show high spawning-site fidelity.

Sprat

Sprat inhabit the Baltic Sea from the Belt Seas and western Baltic (Subdivisions 22 and 24), to the Quark area in the north (Subdivision 30), and to the northeastern part of the Gulf of Finland (Subdivision 32) (Hessle, 1927; Veldre, 1986; Recchlin, 1986). There are three different sprat stocks in the Baltic, and mixing with the Kattegat and Skagerrak stocks is considered to be very low, although there is no significant difference in morphometric characters and vertebrae counts (Lindquist, 1968). Mixing is probably prevented by the salinity gradient and differences in many abiotic factors between the Western Baltic and the Kattegat (Hessle, 1927; Aps et al., 1987). Boundaries between neighbouring stocks are unclear, and stock mixing during feeding and wintering is apparent (Recchlin, 1986). During the feeding period in July–November in the south and central parts
Salmon

Salmon in the Baltic are distributed from the Belt Seas and Western Baltic to the northern parts of the Gulf of Bothnia and the Gulf of Finland and very seldom migrate outside the Baltic (ICES, 1980; Lindroth et al., 1982). There are naturally spawning stocks and artificially reared stocks of various origin. During the marine phase, the Baltic salmon have very clear migration patterns in the coastal and pelagic area. In general, both the wild and hatchery-reared stocks have the same migration patterns, with some exceptions. The migrations are divided into post-smolt, feeding, and spawning phases.

Salmon smolts enter the Baltic usually in April–June, with those from the southern Baltic running a few weeks earlier than those from the north. The wild and hatchery-reared smolts start their post-smolt migration at about the same time. During the first few weeks, post-smolts are relatively stationary, adapting to the new environment, and they remain close to the river mouth or releasing place (Bartel, 1976; Ikonen and Auvinen, 1985). From releases on the Finnish side of Bothnian Bay (Subdivision 31), post-smolts migrate southwards along the Finnish coast to the Quark area where they shift to the Swedish coast. From the Swedish releases, the post-smolts migrate south along the Swedish coast of Bothnian Bay to the Quark where some shift to the Finnish side following the main current northwards along the Finnish coast, and do not leave Bothnian Bay (Larsson and Atheskar, 1979). In the Bothnian Sea (Subdivision 30) stock, the post-smolts behave like the northern stocks, except for the River Neva stock (from Russian origin in the eastern Gulf of Finland, Subdivision 32) releases in the Bothnian Sea (Ikonen and Auvinen, 1982), which seem to have more localized tendencies.

Nearly all Baltic salmon stocks feed in the Baltic Main Basin (Subdivisions 24–29), except those of River Neva origin. From the releases in the Gulf of Finland, about 31% of the Neva-origin fish feed in the Main Basin, while the percentage from the Bothnian Sea releases is less. The most important feeding grounds are the Gotland Deep, the waters around Bornholm, and the Gdansk Basin (Järvi, 1938; Halme, 1964; Carlin, 1959; Thurow, 1973; Christensen and Larsson, 1979; Ikonen and Auvinen, 1984a, 1985). On these feeding grounds, the stocks mix thoroughly, and there is no clear evidence on the preferred feeding areas of individual stocks, although there are some aggregations on the main fishing grounds (Carlin, 1959; Halme, 1964). Feeding salmon are more or less clustered, and changes in density on the feeding grounds reflect their active movement in search of food (Thurow, 1973).

All Baltic salmon stocks exhibit homing behaviour, but in some releases, homing has not developed because of environmental factors (Christensen, 1982).

Sea trout

Sea trout in the Baltic are distributed from the southwestern part to the northern parts of the Gulf of Bothnia and eastern parts of the Gulf of Finland. Their migration may be divided into two patterns: the long-distance migrating stocks and the more stationary stocks (Zannecki and Duszynski, 1961; Ikonen and Auvinen, 1984b). In the Baltic, sea trout occupy an intermediate position between the pelagic and coastal fish communities, and their migration pattern is dependent on stock origin and the dimensions of the archipelago.

During their feeding migration, the stocks in the Bothnian Sea and Bothnian Bay intermix when migrating from the east coast to the west coast and vice versa. The migration southwards from Bothnian Bay to the Bothnian Sea and to the Main Basin has also been observed even if the northern stocks are considered to be more local and less migratory in nature (Carlin, 1965; Ikonen and Auvinen, 1984b). In the Gulf of Finland, the feeding migration encompasses the whole area from west to east, and there appears to be some migration to the Archipelago Sea, the Bothnian Sea, and the Main Basin (Ikonen and Auvinen, 1984b). In the northeastern Baltic near the island of Saaremaa, the stock seems to be quite local, but in some cases it extends into the Bothnian Sea, the Åland Sea, near Gotland Island, and southwards to the Bornholm region (Rannak et al., 1983). In the Southern Baltic, the feeding migrations are more intensive and extend to quite large areas. From the Pomeranian coast and the Vistula region, sea trout migrate mainly eastwards, but parts of the stock also move westward along the Polish coast. The feeding migration of these stocks may reach the Gulf of Riga, the Gulf of Finland, and the Bothnian Sea (Backiel and Bartel, 1963; Chrzan, 1963). The stocks along the Swedish south and east coasts migrate northwards and to the Bothnian Sea, and the Gulf of Finland, the Gulf of Riga, as well as southeasterly to the Gulf of Gdansk (Svärdson and Fagerström, 1982).
Cod

There are two cod stocks in the Baltic which have been shown to differ in many ways. The Western Baltic stock (Gadus morhua morhua L.; the Atlantic cod or Transition Area cod) is distributed west of Bornholm, in the Western Baltic, the Belt Seas, and the Sound (Subdivisions 22–24) and has regular connections to the Kattegat (Division IIIa) and to the southeastern Baltic (Bagge et al., 1994). The Eastern Baltic stock (Gadus morhua callarias L.; the Baltic Sea cod) is distributed east of Bornholm to the northern parts of the Bothnian Sea and to the eastern parts of the Gulf of Finland (Bagge et al., 1994). The border between these two stocks is diffuse, and mixing is evident in the Arkona and Bornholm Basins.

Western Baltic cod migrate in all directions after spawning (Berner, 1981) from the deep waters to more shallow coastal areas to feed. The young, immature age groups usually remain in the coastal areas before joining the mature stock. From the Arkona region, feeding migrations of adults may reach the Belt Seas in the west and extend eastwards to the Slupsk Furrow, the Bornholm region, the Gdansk Deep, and even to the southern Gotland Deep (Lamp and Tiews, 1974; Berner, 1981). Cod in the Arkona Basin are always a mixture of the two main stocks, and the spawning migration occurs in two directions. According to transplantation experiments, the homing of cod is not well developed (Bagge, 1983).

Eastern cod migrate to the Bornholm Basin spawning grounds in December–February from the feeding grounds in Slupsk Furrow, Gdansk Bay, Hanö Bay, and the Gotland Deep (Netzel, 1968, 1974). The spawners in the Gdansk Deep originate from areas south of the Bornholm Basin and from southern parts of the Gotland Deep (Netzel, 1974; Otterlind, 1976). There is also a spawning migration from the Swedish east coast, the Åland Sea, the southern Bothnian Sea, and the Gulf of Finland to the Bornholm Basin, the Gdansk Basin, and the southern parts of the Gotland Basin in December–March (Otterlind, 1976; Sjöblom et al., 1980; Aro and Sjöblom, 1983a). The homing behaviour of cod in the Southeastern and Northern Baltic is also unclear, and cod may use different spawning grounds in successive years (Bagge, 1983; Otterlind, 1984, 1985). During the feeding period, cod are distributed over large areas and may undertake extensive migrations (Otterlind, 1985; Aro 1989) that exhibit no pattern.

Flounder

There are several rather distinct flounder stocks or populations in the Baltic (ICES, 1978). Flounder are regularly distributed in all parts of the Baltic, except Bothnian Bay, the easternmost part of the Gulf of Finland, and the deepest areas of the Gotland Deep (Anon., 1978). There are at least three stocks in the Southwestern and Southeastern Baltic (Subdivisions 22–26), three in the Central and Northeastern Baltic (Subdivisions 27–28), one each in the Åland Sea, Archipelago Sea, and southern Bothnian Sea, and two in the Gulf of Finland (Anon., 1978). Migrations between the mature flounder stocks in the southern and central Baltic are quite rare, extending from the southern part of Öland Island to the Rosewie on the Polish coast (Otterlind, 1965, 1967; Vitinsh, 1976, 1977). Migrations are effectively blocked in the Southeastern and Central Baltic by the Gdansk and Gotland Deep and in the Northern Baltic by the Gotland Deep and the deep southwest of the Åland Islands (Otterlind, 1965; Vitinsh 1972, 1976, 1977; Aro and Sjöblom, 1983b). The annual migration patterns of flounder stocks are quite well known and, because of their general locality, the homing behaviour of flounder is obvious.

Plaice

Plaice are distributed in the Baltic Sea from the Belt eastwards to the Gdansk Bay area and northwards to the southern Gotland Deep (Bagge, 1981). Plaice are very rare in the Northern Baltic. Feeding migrations from the deeper spawning grounds to shallower waters are primarily west and to a lesser extent east from the Arkona Basin. The westward feeding migration may reach the Belt Sea, the Sound, the southern Kattegat, and even the Skagerrak (Otterlind, 1967). Those emigrating out of the Baltic Sea are assumed not to return (Otterlind, 1967). The eastward migration is most intensive from the Arkona Region to the east and southeast of Bornholm during November–February. Plaice feeding in the Gdansk Deep have been shown to migrate to the Bornholm Basin to spawn (Cieglewicz, 1961).

Freshwater species

In the Southern Baltic where the freshwater species are almost totally absent, shallow coastal bottoms and pelagic areas serve as habitat for the young stages of several marine pelagic and demersal species of economic importance. These areas also serve as habitat for a number of other littoral and coastal species of substantial ecological but minimal economic importance. In the Central and Northern Baltic Sea, there is a clear dominance of freshwater species in the littoral and coastal areas (Neuman, 1982), but their abundance decreases towards the seaward limit of their distribution (Lehtonen and Toivonen, 1981). The number of freshwater species is greatest in the archipelagoes, bays, inlets, and river mouths. The migrations of freshwater species are generally local, although some species long distances. Some of the freshwater species lack a migration pattern or their migrations are too short to identify. Two whitefish
Conclusions

The fish fauna in the Baltic Sea may be classified into three different and intermediate communities: a pelagic community, a benthic community, and a littoral and coastal community. The borders between them are not sharp, and individuals from neighbouring communities cross them frequently, particularly the littoral and coastal regions which serve the pelagic community as spawning and nursery areas. In the Gulf of Bothnia, the littoral and coastal community is dominated by freshwater species, which very seldom migrate outside this environment, and the Baltic herring is actually the only native pelagic species using that environment as a spawning and nursery area (Andreason and Petersson, 1982). The migration and movements of the Baltic fish species occur at micro- and macroscales inside and between these communities in annual, diurnal, horizontal, and vertical patterns.

The migration, spatial, and temporal distribution pattern of Baltic fish exhibits an annual cycle between spawning, feeding, and nursery habitats. Homing in spawning migrations and site fidelity has been observed, but results suggest that this link is weak in the case of cod, and the ratio of emigration to other spawning grounds seems to be dependent on the conditions of the spawning grounds. This also applies to spring-spawning Baltic herring and freshwater species. Baltic fish may use different spawning grounds in successive years, and evidence indicates that spawning migrations are more strongly linked to prevailing hydrographical conditions than to homing.

The feeding migration of Baltic fish seems to have different patterns for Baltic herring, sprat, salmon, and sea trout, but not in the case of cod. The movements of Baltic fish from one place to another during the feeding period seem to be once-a-year events. However, they may be just local seasonal movements, dispersals, or "true" migrations. The advantage of movements and migration in a patchy environment is, in general, that the impact of environmental variability on reproduction, survival, foraging, and growth decreases. The migratory behaviour promotes more flexibility in the face of uncertainty. With migration, the risk from predation and cannibalism is balanced against the advantage of remaining in one place to exploit resources.

The freshwater species in the Baltic have unfortunately been more or less neglected in ICES activities even though they are an important component of the ecosystem. The number of original freshwater species in the Baltic is 23 (Lehtonen and Toivonen, 1981). The freshwater species are practically absent in the southwestern part of the Baltic except in some estuaries, fjords, and bays (Henking, 1923; Hempel and Nellen, 1974). There are 18 species in the Central Baltic, and freshwater species dominate in the north and northeastern parts of the Baltic (Lehtonen and Toivonen, 1981).

The general problem in quantifying movements and migrations (feeding or spawning) on a robust and usable spatial and temporal scale is that the tagging data rely totally on commercial fishermen's catch and effort and their willingness to return tags. Tagging of Baltic fish...
was very popular from the 1950s to the early 1980s. Most of these tagging studies and experiments were planned to estimate movements and fishing mortality. The results of these studies have only been partly published in the scientific literature.

The analytical tools for mark-release experiments were developed decades ago and are well described (Seber, 1973; Burnham et al., 1987). However, data analysis is hampered by a lack of essential information on fishing effort, spatial and temporal distribution of fishing activities, systematic determination of tag return rates from the commercial fishery, and so on. Many tagging experiments have neglected these issues by allocating resources mainly to catching and tagging of fish instead of to the recovery and reporting rates of tags.

Before the establishment of the IBSFC in the early 1970s, there were national fishing zones and a huge international fishing zone in the Baltic Sea where fishing activities were largely unregulated. Consequently, detailed information on fishing and fisheries was very scarce, and the systematic collection of fisheries data did not exist on a large scale. The situation has changed considerably since the beginning of the 1970s, and the parameters necessary for the design and analysis of tagging experiments are now accessible. However, Baltic fish tagging experiments are not very appealing because conducting an experiment takes at least 6–8 years before final results are available. Despite these shortcomings, new tagging experiments on Baltic cod and herring should be encouraged.

References


