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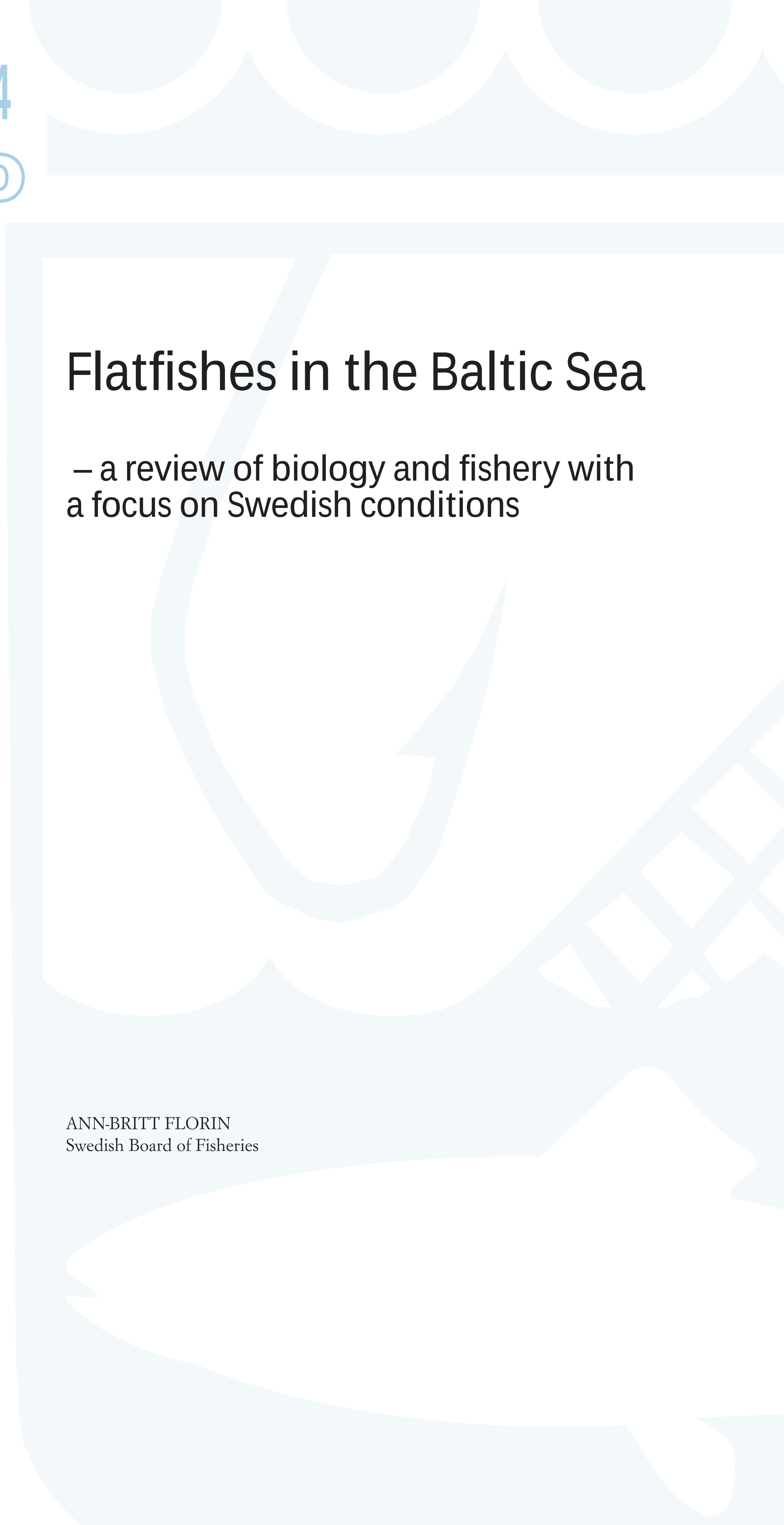

Flatfishes in the Baltic Sea

– a review of biology and fishery with a focus on Swedish conditions

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ISSN 1404-8590

Finfo 2005:14

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Flatfishes in the Baltic Sea

– a review of biology and fishery with a focus on Swedish conditions

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Abstract

The flatfishes in the Baltic Sea are important for both economic and ecological reasons. By taking advantage of the biological knowledge that exists, the development and realization of management plans for flatfish fishery could be improved. This paper is the first comprehensive compilation of knowledge of the flatfishes in the Baltic Sea; turbot (*Psetta maxima*), brill (*Scopthalmus rhombus*), European flounder (*Platichthys flesus*), plaice (*Pleuronectes platessa*), sole (*Solea solea*) and dab (*Pleuronectes limanda*). Subjects addressed are reproduction, recruitment, feeding, growth, population structure, fishery and abundance. During the 20th century, abundance has fluctuated markedly, and also size and age structure has shifted, either as a consequence of intensive fishing or due to environmental changes. Eutrophication can have severe impact on flatfish through oxygen deficiency in deeper areas and an increased occurrence of filamentous algae in nursery areas. However, the increased primary production may also be favourable if it results in increased food availability. A common pattern during the last century is the increased growth, probably due to better food availability, and/or an effect of decreased competition at lower densities. Intensive fishery has also induced evolutionary changes in important life history characteristics, suggesting that the evolutionary consequences need to be considered in future management decisions. Tagging and genetic analyses have revealed that several flatfish species are structured into several distinct spawning and feeding populations. Furthermore, it is evident that some flatfish species have adapted to the special conditions of low salinity in the Baltic. This knowledge will provide information at which geographic scale management is best performed and also how to avoid loss of local adaptations. Another example of biological knowledge relevant to management is the considerable difference in size between sexes that is common among flatfishes. This size difference has consequences for the effect of fishing on a stock and the effect of management decisions.

Svensk sammanfattning

Plattfiskar i Östersjön är viktiga av både ekonomiska och ekologiska skäl. Genom att ta till vara den biologiska kunskap som finns skulle utvecklingen och genomförandet av förvaltningsplaner kunna förbättras. Den här rapporten är den första grundliga sammanställningen av kunskap om plattfiskarna i Östersjön, d v s piggvar (*Psetta maxima*), slätvar (*Scopthalmus rhombus*), skrubbskädda/flundra (*Platichthys flesus*), rödspätta (*Pleuronectes platessa*), tunga (*Solea solea*) och sandskädda (*Pleuronectes limanda*). Ämnen som behandlas är fortplantning, rekrytering, födoval, tillväxt, beståndsstruktur, fiske och beståndsutveckling. Under 1900-talet har plattfiskbestånden fluktuerat påtagligt och även storleks och åldersstruktur har förändrats, antingen som en direkt följd av hårt fiske eller genom miljöförändringar. Övergödningen kan ha stor negativ inverkan på plattfiskar, dels genom den förorsakade syrebristen på djupa bottnar, dels den ökande mängden fintrådiga alger i uppväxtområden. Den ökade primärproduktion kan dock vara gynnsam om den resulterar i ökad födotillgång. Ett vanligt mönster under det senaste århundradet är en ökad tillväxt, troligtvis p g a bättre födotillgång men det kan också vara en effekt av minskad konkurrens vid lägre fisktätheter. Fiske har även visats ge upphov till evolutionära förändringar i viktiga livshistoriekaraktärer, vilket betyder att evolutionära effekter bör tas med i beräkningen i framtida förvaltningsplaner. Märkningar och genetiska analyser har avslöjat att flera plattfiskarter är indelade i distinkta bestånd. Vidare har det upptäckts att några plattfiskarter har anpassat sig till de särskilda förhållanden med låg salthalt som råder i Östersjön. Denna kunskap ger anvisning om på vilken geografisk skala förvaltning bör utföras och också hur en förlust av unika anpassningar kan undvikas. Ett annat exempel på biologisk kunskap som är relevant i förvaltningsarbete är den markanta storleksskillnaden mellan könen som de flesta plattfiskar uppvisar. Den här storleksskillnaden har konsekvenser för hur fisket påverkar ett bestånd och vilken effekt olika förvaltningsbeslut får.

1. Introduction

Flatfishes are among the most important marine fish resources in the North Temperate Zone. Some species, like halibut and turbot, are successfully reared in commercial aquaculture (e.g., Brown 2002) but the main economic value is in fishery. In the Baltic Sea, total international annual commercial landings varied between 12 000 and 24 000 tonnes during the last two decades (Ojaveer and Lehtonen 2001; ICES 2005a). In 2004, the 1 000 tonnes landed by the Swedish fishery corresponded to a value of almost three million Euros (30 million Swedish crowns). Furthermore, the recreational landings of flatfishes might be substantial, and even exceed the commercial fishery in some areas (Svedäng *et al.* 1998; Fiskeriverket 2000; Fiskeriverket and SCB 2005). Despite their great economic value and the effort put into management, sustainable fishing seems hard to achieve. According to an investigation of historical trends in biomass and catch data of flatfish stocks in the Northern Temperate Zone, more than half of the stocks have been overexploited at least during some period (Rice and Cooper 2003). Apparently, the way flatfish resources is managed today is not satisfactory. Several biological parameters like life-history characteristics (size and age at maturity, fecundity etc), species ecology (feeding and breeding habits, predators etc.) and stock structure (extent of migration, existence of local adaptations etc.), will affect how the stock respond to exploitation (e.g., Jennings *et al.* 2001). One way to improve management would be to use the biological knowledge already existing in the scientific community. Recently, after the completion of this review, a book on biology and exploitation of flatfishes was published (Gibson 2005). The excellent work by Gibson and co-workers gives a nice overview of flatfishes in the world, however data from the Baltic Sea are almost completely missing. Hence, this paper is the first thorough compilation of knowledge of flatfishes in the Baltic Sea. Hopefully, this unique collection of data will give a solid ground for development and realization of management plans for flatfish fishery.

This review focuses on flatfishes that are of economic importance in the Baltic Sea and to provide a more complete picture data from Skagerrak and Kattegat are included. The knowledge of biology, ecology and exploitation of these species are retrieved from the literature and the databases at the Swedish Board of Fisheries (SBF, Fiskeriverket). Efforts are also made to include results from the “grey literature” that otherwise is lost to the scientific community. The most thoroughly investigated flatfish species in Sweden is plaice (*Pleuronectes platessa*), which is reflected in this review. Efforts are, however, made to focus on turbot (*Psetta maxima*) and European flounder (*Platichthys flesus*), two important species for coastal fishery. The other flatfish species that occurs regularly in the Baltic Sea: brill (*Scopthalmus rhombus*), sole (*Solea solea*) and dab (*Pleuronectes limanda*), are also investigated.

2. General characteristics of flatfishes

2.1 Morphology

The flatfishes are adapted to a demersal lifestyle. Adults are asymmetrical with a flattened, almost two-dimensional body shape with an upper (dorsal), pigmented eye side and a blind, unpigmented bottom (ventral) side (Molander 1964; Curry-Lindahl 1985) (Figure 1). All flatfishes have the following characters in common: 1) Ontogenetic migration of the eyes, 2) Dorsal fin overlaps cranium 3) An invagination of the wall of the orbit that can be filled with fluid to make the eyes protrude (*Recessus orbitalis*) (Curry-Lindahl 1985; Hensley 1997).

Flatfish begin life as symmetric fish larvae with eyes placed in normal positions and an upright swimming mode. A substantial alteration in morphology, physiology and ecology occur when the juvenile switches from a pelagic, plankton feeding state to a benthic, benthos feeding lifestyle (Molander 1964; Curry-Lindahl 1985; Yamashita *et al.* 2001). The start and end of the eye migration, placing both eyes on the same side of the fish, mark the duration of metamorphosis. At the climax of the metamorphosis the larvae settles at the bottom and ceases to feed for a while. The metamorphosis also involves changes in position of pectoral fins and internal changes such as cranial twist and alterations in digestive system, muscle structure and red blood cell types as well as development of rod cells in the retina of the eye that increase the photosensitivity (Yamashita *et al.* 2001). The size at metamorphosis differs between five and 140 mm depending on species (Yamashita *et al.* 2001).

2.1.1 Sidedness

In some species almost all individuals have their eyes on the left side of the body, they are said to be left-sided or sinistral, while in other species adults have the opposite, right-sided or dextral, asymmetry (Parker 1903). In some species both morphs are common. Parker (1903) suggested that sidedness was under natural selection due to the type of optic chiasmata (the crossing of the sight nerves), assuming that fishes with the migrating eye connected to a dorsal nerve had a higher survival than the opposite arrangement. In symmetric teleosts, and in the sole family (*Soleidae*), Parker found an equal frequency of individuals with their left or right sight nerves dorsal. This is thought to reflect a more primitive state. In contrast, among the 16 investigated species in the flounder family (*Pleuronectidae*), species with only one type of sidedness always had their dorsal nerves connected to the migrating eyes. In species with both dextral and sinistral individuals, the dorsal nerve was connected to the eye that either is the most frequently migrating within the species or the eye that migrates in the closest relative species with a fixed sidedness. The observed higher mortality in reversed individuals of *P. flesus* supports the role of natural selection of sidedness (Parker 1903; Fornbacke *et al.* 2002).

In *P. flesus*, there is a cline in sidedness, with a higher percentage of left-sided individuals (27%) on the west coast than on the

Figure 1. Adult turbot (*Psetta maxima*), foto by A.-B. Florin.

east coast (20%) of Sweden (Fornbacke *et al.* 2002). The same phenomenon is seen in the pacific starry flounder, *P. stellatus*, with an equal frequency of left and right sided individuals off the US coast but almost 100% left-sided individuals in Japanese waters (Policansky 1982). Sidedness in starry flounder is under genetic control and the cline is proposed to be caused by natural selection on some unknown trait associated with sidedness (Policansky 1982).

2.2 Phylogeny

There are about 600 flatfish species in the world out of which 25% are distributed in temperate waters (Hensley 1997) and 15 of these occurs within the Skagerrak, Kattegat or Baltic Sea area (Table 1). All flatfishes belong to the systematic order *Pleuronectiformes*, however, the evolutionary development and history (phylogeny) of flatfishes are disputed (cf. Hensley 1997). The main issue is whether flatfishes are characterised by development from more than one ancestral type, i.e. having a polyphyletic origin, or not. Phylogenetic trees based on morphology (Hubbs 1945; Lauder and Liem 1983) are different from each other, and they also differ from genetic studies (Vernau *et al.* 1994; Exadactylos and Thorpe 2001). For example, in the molecular phylogeny of Vernau *et al.* (1994) (Figure 2a) *Soleidae* was the most primitive family while Exadactylos and Thorpe (2001) concluded, based on allozyme variation, that *Soleidae* evolved from the more primitive *Scophthalmidae* in agreement with the morphologic tree suggested by Lauder & Liem (1983) (Figure 2b). The high degree of genetic diversity within families indicates that the order is older than suggested by morphologic similarity, i.e. earlier than the Eocene time period (40–58 mya) (Vernau *et al.* 1994; Exadactylos and Thorpe 2001). Fossil record, however, suggest that *Scophthalmidae* first appeared in the Oligocene (c. 35 mya) (Chanet 2003). Within this family there are controversies concerning to which genera turbot belongs. Some authors place the turbot in the same genera as brill, *Scopthalmus*, (Desoutter *et al.* 2001; Chanet 2003), other prefer the separate genera, *Psetta* (Nielsen 1973). In the

Table 1. Classification of flatfishes (*Pleuronectiformes*) in Skagerrak, Kattegat and the Baltic Sea. (Kullander, S.O. 2002. Svenska fiskar: Förteckning över svenska fiskar. World Wide Web electronic publication; Swedish Museum of Natural History. http:// www.nrm.se/ve/pisces/allfish.shtml.se, 2005–08–24.)

Family			***Species***		
English	*Latin*	*Swedish*	*English*	*Latin*	*Swedish*
Bothids	*Bothidae*	tungevarar	Scaldfish	*Arnoglossus laterna*	tungevar
	Scophthalmidae	varar	Turbot	*Psetta maxima*	piggvar
			Brill	*Scophthalmus rhombus*	slätvar
			Topknot	*Zeugopterus punctatus*	bergvar
			Norwegian topknot	*Phrynorhombus norvegicus*	småvar
			Megrim	*Lepidorhombus whiffiagonis*	glasvar
Right-eyed flounders	*Pleuronectidae*	spättor			
			Dab	*Pleuronectes limanda*	sandskädda
			Flounder	*Platichthys flesus*	skrubbskädda, skrubba, flundra
			Plaice	*Pleuronectes platessa*	rödspätta
			Lemon sole	*Microstomus kitt*	bergskädda, bergtunga
			Sole witch, witch flounder	*Glyptocephalus cynoglossus*	rödtunga
			American plaice	*Hippoglossoides platessoides*	lerskädda
			Halibut	*Hippoglossus hippoglossus*	hälleflundra, helgeflundra
Soles	*Soleidae*	tungor	Common sole	*Solea solea*	tunga, sjötunga
			Solenette	*Buglossidium luteum*	småtunga

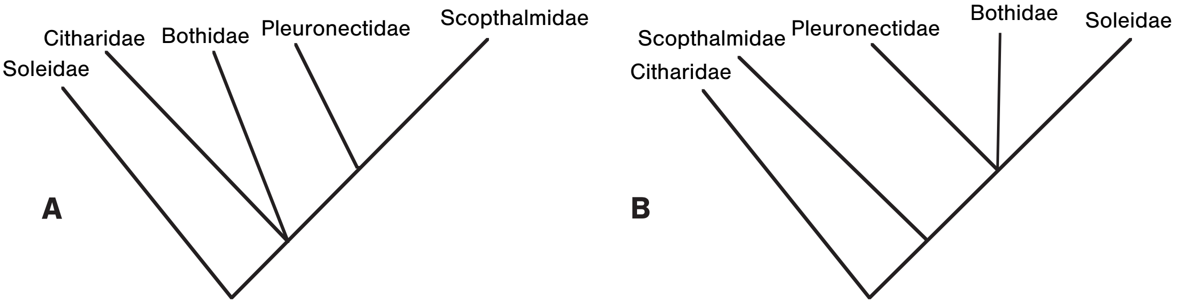


Figure 2. Phylogeny of flatfishes according to a) Vernau *et al* (1994) based on iso-enzyme electrophoresis and DNA/DNA hybridisation or b) Lauder and Liem (1983) based on morphology.

Catalog of fishes (Website version October 17, 2005; http://www.calacademy.org/research/ichthyology/catalog/) both genera are considered taxonomic valid while in Fishbase (http://Fishbase.org; Froese and Pauly 2005), as well as in the Integrated Taxonomic Information Systems on-line database (http://www.itis.usda.gov) and the Swedish Museum of Natural History (Table 1), *Psetta* is preferred. In this paper I have chosen to follow the latter nomenclature and turbot is referred to as *Psetta maxima* instead of *Scophthalmus maximus*.

The most thoroughly investigated group of flatfishes, the right-sided flounders, are either classified as family *Pleuronectidae* (Cooper and Chapleau 1998) or subfamily *Pleuronectinae* (Hensley 1997). Although economically most important, the group consists of only 60 species. The *Pleuronectidae* phylogenetic tree is characterised by large piscivorous species with symmetric jaws on the basal line and by specialised dentition, specialised jaw structure and diverse feeding habits at subsequent lineages (Cooper and Chapleau 1998). In this family the European flounder and plaice are known to hybridise (Kändler and Pirwitz 1957) and the existence of fertile male hybrids (Bagenal 1966; Lincoln 1981a–b) as well as the close genetic similarity (Galleguillos and Ward 1982; Exadactylos and Thorpe 2001) suggests that these two species should be regrouped into the same genus *Pleuronectes* (Hensley 1997). Based on morphologic similarities however, flounder and plaice are two distinct clades (Cooper and Chapleau 1998) with their typical characters derived from different ancestors. It is also argued that *P. flesus* is a paraphyletic species (i.e. not all descendants to the common ancestor are included in the taxa) and that it consists of several subspecies (Borsa *et al.* 1997; Exadactylos and Thorpe 2001).

2.3 Reproduction and recruitment

2.3.1 Sex-determination systems in flatfishes

The sex in fishes can be determined in many different ways (reviewed in Yamamoto 1969; Ward 2002). In some species sex is genetically determined by sex chromosomes, either the male or female is the heterogametic sex, i.e. the sex with different sex chromosomes. Other species lack special sex chromosomes but still have a genetic determination of sex. Environmental factors like temperature and pH can influence the sex of the fish embryos and the genetic sex can be modified into another phenotypic sex. The sex determination could also be of entirely environmental origin. Finally, in some species individuals are born as one sex but changes to the other at a later stage in life.

The mechanisms for sex determination in flatfish are only known for a few species. Yamamoto (1999) revealed that the Bastard halibut (*Paralichthys olivaceus*) has male heterogametic sex determination (XX-female and XY-male). However, sexual development of genetic females (XX-fish) is so unstable that spontaneous sex reversal to physiological males can be caused by exogenous factors, like extreme water temperatures (Tabata 1995; Yamamoto 1999). In plaice females is probably the heterogametic sex since gynogenesis (where the eggs develop without contribution of male DNA) give rise to both male and female offspring (Lincoln 1981b). A possible effect of water temperature was indicated by the extreme number of males among triploid individuals produced by cold-shocked eggs of both plaice and plaice x flounder hybrids in the experiment by Lincoln (1981a).

In turbot sex ratio is supposedly skewed so that there are many more males than females (Muus *et al.* 1999). According to Molander (1964) the ratio was 2:1 in the North Sea and 10:1 in the Baltic. It is unclear if these numbers refer to adults or juveniles and to the catch or the entire stock. In the commercial Swedish turbot fishery in central Baltic Sea today, however, the sex ratio is reversed so that three times more females than males are caught (Fiskeriverket 2005b) mainly because of their larger size. In North Atlantic plaice it is the other way around, more males than females are caught (Solmundsson *et al.* 2003). The higher catchability of males, caused by their higher swimming activity, together with the earlier sexual maturation and longer time spent on the spawning ground can explain the higher occurrence of males in the commercial catches of plaice (Solmundsson *et al.* 2003).

2.3.2 Reproduction

There is a general positive exponential relationship between fish size and number of eggs, i.e. fecundity (e.g., Jennings *et al.* 2001) but there is great individual variability. In most flatfish species fecundity is positively related to age (Kändler and Pirwitz 1957; Bagenal 1966). Variations in fecundity may partly be explained by variations in food availability (Bagenal 1966). Variations in population density, due to e.g. fishing or high larval mortality on exposed coasts, would lead to more food for the survivors while overcrowding could lead to food shortage. An interesting trend is that flatfishes have higher fecundity, measured as number of eggs in relation to body size, in the Baltic Sea compared to the North Sea (Kändler and Pirwitz 1957; Bagenal 1966).

Some fish species in the Baltic Sea, like sprat (*Sprattus sprattus*), cod (*Gadus morhua*), fourbeard rockling (*Enchelyopus cimbrius*), dab and flounder have adapted to the less saline water of the Baltic and enabled their eggs to stay floating by taking up more water and lower their density. This means that the eggs are larger the further into the Baltic Sea from the Öresund strait (Mielck and Künne 1932; Lönning and Solemdal 1979). This is due to different populations having different egg properties rather than just a physical adaptation by the eggs themselves (Solemdal 1973; Lönning and Solemdal 1979; Thorsen *et al.* 1996; Nissling and Westin 1997; Nissling *et al.* 2002). The eggs of plaice are only marginally larger in the Baltic compared to the North Sea and turbot do not seem to have this adaptation at all (Mielck and Künne 1932). There seems to be three types of spawning behaviour among flatfishes in the Baltic (Mielck and Künne 1932; Lönning and Solemdal 1979; Nissling *et al.* 2002). Plaice and dab spawn only in the relatively saline water of the western Baltic Sea and the deeper areas in the central Baltic Sea. Flounder spawns in the more saline water of the western Baltic Sea and the deeper areas in the Baltic Sea as well as in the less saline shallower parts of the central Baltic Sea. This is a consequence of two different strategies, demersal or pelagic eggs, which will be dealt with in the section about flounder. Turbot spawns, apart from the western Baltic, only in the shallower (<12m) parts of the middle Baltic (Mielck and Künne 1932).

2.3.3 Recruitment

Recruitment, i.e. the number of individuals that reach the age of maturity, varies greatly between years (e.g., Jennings *et al.* 2001; Myers 2002). Compared to other temperate species however, flatfish recruitment to maturity varies little, possibly because the concentration of flatfish larvae on nursery areas dampens the variability (Iles and Beverton 2000). In North Atlantic flatfish the magnitude of recruitment is mainly an effect of the transport of eggs and larvae to nursery areas and the quality of these areas for larval development (Beverton and Iles 1992; Bailey 1994; Gibson 1994; van der Veer *et al.* 2000; Wennhage and Pihl 2001; Pihl *et al.* 2005). Although the number of recruits is positively correlated with the quantity of nursery habitats, the carrying capacity (maximum number of supported larvae) is generally not reached. Instead the supply of larvae to the nursery areas sets the limit (van der Veer *et al.* 2000). However, the increasing distribution of algal mats on nursery grounds can become a problem. The occurrence of algal mats on nursery areas in Skagerrak is estimated to lead to a 30–40% reduction of 0-group plaice recruitment (Pihl *et al.* 2005).

Mechanisms that generate variability in abundance occur in all life stages but those operating in the three-dimensional pelagic egg and larval stages are the most important. The variability generating processes seems to be amplified towards the edges of distribution (Rijnsdorp *et al.* 1995; Myers 2002; but seeLeggett and Frank 1997). After settlement to the two-dimensional environment, density-dependent, regulating mechanisms dominate (Beverton and Iles 1992; Rijnsdorp *et al.* 1995; van der Veer *et al.* 2000; Le Pape *et al.* 2003). The power of variability generating, in relation to regulating, mechanisms are modified by four factors (van der Veer *et al.* 2000):

1) Fisheries may reduce adult biomass and remove intraspecific regulating processes.
2) Food and predators are unevenly distributed over the species range.
3) Temperature differences and adaptation to cold (*Pleuronectidae*) or warm (*Bothidae* and *Soleidae*) water may give different responses.
4) Type of food will influence recruitment variability since the availability of epibenthic prey is more variable than benthic prey.

The same pattern of abundance of settling flatfish is found throughout North Western Europe: increasing densities during the period of settlement followed by a continuous decrease during the rest of the season (van der Veer *et al.* 1990). Investigations by Modin & Pihl (1994, 1996) and Pihl et al. (2000) in the Gullmarsfjord on the Swedish west coast showed that the number of settling plaice reached a maximum in May and decreased during the rest of the season. There can be substantial variation in densities on shallow bottoms between years and places (Modin and Pihl 1994; Lagenfelt and Svedäng 1999; Pihl *et al.* 2000; Wennhage and Pihl 2001; Fiskeriverket 2005a). For example, plaice density in mid-may 1998 varied significantly on a regional scale, with ten times higher densities in the northern (22.3 ind. m^{-2}) than southern (2.3 ind. m^{-2}) bays on the Swedish west coast (Pihl *et al.* 2000). The mortality is density dependent some years but environmental factors uncouple the relationship in other years (Modin and Pihl 1994, 1996; Modin 2000; Pihl *et al.* 2000). Survival during the larval stage is also highly affected by temperature and wind. Low temperature increases survival, but retards growth, and strong winds may cause mechanical damages and transport larvae to suboptimal areas (Pihl 1989, 1990).

Many attempts have been made to describe the relationship between stock size and recruitment using the abundance of 0-group (born in this year) or 1-group (born last year) juveniles to predict the future size of stock (cf. Vitinš 1988). A mathematical model for stock recruitment in flatfishes which incorporates the environmental effects as well as the effect of the stock is discussed in Iles and Beverton (1998, 2000).

2.3.4 Predation

Predation is the main mortality factor for juvenile flatfish. In a study by van der Veer *et al.* (1990) the same two types of predators were found everywhere in the North Western Europe: crustaceans (mainly the shrimp *Crangon crangon*) in spring and migratory fish in summer and autumn. The impact of predation by crustaceans on plaice density varied among areas, presumably depending on local temperature conditions (van der Veer *et al.* 1990). In areas characterised by low spring temperatures no impact on the year-class strength was found, while in areas with high spring temperatures, either a reduction or an increase of variation in recruitment was observed (van der Veer *et al.* 1990). The nature of the effect is speculated to depend on the minimum temperature in the nursery area in winter, which affects migration and/or mortality of the shrimps. In areas with low winter temperature, the abundance of shrimps fluctuates between years and hence increases variability in plaice recruitment. In laboratory experiments the functional response of shrimps to prey density show a typical sigmoid type III response curve (Begon *et al.* 1990; Wennhage 2002). Plaice densities in the sigmoid part of the functional response curve represent normal to high field densities of plaice on the Swedish west coast, suggesting that shrimp predation could have a stabilising effect on plaice recruitment. In contrast fish predation in summer and autumn appear to have little impact on the recruitment of plaice (van der Veer *et al.* 1990). The coelenterates *Pleurobrachia pileus* (Sea gooseberry) and *Aurelia aurita* (a jelly fish) predate on both flounder and plaice larvae in the Dutch Wadden sea (van der Veer 1985). However, due to the timing of larval immigration and coelenterate outburst they probably only have an impact on the recruitment of flounder.

Substrate affects the predation pressure. In a laboratory experiment predation by shrimps (*C. crangon*) on newly settled fish was higher on bare sand than on filamentous algae substrate though predation by crabs (*Carcinus maenas*) was unaffected by habitat type (Wennhage 2002). The combined predator pressure was lower among algae than on sand, but settling plaice still chose the sand habitat. The formation of macroalgal mats on plaice nursery grounds, which have been a regular phenomenon in recent years, could lead to a concentration of juveniles in the remaining sand habitats and an increased density dependent predation by shrimps (Wennhage 2002).

Different temporal and spatial strategies have evolved in order to minimise the risk of predation after settlement (Modin and Pihl 1996). Plaice settle during the early phase of 1-group *C. crangon* immigration while the first appearance of flounder occur simultaneously with the peak biomass of predatory shrimp (Modin and Pihl 1996). Plaice, however, occur in the deeper part of the bay together with *C. crangon*, while flounder minimise shrimp predation by staying in the shallow shore waters. In addition, settling larvae avoid habitat with *C. Crangon* if given a choice (Wennhage and Gibson 1998). Furthermore, young plaice show a diurnal movement pattern (Gibson 1997; Gibson *et al.* 1998), they move in-shore at dusk and return to deeper water at dawn. This behaviour could act to minimise predation risk as larger predatory fishes do not move in-shore as far as the plaice, nor do they remain in shallow waters as long as the young plaice (Gibson *et al.* 1998).

2.4 Growth

In flatfish the growth differ between sexes; the females growing faster and reaching a larger size (Devold 1942; Molander 1964; Curry-Lindahl 1985). The mortality of females is also lower so that the sex ratio is strongly female biased in older age groups (Devold 1942; Molander 1964; Curry-Lindahl 1985). After a rapid growth the first year of life there is a considerable reduction in growth rate during the sexual maturation period and afterwards there is a slight decrease with age (Devold 1942). Longevity is positively related to size (review in Beverton and Holt 1959), and for flounder, plaice and turbot maximum recorded age by SBF in present stocks is just above 20 years but without fishing mortality the maximum age could probably be the double (Fiskeriverket 2005b). The mean age is much lower though, for turbot in SD 28 it is close to eight years (Gårdmark *et al.* 2004).

Factors influencing growth can be classified into controlling, limiting, masking, directive, and lethal (Fry 1971). Temperature control growth by regulating metabolism which increases with increasing temperature to an optimum thereafter it decreases with increasing temperature (Yamashita *et al.* 2001; Jobling 2002). Optimum temperature decreases with size (Fonds *et al.* 1992), which might explain why adult flatfish prefers deeper, cooler water. Studies in the southern North Sea show that mean temperature regulate the growth of 0-group plaice and sole during summer (Amara 2003). During winter and autumn, however, the growth of plaice is slower than predicted by the temperature, suggesting that other factors, such as decreased food availability, could limit growth.

The resources used to power metabolism are limiting factors for growth (Yamashita *et al.* 2001). Both quantity and quality of food are important. For visual feeders the decreasing day-length could reduce access to food during autumn and winter (Amara 2003). Low levels of oxygen can also influence metabolism. When dissolved oxygen (DO) levels fall below 5–6 ppm growth is reduced (Yamashita *et al.* 2001), probably as an effect of reduced food intake (Pichavant *et al.* 2001; Person-Le Ruyet *et al.* 2003). In fact, the predation efficiency of juvenile *P. flesus* is significantly lower at lower oxygen levels (Tallqvist *et al.* 1999).

Masking factors, like salinity and pollutants, result in increased metabolic losses and lead to reduced growth (Yamashita *et al.* 2001). The optimum ranges of salinity for growth is species and stage specific. In general flatfish, like many marine teleosts, regulate their plasma ion concentration such that their iso-osmotic salinity is between 10–15‰ (Brett 1979; Gaumet *et al.* 1995; Sampaio and Bianchini 2002). Flatfishes tolerate significant variations in salinity and some species, like turbot and flounder, are considered euryhaline (Holmes and Donaldson 1969; Evans 1984). The latter have sometimes even been recorded in freshwater (Molander 1964; Curry-Lindahl 1985; Kerstan 1991). Experiments with seawater adapted juveniles from a North Atlantic aquaculture show that turbot adapt well when transferred to lower salinities (Gaumet *et al.* 1995). In fact less oxygen and food is consumed to reach similar or better growth in brackish (10–19‰) water compared to sea water. This suggests that growth could be improved by adaptation to brackish water. However, this is in contrast with the observation that adult turbots in the brackish Baltic Sea are smaller than in the saline Skagerrak and Kattegat (cf. Molander 1925; Curry-Lindahl 1985). Furthermore, the significant differences observed in osmolality, plasma ion concentrations and Na^+, K^+-ATPase activity after transfer of juveniles to 5‰ salinity, compared with transfers in higher salinities, suggest that there is a threshold of acclimation of turbot to a hypotonic environment (Gaumet *et al.* 1995).

Directive factors act as cues for transitional changes in life history (Yamashita *et al.* 2001), and many environmental factors, including food, predator presence, DO, temperature, salinity, tidal flow, light intensity, and photo period can act as such cues. Movements induced by or responses initiated by these factors increase survival and growth.

Extreme environmental regimes, for example low water temperature (<4 °C) or depletion of dissolved oxygen, can act as lethal factors and kill fish. Anthropogenic activities have led to an increase in areas depleted of DO. Oxygen deficiency caused by eutrophication in nursery areas could be a reason for the decrease in abundance of many flatfish species in the Baltic during the 20th century (Bagge *et al.* 1990). In experiments with juvenile *P. flesus* from the Åland archipelago 80% of the fish died within 42h at 20% oxygen saturation (Tallqvist *et al.* 1999). Already at 40% the ventilation rate increased and at 30% saturation the flounders showed escape behaviour. Turbot, on the other hand is relatively resistant to oxygen depletion. It can survive shocks of oxygen depletion down to 20% and the recover capacity is high (Pichavant *et al.* 2001, 2002; Person-Le Ruyet *et al.* 2003). Since dab settles on relatively "deep" (ca 10 m) shallow muddy bottoms they do not suffer from the higher mortality due to increased filamentous algae depleting the oxygen in shallow waters, like the plaice do (Bagge and Nielsen 1989). Furthermore, the extended spawning period could make dab less sensitive to oxygen depletion as a result of eutrophication. Sole avoids the oxygen deficiency through spawning in early summer when primary production is reduced and settling in late summer after the algal mats have disappeared (Bagge *et al.* 1990).

2.5 Population structure

Most organisms are not uniformly spread but have a patchy distribution where a group of individuals of a species living in a certain area constitutes a population (Begon *et al.* 1990). The entire species then consists of several, more or less, biologically distinct populations with various amount of exchange between them. Identification of population structure is especially problematic in marine organisms where geographic boundaries are less apparent. Nevertheless, the concept of population structure is fundamental for understanding population dynamics and managing fisheries (cf. Jennings *et al.* 2001; Ward 2002; Laikre *et al.* 2005).

In fisheries science populations are called stocks and are defined as intraspecific groups of randomly mating individuals with spatial and temporal integrity (Ihssen *et al.* 1981). The integrity could either be high, as for genetic stocks (reproductively isolated and genetically differentiated stocks), or relatively low as for harvest stocks (locally accessible stocks with independent dynamics) (Carvalho and Hauser 1994; Bailey 1997). The actual management stock could in turn differ from both the genetic and harvest stock due to incomplete population data or socio-economic or political constraints (Carvalho and Hauser 1994). However, management of fish stocks is more effective if it is based on true biological stocks rather than arbitrary defined stocks (Carvalho and Hauser 1994; Laikre *et al.* 2005). In conservation practices it is important to identify the evolutionary significant unit (Powles *et al.* 2000; Fraser and Bernatchez 2001). In fact, the wrongful lumping of different stocks with little gene flow between them can have detrimental effects in conservation recommendations (Ryman *et al.* 1995; Bailey 1997; Frank and Brickman 2001).

In general marine species seem to be more genetically versatile than anadromous and freshwater species (DeWoody and Avise 2000), and at the same time less differentiated into genetic stocks (Ward 2000). This is thought to reflect the higher effective population size and less restricted migration in marine species (DeWoody and Avise 2000).

The degree of population structure ranges widely among flatfishes. Although large populations tend to be subdivided into local stocks, based on morphological, meristic and reproductive characteristics, these data often conflict with evidence on genetic stock structure, due to the scale and organisation of movement between populations (Bailey 1997). Both the common sole and flounder are species with a high degree of genetic population structure in the North Temperate Zone. On the other hand, plaice, and perhaps also turbot, appear to be species with apparent population structure but little apparent genetic differentiation in Europe (Bailey 1997). However, a genetic differentiation between the eastern and western Mediterranean as well as between the Baltic and Atlantic have been found for turbot (Nielsen *et al.* 2004b; Suzuki *et al.* 2004).

2.5.1 Migration

Flatfishes all over the Atlantic, including the Baltic Sea, show annual micro- and macroscale movements and migrations between spawning, feeding, and wintering areas (Molander 1925; Aro 1989; Gibson 1997; Metcalfe *et al.* 2002; Solmundsson *et al.* 2004). This behaviour decreases the impact of environmental variability on reproduction, survival, foraging, and growth (Aro 1989; Metcalfe *et al.* 2002). Eurythermic and euryhaline species, which tolerate a wide range of temperature and salinity regimes, are usually able to migrate more intensively than the more temperature and salinity sensitive stenothermic and stenohaline species (Aro 1989). It has been suggested that marine species often have both local and migratory stocks (Aro 1989) and there is evidence of a homing behaviour in both plaice (Riley 1973; de Veen 1978a; Gibson 1997; Hunter *et al.* 2003; Solmundsson *et al.* 2004; Burrows *et al.* 2004) and turbot (Aneer and Westin 1990).

The cues for migration can be several (review in Gibson 1997). For example, in plaice darkness stimulates swimming off the bottom and temperature can influence mass movement of newly settled individuals (Gibson 1997). Temperature can also influence the onset of spawning migration. For example, in flounder, off south west England, migration starts earlier in years with low temperature (Sims *et al.* 2004). Although flatfishes have no swim bladder they are capable of detecting pressure changes which could act as cues for migration (Gibson 1997). Internal cues, like endogenous circadian rhythm is recorded in juvenile plaice, flounder and turbot (Gibson 1997). Other possible internal cues are hunger and maturation state (Gibson 1997). The cues for recognising destination can be the land/sea boundary for shallow water species or the substratum (Gibson 1997). Other factors could perhaps be smell (Mitamura *et al.* 2005) or audible cues (Holliday 1969). Despite the rarity of social behaviour the concentration of individuals could act as a cue to recognise spawning area, perhaps by pheromones or spawning products (Gibson 1997).

By taking advantage of tidal water movements both time and energy can be saved during migrations. There is evidence for the use of selective tidal transport in plaice, sole and flounder in the North Sea (Kuipers 1973; de Veen 1978a; Harden Jones *et al.* 1979; Gibson 1997; Hunter *et al.* 2004). Tagging and displacement studies of both juvenile and adult North Sea plaice, however, show that the use of tidal transport is limited (de Veen 1978a). Recently, Hunter *et al.* (2004) showed that, although plaice in the northern North Sea do not use tidal transport, tidal stream have a major roll in migration by providing transport and guidance for the southerly distributed North Sea plaice. Where tidal currents are weak, like in the Baltic, onshore movements might instead be driven by wind as Pihl (1990) showed for plaice in Skagerrak.

Many flatfishes also show a pattern of daily movement. The larvae of sole, plaice and flounder move close to the seabed during the day and rise to the surface at night (Gibson 1997). In *Paralichthys* flatfish species in USA and Japan this diel migration is modified by a tidal component that results, due to tidal water, in net onshore movement of late larval stages (Gibson 1997). Also juvenile turbot show a diel movement, approaching the shoreline during night, supposedly to forage, and returning to deeper water during the day (Støttrup *et al.* 2002). Because of strong diel temperature fluctuation such movements also ensure that the fish remain in a fairly constant temperature (Gibson *et al.* 1998).

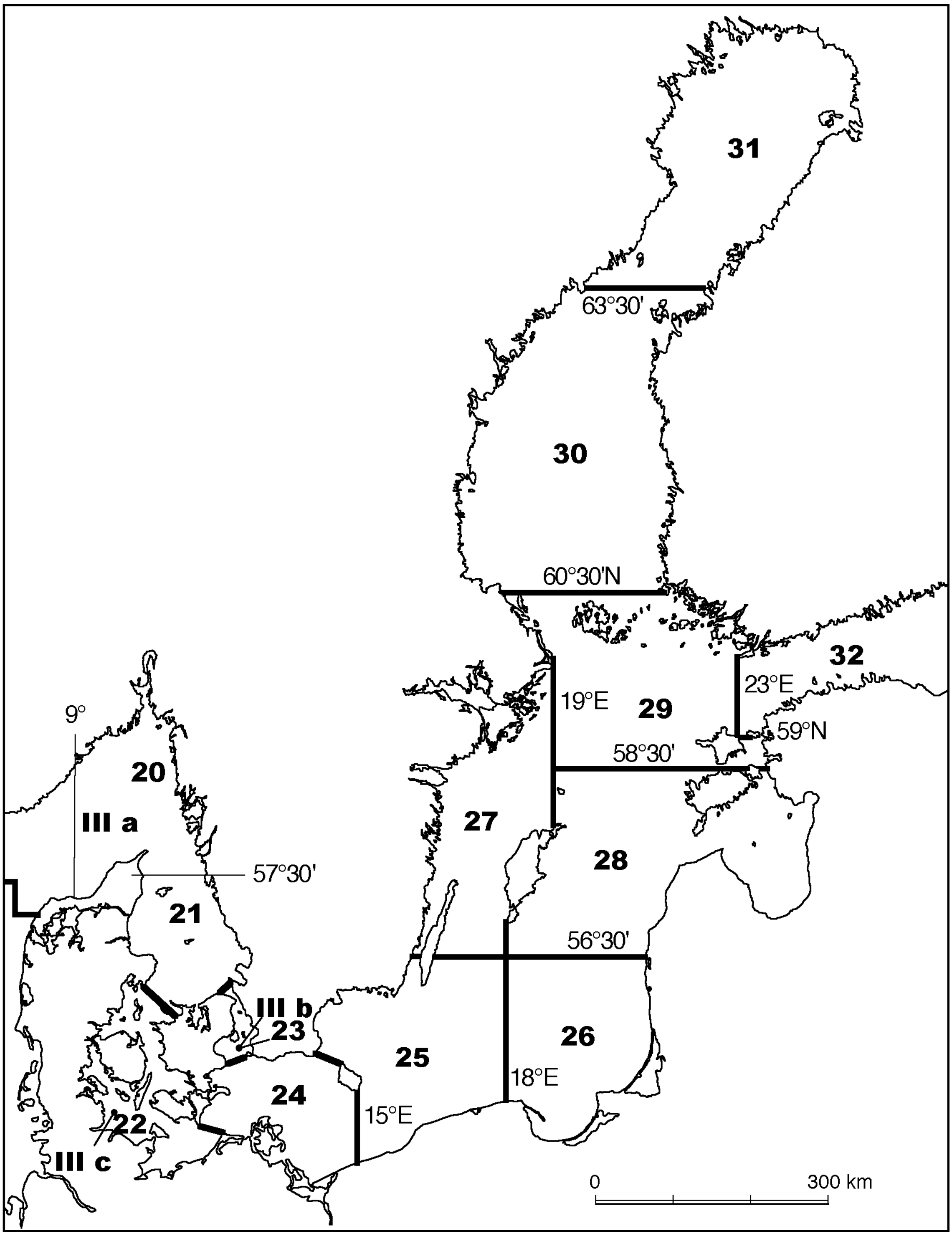


Figure 3. Fishing areas according to ICES (International Council for the Exploitation of the Seas). IIIa is divided into 20 and 21 by Swedish Board of Fisheries.

3. Turbot (*Psetta maxima*) and brill (*Scopthalmus rhombus*)

3.1 Fishery and abundance of turbot and brill

Turbot fishery outside four nautical miles off the coastal baseline is managed within EU, hitherto through the International Baltic Sea Fishery Commission (IBSFC) (Fiskeriverket 2001). The regulation is geographically divided according to the International Council for the Exploration of the Sea's (ICES) subdivisions (SD) (Figure 3). Minimum allowed landing size for turbot and the closely related brill in Sweden is 30 cm and in the southern Baltic Sea they are protected during the spawning time (Table 2). The main part of Swedish turbot fishing, however, takes place in the coastal zone during spawning in the summer. In the 1990's the bar length of meshes was 130 mm or larger but presently mesh size is usually only 110 mm. Turbot is subject to the international monitoring programme initiated and regulated by the EU (EU Council regulation 1543/2000). The purpose is to establish a Community framework for the collection and management of the fisheries data needed to conduct the common fisheries policy. According to the regulation each membership state in the European Union are obliged to monitor fish populations by collecting data every year. In this way yearly estimates on the number of fishes and their mean weight at age are attained as a base for analyses of historic exploitation and prognosis of future catches. Sex distribution and sex maturation are also described on a yearly basis.

Males are smaller than females and their growth curve in the Baltic Sea level out close to 30 cm (Fiskeriverket 2005b). This means that the fisheries land more females than males and that the majority of all discarded turbot are males. Hence, it was suggested that fishing should be regulated through mesh size instead of fish length (Fiskeriverket 2001) or that separate minimum sizes should be used for males and females (Jacobsson 2003). In that way both males and females will be used as a resource and not only the females, which are more crucial to the survival of the stocks.

The main part of turbot fishery takes place in the southern and western part of the Baltic Sea (SD 22–26) within the Danish and German fisheries (ICES 2005a). In 1959 the intensive fishery by Denmark resulted in total Danish landings of turbot of 834 tonnes, compared with the Swedish total landings of 72 tonnes in the same year (Molander 1964). Danish landings of turbot increased 1963–1989, both the total landings and the landings per unit effort (Steffensen and Bagge 1990). The fishery directed towards turbot escalated in the early 1990's in SD 26–28 in the Baltic Sea due to Polish, Russian and Swedish gillnet fishery (ICES 2005a) (Figure 4). Since 1995 however, the total landings of turbot in the Baltic Sea decreased and amounted to 516 tonnes in 2004 (ICES 2005a).

The main part of Swedish turbot fishery occurs on the east of the Island of Gotland, around the Island of Öland and east of the Island of Bornholm (corresponding to ICES SD 28, 27 and 25). Sweden landed 20 tonnes per year in the beginning of the 1990's but catches rapidly increased to culminate in the middle of the decade with landings over 200 tonnes (Fiskeriverket 2005b) (Figure 5). Thereafter the catches decreased and according to Swedish fishermen's log books only 26 tonnes was landed in 2004. In Kattegat the Swedish landings are about 5 tonnes yearly and another tonne is caught in Skagerrak. In 1997 half of the catch

Table 2. Swedish flatfish fishery regulation, FIFS 2004:36. S = south of 59.30 N. C = coastal area. Applying rules 2005-08-11, updates available on the Swedish Board of Fisheries website: www. fiskeriverket.se.

Species	*ICES Subdivision*	*Minimum landing size (cm)*	*Protected spawning period*	*Minimum diagonal mesh size (mm)*
All flatfishes	23–27			120
	28			110
	29S, 32S			100
Turbot & Brill	20–32	30		
	24, 25, 26	30	1/6–31/7	
Megrim	20, 21	25		120
Dab	20, 21	23		100
Flounder	20, 21	20		100
	22–25	25		
	27	21		
	26, 28	21	15/2–15/5	
	29S	18	15/2–15/5	
	32	18	1/2–30/6	
Plaice	20C, 21C	27	1/1–31/5 ripe females	100
	22, 23	25		
	24, 25	25	1/2–30/4 females	
	26–28	21	15/2–15/5	
	29S	18	15/2–15/5	
Lemon Sole	20, 21	25		
Sole witch	20, 21	28		
Sole	20, 21	24		100

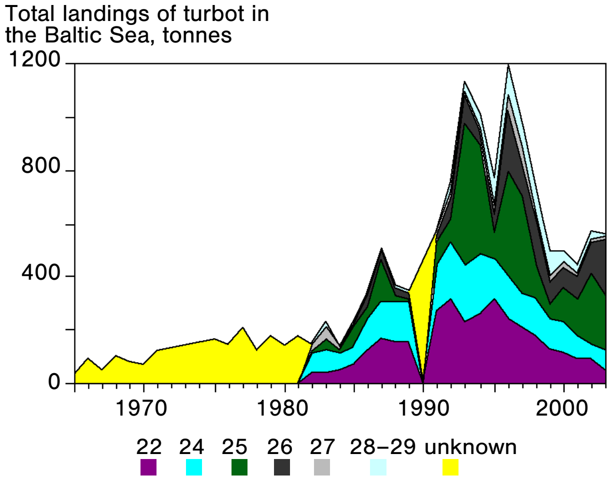


Figure 4. Total landings of turbot in ICES SD 22–32 during the years 1966–2004 according to the report of the Baltic fisheries assessment working group (ICES 2005a). In some years landings are not separated into subdivisions.

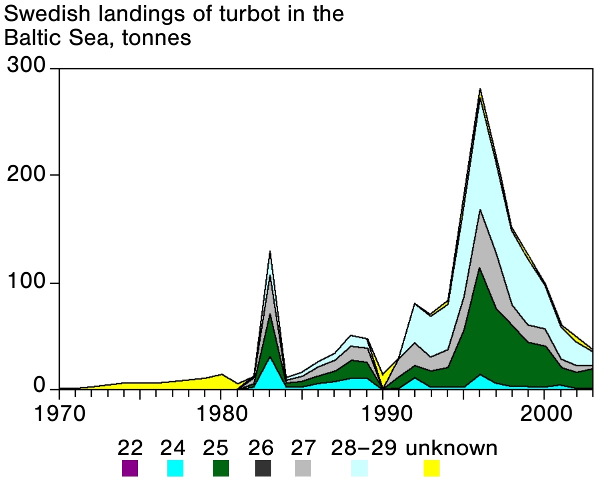


Figure 5. Swedish landings of turbot in ICES SD 22–32 during the years 1970–2004 according to the report of the Baltic fisheries assessment working group (ICES 2005a). In some years landings are not separated into subdivisions.

from the Swedish west coast was taken within the four nautical mile limit (Lagenfelt and Svedäng 1999).

Most brill (>90%) is caught by Denmark in SD 22. In 1959, total Danish landings were 214 tonnes compared to the Swedish landings of 68 tonnes (Molander 1964). The following decades Danish landings of brill decreased, while the landings per effort were constantly low (Steffensen and Bagge 1990). In 2004, the total landings in the Baltic Sea were 41 tonnes (ICES 2005a). The Swedish landings are only a couple of hundred kilos of brill in the Baltic Sea (Lagenfelt and Svedäng 1999) (Figure 6). In Kattegat, however, almost 10 tonnes are landed each year according to Swedish fishermen's log, and half the amount in Skagerrak.

Like many other marine resources abundance of turbot shift between years and the effect of single year classes can be significant. Several attempts have been made to predict the commercial turbot stock recruitment and hence the catch in advance. Monitoring programmes, performed by the Institute of Coastal Research (ICR) at the SBF, east and north of Gotland between 1998–2002 indicated high recruitment but a lack of large individuals (Neuman and Píriz 2000; Fiskeriverket 2001, 2005b). The high level of recruitment was also seen in the Sea of Åland during the 1990's (Andersson 1998). However, the strongly diminishing commercial catches despite high effort and a decrease of older females suggests an unsustainable fishing pressure (Fiskeriverket 2005b). As a consequence of the apprehended decrease in abundance, turbot is listed as a near threatened species in the 2005 Red list of Swedish species (Gärdenfors 2005).

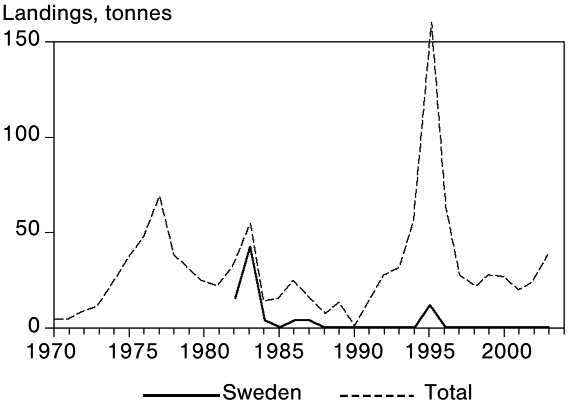


Figure 6. Total and Swedish landings of brill in the Baltic Sea during the years 1970-2004 according to the report of the Baltic fisheries assesment working group (ICES 2005a)

3.2 Population structure in turbot and brill

3.2.1 General distribution

The turbot is a coastal species (Neuman and Píriz 2000) commonly occurring from Skagerrak up to the Sea of Åland (Molander 1964; Curry-Lindahl 1985; Muus *et al.* 1999; Voigt 2002). The depth distribution of fish is size and age dependent, young fish prefers shallower water while older, large fish is found in deeper waters (Molander 1964; Pihl 1989; Støttrup *et al.* 2002). Sparrevohn & Støttrup (2003) showed in a laboratory study that both juvenile and adult turbot prefer sand bottoms to gravel or vegetation.

In spring both young and adult turbot move to the coast while they migrate towards deeper water, although seldom deeper than 70 m (30 m in central Baltic) in winter (Molander 1964; Curry-Lindahl 1985; Voigt 2002). Turbot spawns in shallow waters (10–40 m, 10–15 m in central Baltic) and the metamorphosing post-larvae migrate close to shore to shallow water (down to one meter depth) (Molander 1964; Curry-Lindahl 1985; Voigt 2002; Iglesias *et al.* 2003). In summer and autumn the juvenile fish dwell in the coastal zone (Molander 1964; Pihl 1989; Scherbich

1998; Støttrup *et al.* 2002). The juveniles mainly occur down to 7–8 meters water depth in the eastern Baltic (Scherbich 1998) but less than five meters in Kattegat (Pihl 1989). Støtrrup *et al.* (2002), however, found a substantial number of 0-group juveniles at depths exceeding four meters in Kattegat.

The turbot juveniles show a diel migration pattern moving to shallower waters (<4 meters) at night, possibly to feed, and moving further out at daytime (Støttrup *et al.* 2002). Brill have generally a similar distribution but they rarely occur north of Bornholm in the Baltic (Molander 1964; Curry-Lindahl 1985).

3.2.2 Results from tagging studies

In the period 1965–1970 turbot and brill was tagged occasionally during spring and autumn in the Kattegat near the island of Anholt (Bagge 1987). Recaptures up to five years after tagging showed that both species performed short migrations to deeper water during autumn and winter but returned to the same shallow water in spring. Further migration studies by Aneer and Westin (1990) in the Baltic confirm the relatively sedentary behaviour of turbot. They tagged 401 turbot dorsally with Carlin tags in the Askö area near Stockholm, between 1969 and 1973. Recapture rates varied between 12 and 27% among years. Average distance between capture and recapture was only six km and 90% of the recaptured fish were caught less than 20 km from the point of first capture. Tagging and releasing in the 1990's of reared turbot juveniles in Kattegat by Støttrup *et al.* (2002) further supports the sedentary behaviour of turbot. More than 90% of the fish (in total 100 000 0-group and 40000 1-group juveniles) remained within 10 km of the tagging point during the first year and fish remained close to shore during the first two years after release. Thereafter a movement offshore, possible towards spawning areas, were detected (Støttrup *et al.* 2002). Due to presumably limited dispersal of eggs and larvae in the Baltic (see the section on reproduction) the turbot is considered to consist of several local stocks in the northern and central Baltic (Aro 1989; Fiskeriverket 2001). However, these stocks are not genetically different (see below).

3.2.3 Genetic variation

Allozyme studies of turbot show that genetic variation is low and gene flow substantial prohibiting any genetic differentiation in European specimens (Blanquer *et al.* 1992; Bouza *et al.* 1997). In cultured stocks the variation is even less, suggesting a genetic drift phenomenon involved in the foundation and management of brood stocks. In comparison with flounder and brill from the same area, turbot in northwest Spain have a significantly lower allozyme variation suggesting the existence of a historic bottleneck in turbot (Bouza *et al.* 1997). However, due to their low variability, allozymes may not be useful genetic markers for studying within species differentiation. Using more variable molecular markers, microsatellites (Goldstein and Schlötterer 1999), Bouza *et al.* (2002) found no difference in genetic diversity between turbot and brill, and no evidence of a historic bottleneck in turbot. Assessments of genetic variation in two wild populations and two farmed strains of turbot, from Ireland and Norway (Coughlan *et al.* 1998) showed that despite a considerable loss of rare alleles in the Irish cultured strain, no statistically significant reductions were found in mean heterozygosity or allelic diversity in farmed strains compared to wild stocks. There was, however, significant genetic differentiation between the farmed strains as well as between the farmed and wild samples from each country but not between the wild stocks. The genetic differentiation of the cultured strains is presumably caused by drift (cf. Bouza *et al.* 1997; Coughlan *et al.* 1998). Genetic differentiation by drift of stocks founded by few individuals (as is probably the case for farmed strains) is not uncommon (cf. founder effect, Mayr 1954; Giddings *et al.* 1989; Irvin *et al.* 1998).

Nielsen *et al.* (2004b) found genetic differences (using microsatellites) between turbot sampled from the Atlantic/North Sea area and turbot from the Baltic Sea. There was a sharp cline in the transition area from the low saline Baltic Sea to the high saline North Sea suggesting the existing of two divergent populations connected with a hybrid zone (Nielsen *et al.* 2004b). In a recent study however we found no genetic differentiation between the Baltic Sea and the Kattegat (Florin, A.-B. and Höglund, J. unpublished).

Studies of variations in haemoglobin genotypes reveal a significant difference between turbot from Iceland and west Norway on one hand and southwest Norway, Kattegat and the Baltic Sea on the other (Imsland *et al.* 2003b). There is also differences in haemoglobin subgroup frequencies among the five investigated sites, indicating that turbot in northern European waters belong to more than one panmictic population (Imsland *et al.* 2003b).

In conclusion, the genetic studies hitherto show that although there are some genetic differences on a larger, biogeographical scale, there is no genetic differentiation of turbot stocks within the Baltic Sea.

3.3 Reproduction of turbot and brill

Females mature about the age of four years while males are ready to mate a year earlier (Molander 1964; Jones 1974). Maturity in the Baltic occurs already at a size of 20 cm for females and 15 cm for males while at the Swedish west coast maturity probably occur at about 30 and 25 cm respectively (Molander 1964; Muus *et al.* 1999). In the North Sea, 50% of turbot females are mature at the length of 46 cm, the weight of two kg and an age of 4.5 years (Jones 1974).

Turbot is a summer spawner (Molander 1964; Curry-Lindahl 1985) and investigations of the gonad maturation cycle in wild-caught fish show that turbot spawn in the North Sea from May to Aug (Jones 1974). The onset of spawning is controlled by temperature and day length and in northern Atlantic it is triggered at 13–15 °C and 15–16 h day length (Devauchelle *et al.* 1988). The importance of day length was demonstrated in an experiment by Imsland *et al* (2003a) where exposure to continuous light inhibited spawning in farmed turbot. In addition, increasing day length increased growth but postponed first maturity (Imsland and Jonassen 2003).

The closely related brill mature at the same size but spawns earlier and in somewhat deeper water (Molander 1964; Curry-Lindahl 1985). The closely related brill is also known to hybridise with turbot (Molander 1964; Heap and Thorpe 1987). The close relationship between turbot and brill is underlined by the fact that some authors chose to put them in the same genera (see section 2.2, Desoutter *et al* 2001; Chanet 2003)

Turbot has adapted to the low salinity in the Baltic and spawn successfully up to the Sea of Åland (Molander 1964; Curry-Lindahl 1985; Andersson 1998; Muus *et al.* 1999; Voigt 2002). In experiments, eggs from the Belt Sea develop at 12–18‰ salinity with an optimum at 15‰ (Kuhlman and Quantz 1980) whereas eggs from the North Sea have an optimum at 20–35‰ and does not survive in the low salinity of the Baltic (Karås and Klingsheim 1997). Turbot eggs from east of Gotland, however, hatch successfully in salinities down to seven psu (Nissling 2004). Interestingly, the eggs are not buoyant at salinities below 20‰ (Kuhlman and Quantz 1980; Nissling 2004). This means that the eggs of Baltic Sea turbot are demersal instead of pelagic. The ecological and evolutionary implications of this could be substantial.

3.4 Feeding of turbot and brill

Adult turbot and brill mainly feed on fish (Molander 1964; Arntz and Finger 1981; Curry-Lindahl 1985; Voigt 2002). Turbots have large mouths, compared to other flatfishes (Voigt 2002), thus allowing them to forage on macrofauna (>1mm) from the beginning of their benthic life (Kostrzewska-Szlakowska and Szlakowski 1990; Aarnio *et al.* 1996). Juvenile turbots less than or equal to 30 mm consume mainly amphipods, while >30 mm turbots also eats mysid shrimps and fish (Aarnio *et al.* 1996). The juvenile brill feeds to an equal amount of mysid shrimps, crangon shrimps and fish (Müller 1968).

Turbots and brill are, like all bothids, basically visual, daylight predators foraging on highly mobile prey (de Groot 1971; Arntz and Finger 1981; Holmes and Gibson 1983, 1986). They often leave the bottom to hunt in the open water column. Their feeding behaviour consists of agility, rapid pursuit and stealth of approach (Holmes and Gibson 1983). Turbots use a stalking tactic but rely more on their agility than their stealth. Brill on the other hand approach prey very slowly and perform typical stalking tactics (Holmes and Gibson 1983).

3.5 Growth of turbot and brill

In a laboratory experiment turbot eggs from the North Sea hatched at a mean size of 2.8 mm and larvae metamorphosed at a size of 23 mm after 68 days at a mean temperature of 16 °C (Jones 1972). In the same experiment, brill hatched at 3.8 mm and metamorphosed at 17 mm after 61 days at a mean temperature of 14 °C. Optimal growth temperature for turbot yolk sac larvae was 15 °C (Jones 1972) but for older fish from the North Sea optimum growth temperature is 19–20 °C (Jones *et al.* 1981). Accordingly, juvenile Atlantic turbot (size of 35–50 g) grow fastest at a temperature of 17–20 °C and growth rate is positively correlated to temperature (Burel *et al.* 1996). Larger juveniles (0.5 kg) have a remarkable homeostatic capacity and do not show any changes in metabolism between 16–20 °C (Mallekh and Lagardère 2002) or even between 8 to 20 °C (Burel *et al.* 1996). A comparison between the southern Baltic and the North Sea show that embryonic development is 10% faster in the latter at the same temperature, possibly as an affect of the higher salinity (Karås and Klingsheim 1997). There is an interaction between temperature and salinity so that although growth generally increase with increasing salinity, there can be an optimum temperature–salinity combination for growth at an intermediate salinity, as shown for Norwegian turbot in aquaculture (Imsland *et al.* 2001a). Growth rate differ among fishes from nearby localities. In a study from south west Norway juvenile turbots from two close localities had different growth rates when reared in laboratory (Imsland *et al.* 2001b). On the other hand, growth of juvenile turbot in the North sea seems to be the same in the 1980’s as in the beginning of the 1900’s (Van Leeuwen and Rijnsdorp 1986).

Growth curves of males and females diverge markedly from about age three and onwards, females growing larger than males (Molander 1964; Jones 1974; Fiskeriverket 2001, 2005b). The mean size of both turbot and brill are lower in the Baltic Sea than in the North Sea, and turbots are also slower growing in the northern compared to the southern Baltic Sea (Molander 1964; Bagenal 1966; Curry-Lindahl 1985; Stankus 2001). This is reflected in the values of the parameters of von Bertalanffys growth equation (Table 3). Maximum recorded age in the Baltic Sea is 21 years (Fiskeriverket 2005b).

Table 3. The von Bertalanffy growth parameters for turbot (*Psetta maxima*).

In fish the growth can be described by the von Bertalanffy growth function (Jobling 2002):
$L_t = L_\infty(1-e^{-k(t-t_0)})$ where L_t is length at age t, L_∞ is the asymptotic length the fish would have if it grew for infinity, k describes the instantaneous growth rate and t_0 is the theoretical age when the length is zero. The parameters in the von Bertalanffy function can also be derived using the difference in weight at one time (W_2, t_2) with that of an earlier time (W_1, t_1):

$\frac{\ln W_2 - \ln W_1}{t_2 - t_1} = -mk + mk L_\infty^{(1/L)}$ and the weight-length relationship instead of age: $W = cL^m$ where c and m are constants.

	North Sea		*Western Baltic Sea*		*Eastern Baltic Sea*			*Central Baltic Sea*
	Males	*Females*	*Males*	*Females*	*Males*	*Females*	*Females*	*Females*
L_∞ (cm)	49.2	64.8	34.0	48.3	35.0	53.5	55.0	59.1
W_∞ (kg)	2.4	5.1	–	–	0.78	3.5	–	–
K	0.37	0.26	0.31	0.11	0.30	0.19	0.122	0.06
t_0	0.51	0.05	-1.63	-5.42	0.35	0.28	-2.569	-7.11
reference	(Jones 1974)	(Jones 1974)	(Madsen 1989)	(Madsen 1989)	(Stankus 2001)	(Stankus 2001	(Draganik *et al* 2005)	(Florin *et al.* 2003)

4. Flounder (*Platichthys flesus*)

4.1 Fishery and abundance of flounder

Fishing for flounder is concentrated to the southern part of the Baltic Sea and is dominated by Poland, Denmark and Germany (Thoresson and Sandström 1998; ICES 2005a). Total landings were 17 000 tonnes in 2004 (ICES 2005a) (Figure 7) out of which the Swedish fleet contributed with 200 tonnes (Figure 8). Flounder is mainly caught as a by-catch in cod fishery (ICES 2005a). Fishing is regulated in EU with a minimum landing size of 25 cm in SD22–25 and a minimum mesh size of 120 mm in the Baltic Sea (ICES 2005a). There are additional national rules protecting the flounder during spawning time, and decreasing the minimum landing size to 18 cm and mesh size to 100 mm in the northern Baltic Sea (Table 2). In Skagerrak and Kattegat the minimum landing size is 20 cm and the minimum allowed mesh size is 100 mm. Flounder is subject to a similar national monitoring program as turbot following the extended version of the international monitoring program (EU council regulation 1639/2001).

Swedish fishing for flounder outside the Baltic proper is limited. In 1997 for example, Swedish fishery landed 42 tonnes in the Öresund strait and by-catches in Skagerrak and Kattegat amounted to 70 tonnes out of which 20 tonnes were caught near the coast (Lagenfelt and Svedäng 1999). In 2004 only 13 tonnes were landed in Kattegat and less than one tonne in Skagerrak according to Swedish fishermen’s log.

The stock in southern Baltic (SD24 and 25) was high in the beginning of the 1930’s with annual Swedish landings of 1 000 tonnes but then decreased to become relatively stable in the 1940’s and 1950’s with annual Swedish landings of 200 tonnes (Molander 1955a). Molander (1955a) speculated that, high fishing pressure had caused

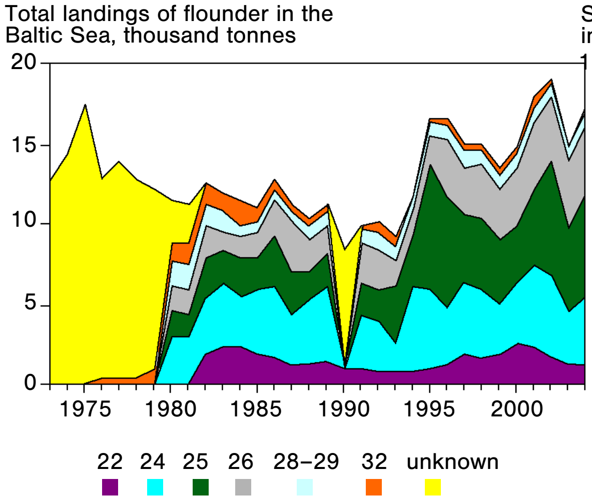


Figure 7. Total landings of flounder in ICES SD 22-32 during the years 1973-2004 according to the report of the Baltic fisheries assessment working group (ICES 2005a). In some years landings are not separated into subdivisions.

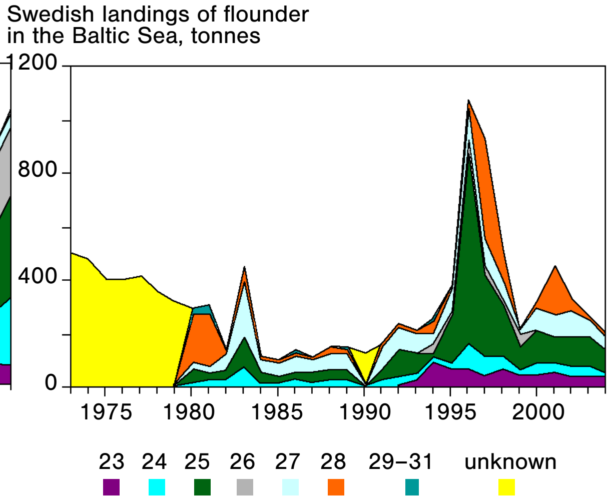


Figure 8. Swedish landings of flounder in ICES SD 22-32 during the years 1973-2004 according to the report of the Baltic fisheries assessment working group (ICES 2005a). In some years landings are not separated into subdivisions.

the decline but since then the low profit of flounder fishing made the fishing intensity balance the recruitment rate, reaching a balance between catches and production of fish. From the 1970's and onwards total landings from SD 24 and 25 varied between four and six thousand tonnes but increased in the middle of the 1990's to 11–13 000 tonnes, the latter increase probably inflated by the misreport of other flatfish as flounder during this period (ICES 2005c). The high level of landings continued, however, into the 2000's, suggesting a true increase of the stock. The stock in the southern Baltic Sea is judged by ICES to be stable since the beginning of the assessments in 1978 (ICES 2005c).

In the northern Baltic Sea the abundance of flounder has increased during the 1990's (Andersson *et al.* 1996; Andersson 1998). The flounder in the Gulf of Finland increased in 1976–1980 probably as a consequence of changed hydrological conditions, for example increased aeration and increased salinity of the homohaline layer, which caused flounder eggs to develop in the upper water layers in more favourable oxygen conditions (Ojaveer *et al.* 1985). High salinity itself also leads to higher fertilisation success and higher egg survival (Solemdal 1967, 1970; Nissling *et al.* 2002). The flounder in Estonian waters also increased in the late 1990's probably as an effect of better spawning conditions due to saltwater inflow (Drevs 1999).

Evaluation of the monitoring programs of SBF along the Swedish west coast 1980–1998 showed that the abundance of juvenile flounder varied greatly between years in some places while others gave low but stable catches (Lagenfelt and Svedäng 1999). The general opinion by SBF is that flounder stocks in the Baltic and the Öresund strait are stable, but the Kattegat stock probably is decreasing (Fiskeriverket 2005b). Furthermore, the individuals caught in Kattegat seem to be smaller in recent years, making the stock more vulnerable to exploitation (Fiskeriverket 2005b).

4.2 Population structure in flounder

4.2.1 General distribution

The flounder is distributed from Skagerrak far up into the Baltic Sea. It is less frequently observed north of the Sea of Åland and rarely north of the N. Quark. (Curry-Lindahl 1985; Bagge and Steffensen 1989; Fiskeriverket 1995; Muus *et al.* 1999; Voigt 2002). The flounder is a "borderline case" between being a warm or a cold-water species and the best catches are made at temperatures between 8–12 °C (Neumann 1979). The flounder mainly occurs on loose clay bottoms but also on sand bottoms. During summer it dwells above the thermocline (Molander 1964). Flounder migrates into less saline waters and closer to the shore in shallower water than other flatfishes (Molander 1964; Lagenfelt and Svedäng 1999; Voigt 2002). In Laholm Bay in Kattegat, Pihl (1989) found that 0-group flounder mainly occurred at 1.5–5 m depth and density decreased while length increased with depth. Metamorphosing post-larvae flounder often migrate to river estuaries and even far into main rivers during spring (Kerstan 1991; Moeller and Dieckwisch 1991; Robin 1991; Hutchinson and Hawkins 1993).

The flounder could be considered both a coastal species and a migratory species. Flounders in some coastal regions in the Baltic Sea are resident inside the belt of skerries during the whole lifecycle, while flounders in other regions migrate far out at sea during the adult stage (Neuman and Píriz 2000). In general, flounders feed in shallow waters and migrate to spawn in deep waters, except for the northern Baltic Sea stocks which also spawn in shallow water (Ehrenbaum 1909; Molander 1925, 1964; Ojaveer *et al.* 1985; Aro 1989). Molander (1923b) showed that flounders in southern Baltic moved out to deeper water (>40 m) in winter whereas flounder from the central Baltic Sea stayed at moderate depth (20–30 m). The length distribution changes with depth in such way that larger fish are found in deeper areas (Draganik and Kuczynski 1993).

4.2.2 Results from tagging studies

Tagging of adult flounders reveals that flounders in the Arcona basin move eastward in the autumn and westward in spring, but the migration is not so substantial and the probability for local populations is relatively high (Otterlind 1967). However, tagging experiments in the Askö area near Stockholm in the end of the 1960's and the beginning of the 1970's, showed that flounder disperse from the Stockholm area to Finland, and to the islands of Öland and Gotland (Aneer, G. and Westin, L. pers. com.). Tagging experiments in SD 22 and 23 (Bagge 1966; Bagge and Steffensen 1989) show that after spawning, flounders migrate to the nearest shallow water to feed. Three local stocks in SD 22 and one in SD 23 are identified. Further tagging studies in SD 24 and 25 indicate that each region support a distinct stock (Otterlind 1967). Tagging experiments in SD 26 and 28 (Cieglewicz 1947; Cieglewics 1961, 1963; Otterlind 1967; Vitinš 1972; Bagge and Steffensen 1989) lead to the conclusion that there are two stocks in each subdivision. The Gotland basin, with low oxygen content, seems to prevent flounder from crossing over and acts as east–west boundary (Aro 1989; Bagge and Steffensen 1989). It is unclear if SD27 supports one (Aro 1989) or two (Bagge and Steffensen 1989) stocks of flounder. Tagging experiments in SD 29, 30 and 32 (reviewed in Aro 1989) suggest that there is one stock of flounder in SD29 and 30 and a separate stock in SD 32. Ojaveer et al. (1985) further speculates that flounders in SD32 are divided into two stocks – one along the Finnish coast and one along the coast of Estonia. This gives in total 15 potential stocks of flounder in the Baltic Sea. It remains, however to discern if these are true biological, genetically different, stocks or "merely" harvest stocks (see the introduction).

4.2.3 Genetic variation

According to allozyme frequencies, the European flounder stocks in the Atlantic and North Sea are similar (subsp. *flesus*) although they differ from flounders in the Adriatic Sea (subsp. *italicus*) or Black Sea (subsp. *luscus*) (Galleguillos and Ward 1982). Diagnostic loci, as well as morphological comparisons using number of fin rays and different body ratios, can be used to differentiate between these subspecies (Galleguillos and Ward 1982). A more extensive study of allozyme variation in flounders from the Baltic Sea, the British Isles, Portugal, western Mediterranean, Adriatic Sea and Japan, showed that there was no genetic differentiation within regions, but fixed differences between regions (Borsa *et al.* 1997).

4.3 Reproduction of flounder

Flounder spawns between February and April in the North Sea, Skagerrak and Kattegat. In the Baltic, spawning is delayed eastwards and northwards so that around Gotland spawning takes place in April–June and in the Gulf of Finland in May–June (Molander 1964; Curry-Lindahl 1985). In the northern Baltic the eggs develop at the bottom while the larvae are pelagic during early summer (Sandman 1906; Mielck 1926; Mielck and Künne 1932; Solemdal 1971; Lönning and Solemdal 1979; Bonsdorff and Norkko 1994; Andersson 1998).

Flounders transferred from high (34.5‰) to low (6.5‰) salinity before spawning develop larger eggs with lower specific gravity (i.e. the ratio of the egg mass to the mass of an equal volume of distilled water at 4°C) (Solemdal 1967, 1971, 1973). Compared to eggs from wild flounders in low salinity areas, however, the experimental change is small (Solemdal 1967, 1971, 1973). The maximum size of flounder eggs with the minimum specific gravity is found in waters of 10–12‰ salinity. This indicates that eggs cannot be buoyant in water of lower salinity. Supporting this conclusion, Mielck (1926) found no floating flounder eggs above 40 m depth to the north and west of Bornholm, not above 50 m in the deep of the Bornholm Basin, and not above 100 m in the deep area in Danzig and east of Gotland. This corresponds to a 10–11‰ isohaline. For flounder in SD 24–25 the appropriate habitat for successful reproduction has a minimum salinity of approximately 12‰ and minimum oxygen concentration of two ml·l^{-1} (ICES 2005c). This means that the recruitment success fluctuates depending on the hydrological conditions on the spawning ground.

Reproductive populations of flounders do, however, exist also on shallow central banks and in eastern part of the Baltic with water of only 5–7‰ salinity. Eggs from these areas are smaller and heavier and they instead develop at the bottom (Mielck 1926; Solemdal 1967; Lönning and Solemdal 1979). Presumably, selection has favoured tougher, heavier, eggs that are better to resist mechanical forces acting at the bottom (Solemdal 1967, 1971). The reproductive success of the demersal spawning flounder could be questioned, however. In marine teleosts low salinity can be a problem for successful reproduction. Low salinity immobilise sperm, rendering many of the eggs unfertilised and also diminish egg survival (Holliday 1969; Nissling *et al.* 2002). According to Molander (1964) only about one third of the demersal eggs will develop, and in the extensive egg trawling survey by Mielck (1926) no eggs in later developmental stages were found on the bottom. There could also be a problem with low oxygen levels at the bottom (Muus *et al.* 1999), however, also pelagic eggs are subjected to oxygen deficiency at deeper areas.

The existence of two separate reproductive patterns in the Baltic is further supported by Mielck (1926) and Mielck & Künne (1932) who caught ripe females at a bank with 6–7‰ salinity. Some of the females had normal, small "bank" type of eggs, but also a few were found with large "deep" eggs. It is uncertain if individual flounders can change spawning behaviour and type of eggs between years, or if it is truly two different, genetically distinct, stocks of flounders. Transferring experiments suggest, however, that flounder, like cod, have distinct populations with distinct egg-properties and a limited ability to adapt egg-properties to new salinity (Solemdal 1971, 1973; Thorsen *et al.* 1996; Nissling and Westin 1997; Nissling *et al.* 2002). The demersal spawning flounder, presumably constituting one distinct stock with respect to salinity requirements for reproduction, may spawn successfully as far north as the southern Gulf of Bothnia and the Gulf of Finland (Nissling *et al.* 2002). For pelagic spawning flounder, salinity of neutral egg buoyancy suggests that successful spawning can take place in three separate areas: the Öresund strait (SD23), the Arcona (SD24) and the Bornholm basin (SD25) (Nissling *et al.* 2002).

The size at maturity in the Southern Baltic increased from 1920's to the 1950's. In 1919 it was 13–15 cm for males but in 1949 spawning males had a mean length of 19–20 cm (Molander 1955b). Likewise, in 1930's females were spawning at a length of 22 cm but in 1949 the size at maturity had increased one cm (Molander 1955b). The age at spawning (3 years) had not changed, however. In more recent years, 1978–2003, the age at maturity is estimated to be between two and three years in SD 24 and 25 (ICES 2005a). In Muus *et al.* (1999) the size at maturity is stated to be 20–25 cm for males and 25–30 cm for females. The increase in size at maturity is most probably an effect of the increased growth (discussed below).

4.4 Feeding of flounder

Adult flounder mainly feeds on crustaceans, bristle worms (polychaetes) and mussels (Molander 1964; Zalachowski *et al.* 1975; Arntz 1978; Karlson 2005). The most intensive feeding occurs in the summer while food is sparse in the winter (Mulicki 1947). Investigations from the Kiel bay (Arntz 1978) and Gdansk bay (Mulicki 1947) suggest that they do not feed during spawning.

Juvenile flounder (0-group and 1-group) feed mainly on polychaetes (in particular *Nereis diversicolor*), amphipods (mainly *Bathyporeia pilosa*) and crustaceans (*Gammarus spp.*), while molluscs are of minor importance in the southern Baltic (Kostrzewska-Szlakowska and Szlakowski 1990). In Kattegat, however, molluscs (mainly *Mya arenaria* and *Cardium spp.*) are important food items for juveniles in the nursery areas (Pihl 1982).

Diet preferences shift as a function of fish size (Mulicki 1947; Pihl 1985; Kostrzewska-Szlakowska and Szlakowski 1990). Aarnio et al. (1996) found that in the Åland archipelago flounder less than or equal to 45 mm mainly consumed meiofauna (animals of 0.1–1 mm size) (dominating taxa: *Harpacticoida*, *Copepoda*) while larger fish (46–101 mm) consumed macrofauna (dominating taxa: *Oligochaeta*, *Amphipoda* and *Chironomidae*). Studies from the Gdansk Bay (Mulicki 1947) showed that during the first year flounder fed mainly on crustaceans, polychaetes and diatoms (algae) and in summer also on chironomus larvae but as they grew there was an increase of the mollusc *Macoma baltica* and the crustacean *Mesidotea etomon* in the diet. Fish of intermediate length (14–17 cm) had the greatest variety of food items (27 animal species) and the less empty stomachs indicating that this is the group of most voracious flounders, not too selective about their food choice, which find food even on spots with poor feeding conditions (Mulicki 1947).

Recent studies in the Gdansk Bay (Karlson 2005) confirm the importance of *Macoma baltica* for both juvenile and adult flounders.

Juvenile *P. flesus* is an important epibenthic predator on shallow sandy bottoms, playing an important role in structuring benthic infaunal communities by both lethal and sublethal (siphon cropping) predation (Pihl 1985; Tallqvist *et al.* 1999). The distributions of algal mats can, however, reduce the efficiency of flounder to catch prey (Aarnio and Mattila 2000; Tarpgaard *et al.* 2005).

4.5 Growth of flounder

Flounder is a good example of the increasing growth in length and especially in weight with increasing salinity (Molander 1964; Sager and Berner 1989; Drevs *et al.* 1999). Growth also increases with temperature and in a laboratory experiment 0-group flounder from the North Sea had optimum growth at a temperature of 20 °C (Fonds *et al.* 1992).

Males are smaller than females and more numerous in the younger age classes, but they have a shorter lifespan and are under-represented among the older age-classes (Molander 1938, 1964). The size of flounders seems to be negatively affected by high population density (Molander 1938) and as a possible consequence of intensive fishing reducing flounder density the mean size of flounders increased drastically in the southern Baltic Sea in the first half of the 20th century. In 1919 the mean size of a 5-year-old flounder was 20 cm while the mean size in 1937 was 31 cm (Molander 1938, 1964). Age distribution also changed during the 1920–1950 period so that there were fewer older fishes in the 1950's (Molander 1955b). In the 1980's, however, the mean size of a five year old flounder is stated to be 26 cm in the Southern Baltic (Curry-Lindahl 1985) indicating that the mean length have decreased again. However, it is risky to compare age data from different sources since results of age-determination are strongly dependent on both the method and the determinator (Beamish and McFarlane 1983; Van Leeuwen and Rijnsdorp 1986; Söderberg 2003; CFÅ 2005).

5. Plaice (*Pleuronectes platessa*)

5.1 Fishery and abundance of plaice

Fishing for plaice mainly takes plaice in Kattegat, Skagerrak and the westernmost part of the Baltic Sea, and more than 90% are taken in the Danish fishery (ICES 2005a–b). Fishing is mainly carried out with bottom trawls and gillnets and occasionally the Danish seine is used (Lagenfelt and Svedäng 1999). The minimum landing sizes ranges from 27 cm in Skagerrak and Kattegat to 18 cm in the Sea of Åland and plaice is also protected during spawning time (Table 2). Within EU, the fishery is regulated with a yearly total allowable catch (TAC) that is decided by the European commission in negotiation with Norway and Russia. In 2005 TAC for plaice is 7 600 tonnes in Skagerrak, 1900 tonnes in Kattegat and 3766 tonnes in the Baltic Sea. The Swedish share of this is 317 tonnes in Skagerrak, 190 tonnes in Kattegat and 203 tonnes in the Baltic Sea.

In the early 1920's an intensive fishery for plaice in the Arcona and Bornholm basins started and in the 1930's the plaice stock was severely depleted in the southern Baltic Sea (Molander 1955a). During World War II fishing was limited and the stock recovered although the surplus was soon harvested at the end of the war. The thinning out of the stock was counteracted by the extremely rapid growth of the remaining plaice and by the contribution from relatively strong year classes (Molander 1955a; Bannister 1978).

Comparisons of trawl surveys between 1953–65 and 1982–85 in SD 22 show that the abundance of plaice continued to decrease in the Baltic Sea (Bagge and Nielsen 1986). This is also reflected in the constantly decreasing landings of plaice since the 1960's (Steffensen and Bagge 1990). Danish landings, which amounts to 95% of the total landings in SD 22, decreased from 4 000 tonnes in 1978 to 600 tonnes in 1986 (Bagge and Nielsen 1989) and 100 tonnes in 1989 (ICES 2005a). Plaice spawning stock biomass (SSB) decreased as well, from 5 000 tonnes in 1970's to 1 000 tonnes in 1980's (Bagge *et al.* 1990). This is a result of low recruitment possibly due to the increasing amounts of filamentous algae hindering settlement (Bagge *et al.* 1990; Pihl 2001). From the early 1990's landings increased and are above 1 000 tonnes since 1999 (ICES 2005a). In 2004 total landings of plaice in the Baltic Sea were 1 800 tonnes out of which Sweden landed 78 tonnes (ICES 2005a) (Figure 9 and 10).

In the 1970's total landings in Kattegat and Skagerrak each amounted to 10 000 tonnes whereof Danish landings accounted for > 90% whereas Swedish landings were only 300 and 100 tonnes, respectively (ICES 2005b). Thereafter landings decreased and since the beginning of the 1990's total yearly landings are around 2 000 tonnes in Kattegat and 7 000 in Skagerrak (ICES 2005b) (Figure 11). In 1997 500 tonnes of plaice was harvested by Sweden in Skagerrak and Kattegat out of which 130 tonnes were caught within the four nautical mile limit (Lagenfelt and Svedäng 1999).

The recruitment variability is reflected in the variation in year class strength of plaice in southern Baltic Sea (Molander 1955a; Bannister 1978). However, abundance of plaice in the southern Baltic Sea is also believed to be dependent on migration of plaice from Kattegat (ICES 2005c). Based on meristic characters and the correlation of abundance of 0-group plaice and wind data, a good year class in Kattegat in its turn seems to depend on input from Skagerrak (Bagge and Nielsen 1993; Nielsen *et al.* 1998). On the other hand, an examination of female maturity in bottom trawl surveys in February 1990 to 1992 (Ulmestrand 1992), indicated

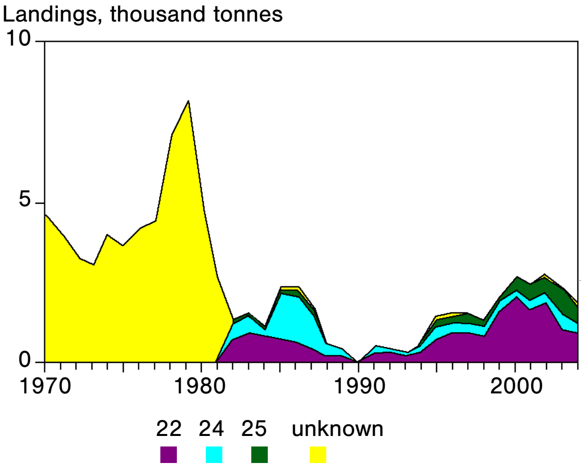


Figure 9. Total landings of plaice in ICES SD 22–32 during the years 1970-2004 according to the report of the Baltic fisheries assessment working group (ICES 2005a). In some years landings are not separated into subdivisions.

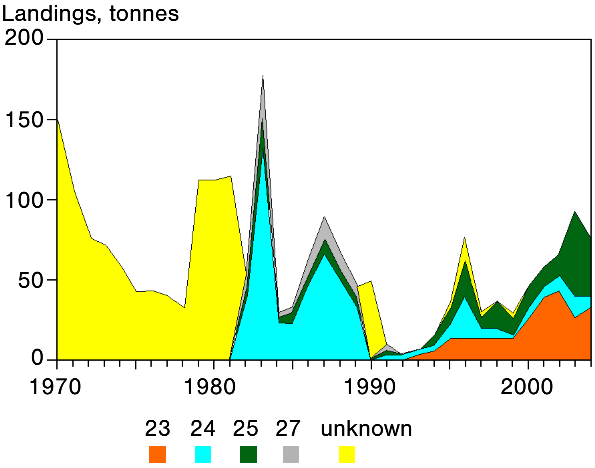
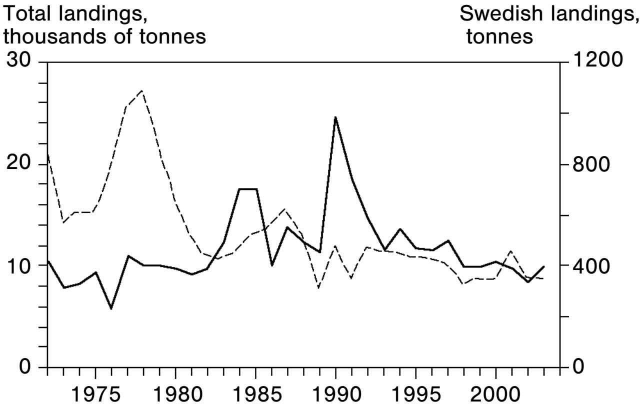


Figure 10. Swedish landings of plaice in ICES SD 22–32 during the years 1970-2004 according to the report of the Baltic fisheries assessment working group (ICES 2005a). In some years landings are not separated into subdivisions.

Figure 11. Total and Swedish landings of plaice in Div. IIIa (Skagerrak and Kattegat) during the years 1972–2003 according to the report on the assessment of Demersal Stocks in the North Sea and Skagerrak (ICES 2005b).



that Skagerrak and Kattegat were insignificant as spawning areas for plaice. Instead, Ulmestrand (1992) suggested recruits of plaice in the Skagerrak and the major parts in the Kattegat originate from parental plaice stocks in the North Sea. However, Nielsen *et al* (2004a) discovered the existence of at least one main spawning area in southern Kattegat, although only areas of less importance was found in northern coastal Kattegat.

Plaice in Kattegat decreased during the 1980's from a large SSB in 1978 (27 000 tonnes) to only 1 700 tonnes in 1989 (Bagge *et al.* 1990). This happened in spite of a decreased fishing mortality (F=0.3 in late 1980's compared to F=0.6 in the 1970's). The reason is assumed to be poor recruitment (Bagge *et al.* 1990). Furthermore, there was a decrease in length composition from 1981 to 1992 (Ulmestrand 1992), continuing to 2000 (Nielsen *et al.* 2004a), probably as a result of a decreased amount of older age groups. This change in age composition could have caused the decline in the Kattegat population since reproductive success is lower for first-time spawners than for older fish (Rijnsdorp *et al.* 1991). In the late 1990's, however, research surveys of 0-group plaice in the Skagerrak, Kattegat and the Öresund strait showed a stable occurrence of juvenile fish (Lagenfelt and Svedäng 1999). The recruitment in 1998 and 1999 were unusually high, and SSB in Skagerrak and Kattegat jointly were estimated to be close to 50 000 ton in 2004 (ICES 2004). Nevertheless, the stock is at risk of being harvested unsustainably since fishing mortality is above the recommended level (ICES 2004; Fiskeriverket 2005b).

5.2 Population structure in plaice

5.2.1 General distribution

Plaice is mainly found in the North Sea, Skagerrak and Kattegat area but it is also common in the western and southern Baltic Sea (Molander 1964; Fiskeriverket 1995; Neuman and Píriz 2000). Plaice is a cold adapted species and a laboratory study on metabolism of Atlantic 0-group plaice showed that plaice was adapted to 5–10 °C with an upper limit of 20 °C (Edwards *et al.* 1969). In the Northeast Atlantic metamorphosing plaice larvae settle in sheltered, shallow (<1m) bays in March–May, and migrate to deeper water in August–December (Modin *et al.* 1996). In Laholm Bay in Kattegat, Pihl (1989) showed that juvenile plaice mainly occurred above five meters depth and that density decreased while length increased with depth. With increasing age, plaice move to deeper areas, usually less than 100 m depth, where it will spawn (Molander 1928; Fiskeriverket 1995).

Feeding migration occurs from deeper spawning grounds to more shallow areas (Aro 1989). In the North Sea, plaice migrate from northern feeding grounds to more southern spawning areas by selective use of tidal currents (Harden Jones *et al.* 1979; Hunter *et al.* 2004). In the Baltic Sea, however, tidal currents are most probably too weak to be of use for migration.

5.2.2 Morphology

Meristic characters, like number of vertebrae or number of anal fin rays, differ in plaice from different locations (Mielck 1929; Poulsen 1938; Devold 1942; Molander and Molander-Swedmark 1957; Bagge *et al.* 1990; Bagge and Nielsen 1993). Based on meristic characters Poulsen (1938) identified three stocks of plaice in the Northeast Atlantic: one Atlantic stock in the North Sea, a true Baltic stock in SD24 and 25 and a Belt stock in SD22. Furthermore, Skagerrak and Kattegat are considered to have separate stocks of plaice. The Skagerrak stock has a high number of anal fin-rays (>56) while the Belt Sea stock has a low number (<54) of anal fin-rays (Bagge and Nielsen 1993). Meristic characters of newly settled plaice in the Kattegat show that Skagerrak input dominate the northern Kattegat while Belt Sea immigration influence the southern part (Bagge *et al.* 1990). There also seem to be a local Kattegat component in the centre of Kattegat, with an intermediate number of anal fin rays (Bagge and Nielsen 1993). However, the use of morphological characters to differentiate between stocks can be questioned. For example, the number of vertebrae in plaice along the outer Norwegian coast change gradually and the variation in anal fin rays in the Trondheim Fjord stock must be of environmental and not genetic origin (Devold 1942). However, experiment by Molander & Molander (1957) showed that although offspring of the “Atlantic form” reared under different temperatures (6–10 °C) varied in meristic characters, the variance was still distinct from that of the “Baltic form”. This supports the existence of genetic differences apart from environmental factors as a cause of morphological differentiation.

5.2.3 Tagging experiments

Tagging studies by Blegvad (1934) and Otterlind (1967) suggest that there is only one stock in SD24 and 25, and that this is separated from the stock in SD22. Tagged adult plaice, recaptured at a rate of 35%, showed an intensive east–west migration within the Baltic proper (Otterlind 1967). In November to January the fish migrated from the Arcona basin eastwards – in spring the direction was the opposite. During spring fish also migrated towards coastal areas while they moved towards deeper oceans during autumn. Some places, however, seemed to harbour more stationary plaice (Otterlind 1967). In autumn 1987, over 2000 plaice, ranging between 17–28 cm, was transplanted from Kattegat to Skagerrak (Ulmestrand 1989). During the following year two percent were recaptured showing a southwestern migration towards the North Sea. This could possibly be a spawning migration.

In a tagging experiment, adult plaice transplanted from the North Sea to the Kattegat showed northwards migration (Staehr and Stoettrup 1991). This homing behaviour, earlier suggested by de Veen (1978a), was confirmed by Hunter *et al.* (2003). Spawning and feeding area fidelity is also demonstrated in Icelandic plaice (Solmundsson *et al.* 2004). In addition, juvenile plaice transplanted along the shore of south-west Scotland, show clear homing behaviour (Burrows *et al.* 2004). Despite the apparent spawning area fidelity, the same fish can visit more than one spawning area within one season (Metcalf and Arnold 1997). Furthermore, electronic tagging studies revealed that plaice in the North Sea split into three discrete subpopulations during the non-breeding season, but mix in two populations during spawning time (Hunter *et al.* 2004).

5. 2. 4 Genetic variation

Microsatellite investigations in plaice from the north Atlantic differentiate between the Icelandic stock and plaice from the Eurasian continental shelf, suggesting a deep-water barrier to dispersal (Hoarau *et al.* 2002). However, there was no differentiation within the continental shelf populations themselves. This suggests that the apparent regional stocks in fact are composed of several genetic stocks in panmixia on the spawning grounds, exactly what Hunter *et al.* (2004) found in their tagging studies (see the section above). Using mitochondrial DNA, Hoarau *et al* (2004) confirmed the difference between shelf and offshore samples and also detected a North Sea–Irish group distinguishable from the Norway, Belt Sea and Bay of Biscay samples.

Genetic analysis of plaice from the North Sea and Iceland during the 1900´s reveal that plaice from after 1970 show evidence of inbreeding and that effective population size is five times smaller than cencus size (Hoarau *et al.* 2005). The emergence of inbreeding coincides with the increase in fishing mortality after World War II.

5. 3 Reproduction of plaice

Tagging experiments in the fjords of Bohuslän in western Sweden have shown that large, mature individuals migrate to the sea to spawn at an age of four years, while young, immature individuals find their way into the fjords, possibly to feed (Molander 1923a, 1928). Females mature at 2–4 years age in the Baltic, and as for most flatfishes, males mature somewhat earlier (Curry-Lindahl 1985). In the north Atlantic age at maturity are for males (3–6 years) and for females (4–7 years) (Devold 1942). Size at maturity is 20–25 cm for males, and 30–35 cm for females (Muus *et al.* 1999). Plaice spawn during winter, December–February in the Baltic Sea and January–April in the North Sea (Curry-Lindahl 1985), at a depth of 30–40 m (Nielsen *et al.* 2004a). In the Baltic Sea successful spawning occurs regularly in the deeper parts of the Arcona (SD24) and Bornholm (SD25) basins, and occasionally during favourable salt-water inflow, in the Gdansk (SD26) and Gotland (SD28) basins (Nissling *et al.* 2002).

5.4 Feeding of plaice

Plaice is a visual feeder taking mostly slow-moving bottom living food, but also more active prey (Holmes and Gibson 1983). It shuffles with frequent pauses to scan for prey. When prey is located, the fish moves forward cautiously to bring its head down upon its prey (Holmes and Gibson 1983). Adult plaice feeds mainly on benthic fauna like bristle worms and molluscs (Arntz and Finger 1981) but also small fish like sand lances (*Ammodytes* sp.) are eaten (Fiskeriverket 1995; Hoeines and Bergstad 2002). Plaice show a clear seasonal pattern with more feeding in the summer and autumn, and less feeding in the winter (Arntz and Finger 1981). In the North Sea, 0-group plaice at nursery areas eats polychaetes, crustaceans and siphons of molluscs (Müller 1968; Thijssen *et al.* 1974; Pihl 1985; Amara *et al.* 2001). In the Baltic the diet of juveniles mainly consists of polychaetes and oligochaetes (Müller 1968).

5.5 Growth of plaice

The length at metamorphosis (10–17 mm) is less variable than age at metamorphosis (8–12 weeks with an average age of 68.5 days) (Modin *et al.* 1996). Differences in timing of settling in combination with differences in water temperature result in a wide range of mean lengths (30 to 78 mm) at the end of August in various areas in northwestern Europe (van der Veer *et al.* 1990). Optimal growth of 0-group plaice from the North Sea is at a temperature of 18 °C (Fonds *et al.* 1992).

In newly settled plaice growth rates show negative, and mortality rates positive, density-dependent relationships with plaice density on the Swedish west coast (Pihl *et al.* 2000). Among females growth during the first year is related to size 1.5–2.5 years later (Modin 2000), and since size is related to fecundity early growth can have large effects on the future fitness of females. However, investigations in the Dutch Wadden Sea on 0-group plaice, showed that difference in growth rate do not necessarily originate from competition for food and density-dependent growth. It could equally well be explained by differences in food composition and availability (Van der Veer and Witte 1993).

Annual growth of plaice in the southern Baltic Sea increased strongly during the years 1919–1951; presumably as a result of the thinning of the stock due to the development of more efficient fishing methods in the 1920's (Molander 1955b). The maximum length, 50 cm, has not been exceeded however. Age distribution also changed, resulting in fewer older fishes in the 1950's (Molander 1955b).

After a slight decrease in the 1970's, growth of plaice in the Belt Sea increased dramatically in the 1980's (Bagge *et al.* 1990). The increase in growth is believed to be caused by an increasing number of the mollusc *Abra alba* on which both plaice and dab feed. No relationship between density and growth were found (Bagge and Nielsen 1989).

In the North Sea somatic growth of juvenile plaice increased between the 1950's and the 1980's, probably as a response to an increase in food availability (Bannister 1978; Bagge and Nielsen 1986). In fact, there was a positive effect of both eutrophication and beam trawling (two processes affecting availability of benthic food) on the growth rate of juveniles (Rijnsdorp and Van Leeuwen 1996). Furthermore, back-calculated growth rate in archaeological otolith samples revealed that for juvenile plaice pre-industrial (before the 19th century) growth rate was similar to growth rate in the 1930's but well below present day (1970's and 1990's) growth rate (Bolle *et al.* 2004). This suggests that the observed increase in growth is not due to the decreased density caused by the onset of industrial fishery. The intensive fishery may have had other consequences though. Since the 1950´s the size at maturity has decreased as a possible effect of fisheries selecting against individuals who postpone maturation (Rijnsdorp 1993). This is the first indication that fisheries have led to genetic changes in life-history traits in a fish stock. The evolutionary changes in maturation during the last half of the 20th century where further confirmed by Grift *et al* (2003).

The annual growth of plaice in Kattegat has decreased during the 1980's (Bagge *et al.* 1990). The decreased growth could be due to low oxygen levels, which may affect composition of the benthic fauna as well as changing the metabolism, and reduce consumption. There was also a change towards earlier maturation from the 1990's to the 2000's (Nielsen *et al.* 2004a).

6. Sole (*Solea solea*)

6.1 Fishery and abundance of sole

Sole is mainly caught in Kattegat using crayfish- or fish-trawl during summer, but also special sole gill nets are used (Lagenfelt and Svedäng 1999; Sjöstrand 1999). In Skagerrak and Kattegat the minimum landing size is 24 cm and the minimum allowed mesh size is 100 mm (Table 2). Sole, like plaice, is regulated by TAC's. In 2005, TAC for Skagerrak and Kattegat jointly is 520 tonnes whereof the Swedish share is 16 tonnes. There is no restriction on catch in the Baltic Sea. Denmark is totally dominating with 95% of the fishing in Skagerrak and Kattegat. The stock was harvested with a total of 250–450 tonnes annually for 35 years before the strong year classes 1989–93 when international harvest averaged 1 000–1 400 tonnes (Sjöstrand 1999; ICES 2005a) (Figure 12). Since 1994, catches decreased and the total catch in 2004 was barely 400 tonnes (ICES 2005a). The Swedish fishery accounts for only a small proportion of the total catch. In 1997, 48 tonnes was landed by Swedish vessels in Kattegat out of which 20 tonnes was landed by the coastal fisheries (Lagenfelt and Svedäng 1999). In 2004 the total Swedish landings reported by fishermen's log was only 15 tonnes out of which 130 kg was caught in the Baltic Sea.

Sole abundance increased during the 1980's in Kattegat and recruitment increased from 1960's to late 1980's with a factor of seven (Bagge *et al.* 1990). After 1995 the stock diminished but it is still judged to be harvested sustainable with a spawning stock biomass above 4 000 tonnes in 2004 (ICES 2005c). A drastic increase was also seen in the North Sea where the stock increased threefold during the last half of the 20th century (de Veen 1978b; Millner and Whiting 1996).

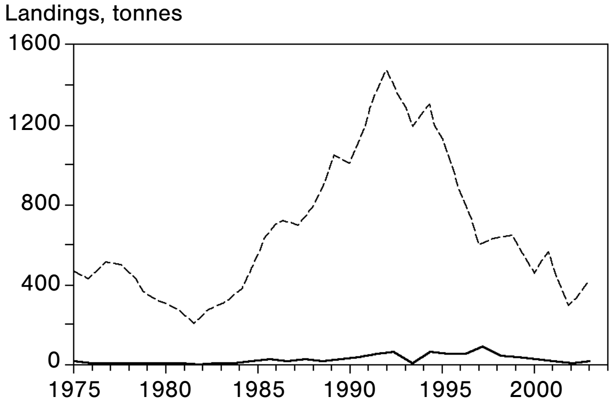


Figure 12. Total and Swedish landings of sole in Skagerrak and Kattegat during the years 1975–2004 according to the report of the Baltic fisheries assessment working group (ICES 2005a).

6.2 Population structure in sole

6.2.1 General distribution

Sole occurs regularly in the Skagerrak and Kattegat areas and occasionally also in the western parts of the Baltic Sea (Molander 1964; Muus *et al.* 1999). Catches of young fish in SBF's monitoring fishing in Kattegat varies with a mean factor of two between years (Lagenfelt and Svedäng 1999). In the Öresund strait the species occurs at low density with a small variation between years (Lagenfelt and Svedäng 1999). During autumn and winter, sole stays in deep water but migrates to shallower waters in early summer to spawn (Fiskeriverket 1995). In Laholm Bay in Kattegat, Pihl (1989) found juvenile sole mainly at 0–5 m depth and density decreased whereas fish length increased with depth.

6.2.2 Genetic variation

Kotulas *et al* (1995) investigated the genetic structure of sole at several spatial and temporal levels using allozymes (Kotoulas *et al.* 1995). They collected flatfish between 1981 and 1986 on the following successive spatial scales: geographic regions (biogeographical scale, thousands of kilometres apart: North East Atlantic, Western and Eastern Mediterranean), zones within each region (regional scale, hundreds of kilometres;) and localities within zones (intrazone scale, tens of kilometres;). They discovered no differentiation at the temporal scale, some differentiation at the regional scale in Eastern Mediterranean, and clear differentiation between biogeographical regions. Furthermore, there was an isolation-by-distance pattern (significant correlation between genetic and geographic distances). The analysis suggested that the geographic unit of population structure (*i.e.* a geographical area corresponding to a panmictic or nearly panmictic population) lies within a radius of the order of 100 km (Kotoulas *et al.* 1995).

6.3 Reproduction of sole

Sole spawns at moderate depth in early summer (Molander 1964; Muus *et al.* 1999). It becomes sexually mature at an age of 3–5 years and a size of 25–30 cm (Molander 1964; Muus *et al.* 1999). In the time period 1957–1973 mean size as well as fecundity at age and length at maturity increased in the North Sea (de Veen 1978b).

6.4 Feeding of sole

Adult sole is a night active animal, feeding on thin-shelled mussels, bristle worms, small crustaceans, and to a lesser degree, fry of sand lances and gobies (*Gobiidae*) (Fiskeriverket 1995; Muus *et al.* 1999). Newly settled sole mainly feeds on copepods and when bigger than 50 mm, it switches to polychaetes (Amara *et al.* 2001). Soles use their small, elongated, protuberances (papillae) near the mouth to search for sessile or barely mobile organisms that are concealed in the substratum (Holmes and Gibson 1983). During daytime sole is often burrowed in the bottom substrata (Fiskeriverket 1995).

6.5 Growth of sole

Growth rate of sole in the North Sea increased during the last half of the 20th century (de Veen 1978b; Millner and Whiting 1996). Female sole growth rate was at it lowest directly after World War II, but increased during the 1960’s when the stock was small. Growth rate remains high today. The increased growth rate could be due to changes in temperature or lowered competition due to the thinning of the stock by fishing. The beam trawling in itself could also have favoured flatfishes that feed on benthic fauna that is uncovered and wounded by trawling (Millner and Whiting 1996). As a fourth reason, eutrophication, may have a positive effect on flatfish growth, since an increased amount of nutrients can lead to an increase in bottom fauna biomass (Cederwall and Elmgren 1990). In Kattegat, however, a decrease in growth is seen in the late 1980’s (Bagge *et al.* 1990).

7. Dab (*Pleuronectes limanda)*

7.1 Fishery and abundance of dab

In the Baltic Sea, the majority (95%) of landed dab come from by-catches in Danish and German cod fishery in SD 22 and to a lesser degree in SD 24 (ICES 2005a) (Figure 13). In Sweden, dab is caught to a minor degree in coastal fishing in Skagerrak, Kattegat and the Öresund strait (Lagenfelt and Svedäng 1999). According to Swedish fishermen's log, the yearly landings are nowadays only a few tonnes in Kattegat and even less in other areas (Figure 14). Mesh size and minimum landing sizes regulate the fishery (Table 2). The Danish landings of dab were constant from 1930 to1980 when they increased threefold. The catch per unit effort (CPUE) decreased in the 1960's, but was constant until 1980 when it increased threefold. CPUE was on a constant higher level in the period 1983–1991 compared to 1953–1963 (Steffensen and Bagge 1990; Bagge *et al*. 1994). Judging from the catch per unit effort, dab in Kattegat, as well as in SD22, increased in numbers from the 1980's (Bagge *et al.* 1990). The increase in stock is thought to be due to increased larval survival due to increased primary production (Bagge and Nielsen 1989). In the Baltic proper, landings increased during the beginning of the 20th century but since 1940's have been insignificant (Temming 1989a). The breakdown of the stock is speculated to depend on overfishing, predation by cod or hydrographical conditions and the increasing oxygen deficiency in the bottom water are assumed to prohibit a regeneration of the stock (Temming 1989a). The apparent drastic decrease in total landings of dab in the Baltic Sea from 3 000 tonnes in 1995 to 715 tonnes in 2002 might be an artefact due to misreporting in 1994–1996 (ICES 2005a). In 2004, total landings in the Baltic Sea is barely 2 000 tonnes whereof Swedish landings amount to 2 tonnes (ICES 2005a).

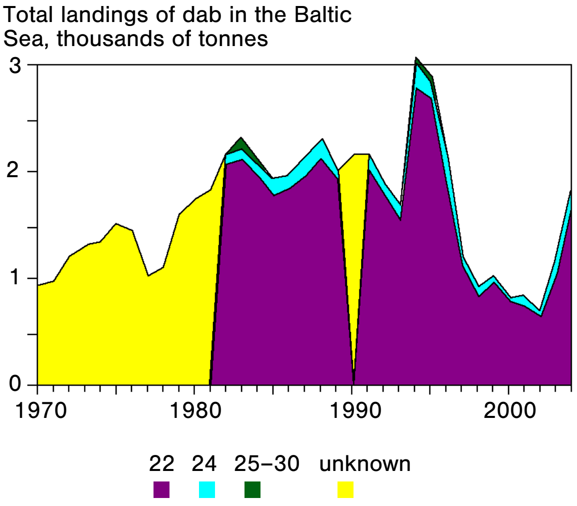


Figure 13. Total landings of dab in ICES SD 22–32 during the years 1970–2004 according to the report of the Baltic fisheries assessment working group (ICES 2005a). In some years landings are not separated into subdivisions.

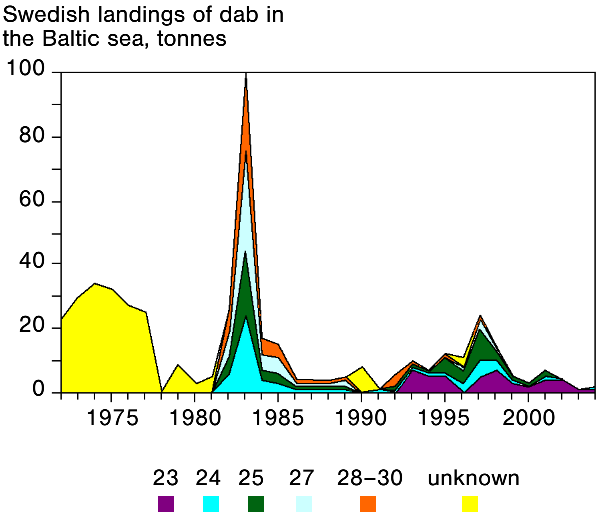


Figure 14. Swedish landings of dab in ICES SD 22–32 during the years 1972–2004 according to the report of the Baltic fisheries assessment working group (ICES 2005a). In some years landings are not separated into subdivisions.

7.2 Distribution and reproduction of dab

Apart from in Skagerrak and Kattegat dab mainly occurs in the southern part of the Baltic Sea (Lagenfelt and Svedäng 1999), but can be found all the way up to Gotland (Molander 1964). In Laholm Bay in Kattegat, Pihl (1989) found that juvenile dab dwell at 5–11m depths and that density increase while length decrease with depth. Dab has an extended spawning period from Feb.–May in Kattegat and March–June in SD22 (Molander 1964; Lagenfelt and Svedäng 1999).

Fecundity is related to age, older females of the same size have more eggs than younger ones (Bagenal 1966). By assessment of spermatozoa mobility, fertilisation and egg buoyancy, Nissling *et al.* (2002) studied the salinity requirements for egg development. The results suggested that there is one western and one eastern stock of dab in the Baltic Sea and that successful spawning may occur in the Öresund strait (SD 23), the Arcona basin (SD 24) and occasionally in the Bornholm basin (SD 25) (Nissling *et al.* 2002). Transferring of dab from high to low salinity show the same effect on eggs as flounder, i.e. increased size and lowered weight. However, dab do not tolerate the low salinity and mortality among transplanted females are high (Solemdal 1971).

In a study from 1988, the age structure was skewed towards larger and older individuals from Southeast to the Northwest Atlantic Sea, i.e. dab from Iceland were larger and older than dab from western Baltic, and dab from the North Sea was intermediate (Lozan 1988). Furthermore, the number of dorsal and anal fin rays was different in the Baltic–Kattegat compared to the North Sea, which in turn differed from the British Seas (Lozan 1988). Dab in the Bornholm basin are also different from dab in the Belt Sea area (Temming 1989b) .This suggests the existence of several separate stocks of dab.

Recent phylogenetic research have concluded that dab should be placed in a new separate genus, *Limanda*, both according to morphological (Cooper and Chapleau 1998) and molecular (Exadactylos and Thorpe 2001) characteristics.

7.3 Feeding and growth of dab

Adult dab on the Swedish west coast mainly feeds on crustaceans, mussels and bristle worms (Lagenfelt and Svedäng 1999). However, on a coastal bank off Norway sandeels were the dominant prey (Hoeines and Bergstad 2002). Small 0-group dab (<40 mm) consumes mainly polychaetes but later also amphipods and hydrozoans are eaten (Amara *et al.* 2001).

The dab is similar in initial growth when compared to the flounder, but its increase in length and weight soon decreases and thus it attains smaller final values (Molander 1964; Sager and Berner 1989). Like in most flatfishes, the length at age is greater for females than males (Bagge *et al.* 1995b). Trawl surveys carried out 1953–65 and 1982–85 in SD 22 showed that the growth increased with time (greater mean length at age) (Bagge and Nielsen 1986). This could be an effect of eutrophication, changing the bottom fauna towards increased amount of the mollusc A*bra alba* on which both plaice and dab feeds (Bagge and Nielsen 1986). Using commercial landing samples from 1962–1985 in SD 22, it was shown that growth was higher in the 1970's compared to the 1960's and 1980's (Bagge and Nielsen 1989). No relationship between density and growth was found (Bagge and Nielsen 1989). Mean length at age for dab in Århus Bay decreased in trawl surveys when the period 1954–1962 was compared with the period 1991–1994 (Bagge *et al.* 1994, 1995b). This was true for both males and females. The reduced growth in the 1990's is speculated to be caused by oxygen deficiency lowering the appetite (Bagge *et al.* 1995a).

8. Summary

There are about 600 flatfish species in the world out of which 25% are distributed in temperate waters. Fifteen of these occurs within the Skagerrak, Kattegat or Baltic Sea area and five occur regularly in the Baltic Sea. The distribution in the Baltic is limited by the decreasing salinity. The most tolerant species, the European flounder (*Platichthys flesus*), occur in the whole Baltic Sea although it is less frequently observed north of the Sea of Åland and rarely found north of the N. Quark. Turbot (*Psetta maxima*) is common up to the Sea of Åland while plaice (*Pleuronectes platessa*) and dab (*Pleuronectes limanda*) have their northern limit in the central Baltic Proper. Brill (*Scopthalmus rhombus*) and sole (*Solea solea*) rarely occur north of Bornholm.

8.1 Fishery and abundance

The growth of turbot males in the Baltic level out close to the minimum landing size of 30 cm, hence the fisheries land more females than males and the majority of discards are males. The main part of turbot fishery takes place in the southern and western part of the Baltic Sea within the Danish and German fisheries. The fishery directed towards turbot in central and eastern Baltic escalated in the early 1990's due to Polish, Russian and Swedish gillnet fishery. The main part of Swedish turbot fishery occurs in SD 25, 27 and 28. Since 1995, landings have decreased and the total landings amounted to 516 tonnes in 2004, whereof Sweden landed 26 tonnes. The strongly diminishing commercial catches despite high effort and a decrease of older females suggest an unsustainable fishing pressure.

Most brill is caught by Denmark in SD 22. In 2004, the total landings in the Baltic Sea were 41 tonnes wheras the Swedish landings are only a couple of hundred kilos. No assessment of the stock has been made.

Flounder is mainly caught as a by-catch in cod fishery in the southern part of the Baltic Sea dominated by Poland, Denmark and Germany. From the 1970's and onwards total landings from SD 24 and 25 varied between four and six thousand tonnes and was doubled in the middle of the 1990's. ICES judged the stock in the southern Baltic Sea to be stable since the beginning of the assessments in 1978. In the northern Baltic Sea the abundance of flounder increased during the 1990's probably as a consequence of better spawning conditions due to saltwater inflow. Total landings of flounder in the Baltic Sea were 17 000 tonnes in 2004 out of which the Swedish fleet contributed with 200 tonnes. The general opinion by SBF is that flounder stocks in the Baltic are stable at present while the Kattegat stock is decreasing. In addition, individuals caught in Kattegat seem to have become smaller in recent years, making the stock more vulnerable to exploitation.

Fishing for plaice mainly takes place in Kattegat, Skagerrak and the westernmost part of the Baltic Sea, and more than 90% are taken in the Danish fishery. In the early 1920's an intensive fishery for plaice started in SD24 and 25, and in the 1930's the plaice stock was severely depleted. During World War II fishing was restricted and the stock recovered although the surplus was soon harvested. The abundance of plaice continued to decrease in the Belt Sea. Danish landings decreased from 4 000 tonnes in 1978 to 600 tonnes in 1986 and 100 tonnes in 1989. From the early 1990's landings increased and in 2004 total landings of plaice in the Baltic Sea was 1 800 tonnes out of which Sweden landed 78 tonnes. Abundance of plaice in the southern Baltic Sea is believed to be dependent on immigration of plaice from Kattegat. Plaice in Kattegat decreased during the 1980's from a large stock spawning biomass of 27000 tonnes in 1978 to only 1 700 tonnes in 1989. Both ICES and SBF judge the stock in Kattegat and Skagerrak to be at risk of being harvested unsustainably since fishing mortality is above the recommended level. No assessment is presently being made in the Baltic.

Sole is mainly caught in Kattegat in Danish fishery. The stock was harvested with a total of 250–450 tonnes annually for 35 years before the strong year classes 1989–93 appeared and the yearly international harvest exceeded 1 000 tonnes. Since 1994, catches decreased and the total catch in 2004 was barely 400 tonnes. The same year total Swedish landings were only 15 tonnes out of which 130 kg was caught in the Baltic Sea. The stock is still judged by ICES to be harvested sustainable with a spawning stock biomass above 4 000 tonnes in 2004.

The majority (95%) of landed dab come from by-catches in Danish and German cod fishery in SD 22 and to a lesser degree in SD 24. In Sweden, dab is caught to a minor extent in coastal fishing in Skagerrak, Kattegat and the Öresund strait. The Danish landings of dab were constant from 1930 to1980 when they increased threefold as did the catch per unit effort. The increase is suggested to be an effect of an increased larval survival due to increased primary production. In 2004, total landings in the Baltic Sea is 2 000 tonnes whereof Swedish landings amount to 2 tonnes. No assessment has been made.

8.2 Population structure

Turbot, brill and sole perform short migrations to deeper water during autumn and winter, and returns to shallow waters in early summer to spawn. In contrast, flounders and plaice generally feed in shallow waters and migrate to spawn in deep waters, except for the northern Baltic Sea where stocks of flounder also spawn in shallow water. Flounders and plaice in the Arcona basin move eastward in the autumn and westward in spring. A homing behaviour has been detected in both plaice and turbot.

Tagging experiments suggest that there are up to 15 stocks of flounder in the Baltic: Three local stocks in ICES statistical subdivision (SD) 22, one in each of SD 23–25, 29 and 30 and two stocks in each of SD 26–28 and 32. However, it remains to discern if these are true biological, genetically different, stocks or merely harvest stocks. Based on meristic characters and tagging four stocks of plaice are identified: Baltic, Belt Sea, Kattegat and Skagerrak. For dab meristic characters, and the requirements for successful reproduction, suggest that there is one western and one eastern stock in the Baltic Sea.

The genetic studies hitherto show that although there are some genetic differences at a larger, biogegraphical scale, there is no genetic differentiation of turbot or flounder stocks within the Baltic Sea. In the North Sea, a genetic isolation-by-distance pattern is found in sole, while plaice on spawning grounds comprise a mix of several genetic stocks.

8.3 Reproduction and recruitment

Age at maturity is between 3–5 years and males mature earlier and at a smaller size than females. Fecundity is positively related to size and age and, measured as number of eggs in relation to body size, it is higher in the Baltic Sea compared to the North Sea. The size at maturity is, however, smaller in the Baltic Sea.

Three types of spawning behaviour can be detected among flatfishes in the Baltic Sea: Plaice and dab spawn only in the relatively saline water of the western Baltic and the deeper areas in the central Baltic (PSU ranging from 15–20). Flounder spawns with pelagic eggs in the more saline water of the western Baltic and the deeper areas in the Baltic Sea and have demersal eggs in the less saline shallower parts of the central Baltic Sea (PSU less than 10). Turbot spawns, apart from the western Baltic, only in the shallower parts of the central Baltic Proper where the eggs are demersal instead of pelagic.

Turbot, brill and sole spawns in the summer, flounder and dab in spring and plaice during winter. Spawning is delayed eastwards and northwards so that spawning in Kattegat is followed by spawning in the southern Baltic and lastly in the northern Baltic Proper.

Flatfish begin life as symmetric, pelagic fish larvae. The metamorphosing post-larvae migrate close to shore to settle at the bottom of shallow water. The magnitude of recruitment is mainly dependent on the transport of eggs and larvae to nursery areas and the quality of these areas for larval development. There can be a substantial variation in densities between years and localities. The mortality and growth rate are density dependent some years but environmental factors may uncouple this relationship in other years. Predation by shrimp and fish is suggested to be the main mortality factor. The formation of macroalgal mats could lead to a concentration of juveniles in the remaining habitats, resulting in an increased density dependent predation.

8.4 Feeding and growth

Turbot and brill are visual, daylight predators foraging primarily on fish. Flounder, dab and the night active sole, feed mainly on crustaceans, bristle worms and mussels. Plaice feed mostly on slow-moving bottom living food, like bristle worms and molluscs but also on small fish. Juvenile flatfish play an important role in structuring the benthic infaunal communities on shallow sandy bottoms, by both lethal and sublethal (siphon cropping) predation. The distributions of algal mats can, however, reduce the efficiency to catch prey.

In flatfish the growth differ between sexes; females growing faster and reaching a larger size than males. For flounder, plaice and turbot maximum recorded age by the Swedish Board of Fisheries in present stocks is just above 20 years. The mean sizes of flatfishes are generally lower in the Baltic Sea than in the North Sea, and they grow slower in the northern compared to the southern Baltic Sea.

Growth can be negatively affected by high population density due to intraspecific competition. As a possible consequence of intensive fishing thereby reducing fish density, mean size of flounders and plaice increased drastically in the southern Baltic Sea in the first half of the 20th century. Furthermore, growth rate of sole and plaice in the North Sea, and dab and plaice in the Belt Sea, increased during the last half of this century. However, pre-industrial growth rate in North Sea plaice was similar to growth rate in the 1930's, although well below present growth rate. This suggests that the observed increase in growth is not due to a decreased density caused by the onset of industrial fishery. Alternative explanations may be temperature changes or that beam trawling itself may favour flatfishes feeding on benthic fauna that is uncovered and wounded by trawling. Eutrophication may also have a positive effect on flatfish growth, since it can lead to an increase in bottom fauna biomass. In fact, the bottom fauna has, possibly due to eutrophication, changed towards increased amount of the mollusc *Abra alba* on which both plaice and dab feeds. In the last decades of the 1900's growth of plaice, sole and dab decreased in Kattegat.

Since the 1950's the size at maturity in plaice has decreased as a possible effect of fisheries selecting against individuals who postpone maturation. This is the first indication that fisheries have led to genetic changes in life-history traits in a fish stock.

9. Conclusions

The flatfishes in the Baltic Sea are important for both economic and ecological reasons. During the 20th century abundance has fluctuated markedly, and size and age structure has shifted, either as a consequence of intensive fishing or due to environmental changes. Eutrophication may have severe impact on flatfish through oxygen deficiency in deeper areas and increased occurrence of filamentous algae on nursery areas. However, the increased primary production may also be favourable if it results in increased food availability. A common pattern during the last century is the increased growth, probably as an effect of better food availability. However, it could also be an effect of decreased competition at lower densities. It is evident that fishery has induced evolutionary changes in important life history characteristics, suggesting that the evolutionary consequences need to be considered in future management plans.

Tagging and genetic analyses have revealed that several flatfish species are structured into several distinct spawning and feeding populations. Furthermore, it is evident that some flatfish species have adapted to the special conditions of low salinity in the Baltic. This knowledge will provide information at which geographic scale management is best executed and also how to avoid loss of local adaptations.

Another example of biological knowledge that is relevant for management is the considerable difference in size between sexes that is common among flatfishes. This size difference has consequences for the effect of fishing on a stock and the effect of management decisions.

Nursery habitats in shallow coastal areas are highly important for flatfish recruitment and juvenile flatfishes are important structuring predators in these habitats. This should be considered in coastal zone management.

Acknowledgement

Thank is due to Johan Modin, Gunnar Aneer, Anders Nissling, Magnus Appelberg, Teija Aho and Alfred Sandström for valuable comments on earlier drafts of this report. I would also like to thank Wolf Arntz, Anders Nissling, Ole Bagge and Tine Kjaer Hassager for providing me with material.

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