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Fish species interactions in the Baltic Sea

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Abstract

The Baltic fish community is dominated by cod, herring, and sprat. These constitute about 95% of the commercial catch of fish in the Baltic, which has been between 580 000 t and 970 000 t per year since 1980. The biomass of cod (ICES subdivisions 25-32), herring (ICES subdivisions 25-29), and sprat (ICES subdivisions 25, 26, and 28) has in the same period varied between 2.5 and 3.7 million t. The biomass of other species is not known but it is not likely to constitute a higher fraction of the biomass than of the commercial catch. Cod preys heavily on cod, herring, and sprat. Two Multi-Species Virtual Population models (called MSVPA) have been developed for the Baltic: one for the western part and one for the central part. Only the model for the central part is dealt with here. More than 43 000 cod stomachs from the central Baltic have been sampled and analysed and a major effort has been devoted to estimating the consumption rations of cod. About half of the diet of cod is herring and sprat. The model suggests that cod has on average (1978-1987) consumed 62 000 t cod, 309 000 t herring, and 232 000 t sprat per year. For herring and sprat this is more than landed by the fishery. The cod cannibalism is almost exclusively on 0 and 1 year old cod. The efficiency with which cod utilize its food has been found to be surprisingly high. Between 35% and 45% of that consumed goes to growth or to gonadal production. The magnitude of cannibalism suggest a rather strong self-regulatory mechanism of the cod stock. This has important implications for the long-term management of the Baltic cod stock. Salmon, trout, pike, pikeperch and perch are other piscivorous fish in the Baltic. Herring, sprat and juvenile cod are parts of their diet. The biomass of these predators is low compared to the biomass of cod. The effect on herring, sprat and cod of these predators can be neglected.

Keywords: Baltic, fish interactions, MSVPA/MSFOR model, cod cannibalism, stock–recruitment relationship.

Introduction

Species interaction is regarded here as the influence between and within species by predation and food competition. Interaction by predation and food competition can result in secondary effects such as changes in numbers, natural mortality, growth, fecundity and age and size at first maturity. However, fish species interactions in the Baltic have only been demonstrated to be significant for fish mortality through predation. This paper will only deal with this kind of species interaction.

The importance of fish interactions has long been recognized. Analysis of fish stomachs was one of the first issues to occupy fish biologists (see e.g. Smith 1890, Todd 1907) and it soon became evident that mathematical models were needed in order to quantify these interactions. Volterra (1928) used fish landings from the upper Adriatic to develop one of the first multispecies models. Jensen (1929) speculated about the apparent negative correlation in the cod catches and the herring catches two years later in the western Baltic and considered predation to be a likely explanation. But, surprisingly, multispecies models have had little influence on fisheries management. The International Council for the Exploration of the Sea (ICES), responsible for the biological advice on fish stock management in the North East Atlantic area, in 1993 based its advice on singlespecies considerations for some stocks where multispecies interactions are strong. The Beverton & Holt's (1957) singlespecies Yield/Recruit (Y/R) curves and F_{max} concepts are still used in describing the stock dynamics, although it has been shown to be seriously misleading for many stocks in some areas like the North Sea (Gislason 1991). Although the quantitative population dynamics approach has been used widely, attention has mainly focused on the interaction between individual stocks and the fishery. A comprehensive theory on the dynamics of exploited fish populations has been developed following the initial work by Beverton & Holt (1957).

Fisheries management advice requires knowledge of interaction between species, but the general belief formerly was that the effect of predation and competition was subordinate to the direct effects of fishing. However, the work of Daan (1973, 1975) on feeding of North Sea cod and of Ursin (1973), Andersen & Ursin (1975, 1977) and Ursin & Andersen (1975) on a comprehensive North Sea ecosystem model clearly demonstrated that this was wrong.

The ecosystem simulation model developed by Andersen & Ursin (1977) for the North Sea was a first attempt to quantify the interaction between fish stocks, and to estimate the integrated effects of fisheries on the entire ecosystem. Although this model can aid to understand the causes of the many changes which had occurred in the North Sea, a general criticism was, according to Sissenwine & Daan (1991), that the model required too many untested assumptions and required too many parameters to be estimated and to be relied upon for evaluating the effects of the fishery. However, elements of the model, such as the concept of predator-specific prey suitability, were important breakthroughs which made it possible to integrate species interaction with traditional stock assessment techniques.

The studies cited above produced a paradigm in fisheries biology for analysing and developing models of fish interactions. Following this, several of the popular single-stock Virtual Population Models (VPAs, developed by Fry 1949 and Gulland 1965) were combined into one model: a Multi-Species VPA (MSVPA) proposed independently by Pope (1979) and by Helgason & Gislason (1979). The MSVPA links the VPA for each stock by the predation by other stocks. The total number predated is estimated and the predation mortality, M, is then estimated in the same manner as the fishing mortality, F.

The MSVPA is conceptually a simple multispecies model only taking into account the effect of predation on natural mortality. The only additional input needed compared to the VPA are data on food composition and consumption rations of predators. It is assumed that the consumption rations, growth, and predator-specific prey suitability do not vary over the years. The MSVPA has been applied to the North Sea (e.g. Pope 1991), the Baltic Sea which will be dealt with here (e.g. Sparholt 1991), and the Barents Sea (Mr Dankert Skagen, pers. comm.).

A forecast version, called MSFOR, of the MSVPA was developed by Sparre (1980) and Gislason & Sparre (1987). This is a simulation model using the estimated stock numbers and suitabilities from the MSVPA to forecast the change in fish stocks for various scenarios of fishing mortalities and recruitment.

Large fluctuations in the cod, herring, and sprat stocks in the Baltic have previously been observed and explained by predator–prey interactions (e.g. Jensen, 1929, 1962, 1967, Lishev & Uzars 1967). It is considered here that the MSVPA might explain the observed phenomena and be used as a valuable tool in the preparation of management advice.

Cod, herring, and sprat are by far the most important fish species in the Baltic and constitute about 95% of the commercial catch in weight (see next section). Thus, the MSVPA used here has concentrated on these species and cod has been regarded as the predator and cod, herring, and sprat as prey.

The MSVPA requires extensive data on the food composition of the dominant predator species and reliable estimates of consumption rates. In the Baltic, stomach analysis studies have been carried out in several countries since the beginning of the 1970s. These investigations were not co-ordinated and not all samples have been fully analysed, but from 1977 onwards useful data are available (Anon. 1989a). To date, data from more than 55 000 cod stomachs are available. However, only data from the central Baltic (ICES subdivisions 25-32) are in a format readable by the MSVPA. Some seasons and some areas of the central Baltic are still not well represented and therefore sampling has to be continued although this is expected to influence the outcome of the MSVPA only to a small degree (Anon. 1992a).

Since 1980 experiments on digestion rates of cod and other piscivorous fish have been carried out. These now allow the estimation of consumption rates, although there still exist some controversy about the best evacuation model to apply on the experimental data (e.g Bromley 1991).

Beverton & Holt's (1957) singlespecies yield/recruit curves and F_{max} has previously been the main basis for the long-term management advice. As an example Figure 1 gives the singlespecies yield/recruit curve for the cod stock in the North Sea. The fishing mortality corresponding to the maximum of the curve is the F_{max}.

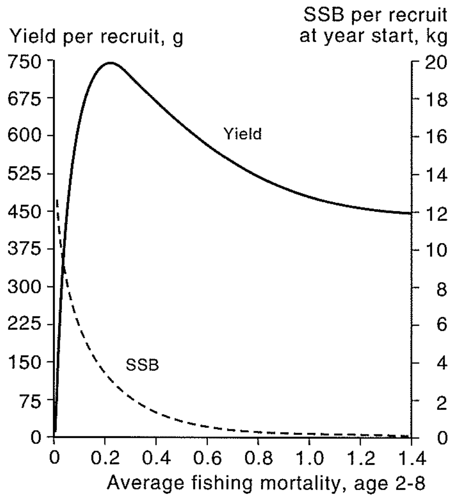

Figure 1. Yield and spawning-stock biomasses (SSB) per recruit for North Sea cod. From Anon. (1992b).

At this fishing mortality, the long-term yield of a given recruit will be higher than of any other fishing mortality level. Thus, independent of a big or a small year class, by this procedure it was claimed possible to advise on the optimal exploitation of a given fish stock. This gave the optimal means of exploiting a fish stock even though it was not possible to state the actual catch, which will be dependent on the strength of the year classes.

Figure 1 also shows that if F on cod in the North Sea is decreasing from the present level of about 1.0 to F_{max} then the stock biomass will increase significantly. This means that the cod stock consumption will increase, including small cod. According to the MSVPA for the North Sea this will counterbalance the gain by decreasing F as indicated in the singlespecies yield/recruit calculations (Gislason 1991).

In 1993, ICES had still not considered multispecies interactions in its advice on the management of cod in the Baltic.

The present paper gives the MSVPA model for the central Baltic as this is the most comprehensive data-based model for the interaction between fish in the Baltic. The fish interactions will be described mainly in terms of predations mortalities and biomasses predated. Implications for the fisheries management regarding optimal exploitation (in term of yield) of the fish stocks will be touched upon.

The Baltic Sea fish

The fish fauna is characterized by a relatively small number of species and the occurrence of both marine and freshwater species. Cod (*Gadus morhua*), herring (*Clupea harengus*), and sprat (*Sprattus sprattus*), constitute about 40, 50 and 5% (means for 1980-1984), respectively of the total commercial catches in the area (Table 1). Other marine species are flounder (*Platichtys flesus*), plaice (*Pleuronectes platessa*), dab (*Limanda limanda*), whiting (*Merluccius merluccius*), and garfish (*Belone belone*). The typical freshwater species include bream (*Abramis brama*), pike (*Esox lucius*), perch (*Perca fluviatilis*), pike-perch (*Lucioperca lucioperca*), roach (*Rutilus rutilus*), and burbot (*Lota lota*). Compared to truly marine areas, the contribution of diadromous species is large. They mainly consist of salmon (*Salmo salar*), trout (*Salmo trutta*), eel (*Anquilla anquilla*), and smelt (*Osmerus eperlanus*). In some years sticklebacks (*Gasterosteus aculeatus*) occur in large numbers and occasionally an industrial fishery on this species has been established.

In general, more marine species are found in the western Baltic and more freshwater species in the northern and eastern parts of the Baltic due to the salinity conditions.

Commercial catch statistics are not an accurate reflection of the species composition in an area. Some abundant species in the Baltic are never landed by fishermen. As an example, the four-bearded rockling (*Enchelyopus cimbrius*) is in some years caught in large numbers in the trawl surveys and often found in cod stomachs (Fester 1974), while its commercial catches are insignificant.

Thurow (1984) estimated the biomass of species other than cod, herring, and sprat to be 1.1 million t in 1970 and 0.5 million tonnes in 1977. These estimates were based on catch statistics, best estimates, unreported and discarded catches,

Table 1. The mean annual commercial landings in the Baltic Sea by species (groups) in 1980-1984. Data from E.D. Andersson (1986, 1987) and K. Høydal (1982, 1983, 1985).

Species	Landings, t
Freshwater fish	18 983
Eel	2404
Salmon	2783
Smelt	3803
Trout	774
Various diadromous	3797
Brill	19
Dab	2091
Flounder	8989
Lemon sole16	
Plaice	2145
Sole	3
Turbot	132
Various pleuronectiformes	3466
Cod	393 260
Ling	1
Pollack	3
Saithe	2
Tusk	–
Whiting	3707
Catfish	2
Sandeel	25
Various demersal percomorphs	3579
Garfish	1086
Horse mackerel	291
Herring	452 219
Sprat	47 558
Mackerel	24
Unidentified	14 226
Total	965 343

assuming that the yield:biomass ratio for these other species was the same as for cod, herring, and sprat. For comparison, the biomass of cod, herring, and sprat in 1980-1984 has been estimated at 4.1 million t (Anon. 1989b,c).

Cod, herring, and sprat

Commercial catches

The commercial catches of cod, herring, and sprat have fluctuated widely during the past 80 years, but there has been an increasing trend from a total of less than

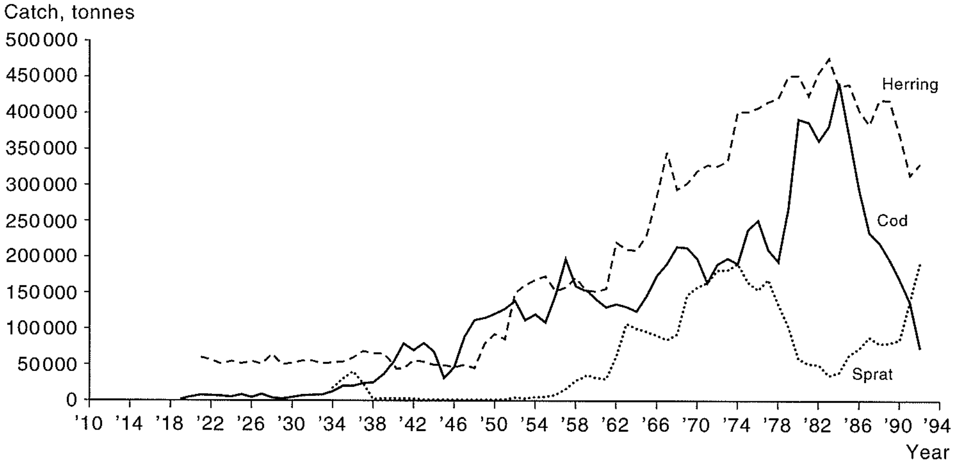

Figure 2. Commercial catches in the Baltic Sea (subdivisions 22-32).

100 000 t in the 1930s to over 900000 t in 1984. Thereafter, landings decreased again to 550000 t in 1992 (Figure 2).

The catch of cod was only about 5000 t per year at the beginning of the century until 1935. From 1935 to 1950 the catches increased gradually, and from 1950 to 1978 they were relatively stable at around 150 000 t per year. From 1979 onwards, the cod catches increased sharply reaching a maximum in 1984 of 441 000 t. Since 1984, a steady decline has been observed to 71 000 t in 1992 (Anon. 1993a).

Throughout the 1980s cod have been heavily over-exploited in the Baltic with a fishing mortality coefficient (F) of about 1.0 y^{-1} (Anon.1993a).

The commercial catches of herring have fluctuated less than the cod catches. In the first half of the century they were fairly stable at around 50 000 t. From 1945 onwards, herring catches increased rather steadily to about 400-500 000 t in the beginning of the 1970s and have remained at this level since then.

Herring is heavily exploited in the western parts of the Baltic (F around 0.8) but in the eastern parts it is only moderately exploited (F below 0.4) and in some areas even under-exploited (Anon. 1993b)

Several thousand tonnes of sprat were landed per year in the 1930s but catches decreased to virtually zero until the middle of the 1950s. Thereafter, they increased to a maximum of about 200 000 t in the middle of the 1970s, followed by a steep decline to about 50-100 000 t until 1991, and raised again to 140 000 t in 1992. Sprat are generally lightly exploited in the Baltic (F below 0.3) (Anon. 1993b).

The interpretation of these data is difficult due to doubts about the reliability of data prior to 1970.

Sparholt (1991) suggested that the exploitation level in the cod stock must have increased after 1929 in all important fishing areas as the mean age in the catch decreased. However, the change has not been large enough to explain the large increase in the cod catches beginning at the end of the 1930s. According to J. Netzel (pers. comm.), the Polish fishermen complained in the 1930s of poor catches of cod compared to the situation in the 1880s and 1890s. Thus, the cod stock has probably been considerably less in the first half of this century than before, possibly due to low recruitment. Since cod eggs can survive only at salinities above 10 psu (Bagge 1981a), it is of note that salinity was low at that time (Anon. 1987). According to Anon. (1987), salinity reached a peak by the end of the 1970s, and this would correspond to the appearance of strong year classes of cod, giving rise to the sharp increase in the catches between the 1970s and 1980s (Anon. 1993a). This hypothesis about a relationship between salinity and cod recruitment should, however, be considered against other changes in the Baltic, e.g. the increased input of nutrients (Anon. 1987). This eutrophication might have increased the food supply to the fish larvae and enhanced survival, although negative effects might be expected from associated reduction in the oxygen content of the deep parts of the Baltic. From a multispecies modelling point of view these anthropogenic changes are relevant as they could have a major impact on the fish community in the Baltic.

The increase in the herring catches beginning at the end of the 1940s can be explained by a substantial increase in effort (Ojaveer 1981).

The fluctuation in the sprat catches reflects, according to Aps (1989), fluctuations in the stock caused by large year classes in 1955-1957, 1959, 1967, 1969, 1972, and 1975. Aps (1989) investigated a large array of environmental parameters in relation to sprat recruitment but did not find any significant correlations.

As cod predate heavily on both herring and sprat (see section The Central Baltic MSVPA, p.147 ff.) fluctuations in predation pressure might also explain some of the observed fluctuations in the herring and sprat stocks.

Stock units

In the Baltic there are two *cod* stocks, which differ in morphometric and meristic characters, in haemoglobulin types, in otolith structure, and in allele-frequencies (Bagge & Steffensen 1989). Also the weight-at-age differs between the two stocks (Anon.1993a). The western Baltic Sea cod stock is distributed west of the Bornholm Island, in the Belt Seas and the Øresund (subdivisions 22-24; Figure 3, next page) and is connected with cod in the Kattegat and Skagerrak (division IIIa) as well as with cod in subdivision 25. The eastern Baltic Sea cod stock is distributed east of Bornholm to the northern parts of the Bothnian Sea and to the eastern parts of the Gulf of Finland (subdivisions 25-32). Although the border between these two main stocks is diffuse and there appears to be mixing in the Arkona Basin (subdivision 24) and in the Bornholm Basin (subdivision 25), tagging experiments indicate that a line from Sweden to Poland/Germany over Bornholm marks an appropriate border line between the two stocks (Bagge & Steffensen 1989). The migrations of Baltic cod have been reviewed by Aro (1989).

The stock structure of *herring* in the Baltic is rather complex with many stocks and a large degree of overlap between the stocks. In routine ICES stock assessment, herring is separated into four different stock units (Anon. 1993b) which differ by morphological, meristic, and biological characters. However, unlike cod, these differences are probably not genetic (Ryman *et al.* 1985), but are more likely a phenotypical reflection of the environmental gradient from the south to the north-east.

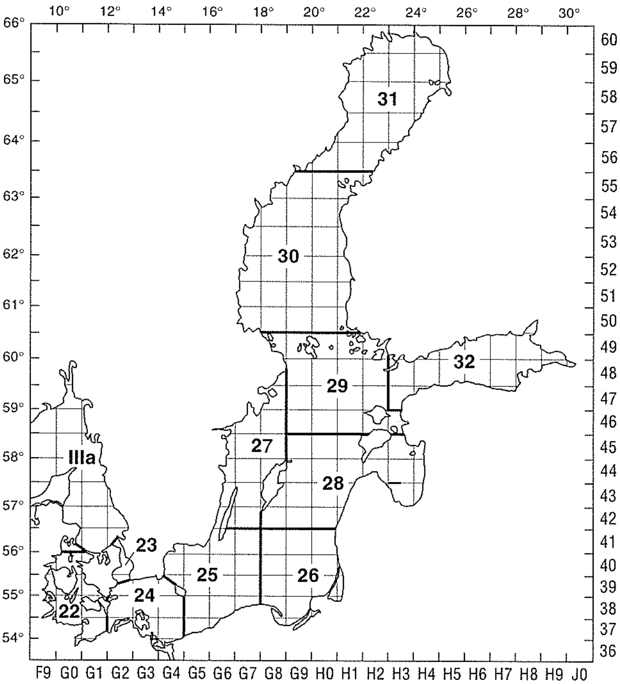

Figure 3. The ICES subdivisions for the Baltic Sea.

Herring in the western Baltic (subdivision 22-24) spawn during spring and migrate to Kattegat-Skagerrak to feed during summer. Migration of herring between subdivisions 24 and 25 is rare (Otterlind 1984). The borders between the stocks east of Bornholm are less well defined or documented and an analysis made by Anon. (1989c) indicates that at least some of these might better be combined together in one common unit.

The stock structure of *sprat* in the Baltic is less complex than the herring stock structure, and in the routine stock assessment only one stock unit is used (Anon. 1993b). Previously, three stocks were assumed in the routine assessments. The boundaries between neighbouring stocks were, however, less clear and apparently the stocks mixed during feeding and overwintering (Rechlin 1967, 1975, 1986). The ranges covered during migration and the rate of mixing were not well known. Some authors have in the past been in favour of more localized stocks (Aps & Lotman 1984, Aps *et al.* 1987), whereas others suggest that there is considerable migration and mixing between the stocks (Grauman 1976, Khoziosky *et al.* 1983). An analysis by Anon. (1989c) indicates that all three sprat stocks are interrelated as regards year-class strength and that the stock assessments are more accurate when they are considered as one stock.

Growth

Weight-at-age of *cod* is in general higher in the western part than in the eastern part of the Baltic according to data given by Anon.(1993a). The differences between subdivisions 25-32 appear to be small. Thurow (1974) found no differences in mean length-at-age for age 1-9 between the Bornholm Deep and the Gotland Deep. Comparison of these data with data from Modin (1987) for the Bothnian Sea (subdivision 30) also showed no significant differences. This agrees with the observation that cod migrate widely around in the Baltic east of Bornholm (Aro, 1989) and confirms that this part is inhabited by one unit stock.

Several authors have tried to relate changes in growth of cod to changes in feeding conditions and stock abundance from year to year (Horbowy 1984, Baranov & Uzars 1986, Baranov 1989). However, the observed changes in mean weight-at-age in the commercial catches have been comparatively small (e.g. Anon. 1993a) and could be biased by changes in fishing selectivity, changes from demersal to pelagic trawling, etc. Therefore, they may not represent actual changes in growth. During the period 1981-1988 the cod biomass changed from over 1.0 million to about 0.4 million t and yet the mean weights-at-age have not changed significantly between the years according to an ANOVA test with age and year as class variable ($p \leq 0.05$ for the year effect). Only cod age 4 and older were used in this analysis as they were considered to be fully recruited to the exploited stock (Anon. 1993a). Furthermore, annual weight increments during the same period showed no correlation to year-class abundance. Also, over a longer time span, data from Kiel Bay, Bornholm Deep, Gdańsk Deep, and Gotland Deep on mean length of 3-group cod do not indicate a significant change in growth between 1931 and 1977 (Bagge 1981a). Recently, at a very low stock level, the growth might, however, have increased slightly (Bagge *et al.* 1992).

The growth of *herring* differs significantly between areas as in general the length-at-age decreases from the south-western to the north-eastern parts (Table 2). In addition, the growth within a subdivision varies substantially over time. Ojaveer (1981) and Anon. (1993b) indicate a gradual increase in weight-at-age in both the southern Baltic and in the Gulf of Riga from 1960 to 1980, followed by a reduction. In some of the major stocks differences in weight-at-age between years are in the order of 40%.

Table 2. Theoretical asymptotic length (L_∞) and mean length of 3-ringers (L_3) in cm of spring- and autumn-spawning herring and sprat in different areas. (From Ojaveer 1981.)

Area	Subdivision	Spring herring L_∞	Spring herring L_3	Autumn herring L_∞	Autumn herring L_3	Sprat L_3
Bothnian Sea	30	20.3	15.9			
Western Gulf of Finland	32	19.1	15.9	18.4	16.2	11.9
Gulf of Riga	28	20.6	15.2	19.8	16.1	
Hiiumaa	29	21.8	16.9	19.7	16.6	11.8
Saaremaa	28	21.8	18.2	21.0	18.4	
Gulf of Gdańsk	26	25.2	19.6	24.4	21.6	12.7
Bornholm	25			27.9	23.2	13.3
Rügen	24	28.3	22.0			
Southwestern Baltic	22-24		23.9		24.8	

Table 3. Mean weight-at-age (g) of sprat in October 1987 according to hydroacoustic survey data (Anon. 1989d).

	Subdivision					
Age	24	25	26	27	28	29S
0	3.7	3.0	3.5			
1	10.5	11.2	9.9	10.2	10.0	10.9
2	12.9	12.4	12.4	13.6	12.6	13.6
3	15.6	15.1	14.7	15.2	14.5	15.0
4	16.5	16.9	16.0	16.1	15.8	15.8
5	17.9	17.4	17.1	17.1	15.5	16.4
6	19.3	17.0	17.0	16.2	18.0	19.8
7	18.2	24.0	20.8	17.7		17.2
8		19.0	16.0	19.6	19.1	17.8
9	18.2	16.5		16.0	19.8	17.5
10+						19.0

There are only minor differences in the weight-at-age of *sprat* between subdivisions (Table 3), which confirms the observation that this species migrates extensively around the area (Aro 1989). Data given by Anon. (1993b) suggest that the annual variations in weight-at-age have been minor between 1970-1988. Since sprats are difficult to age in some parts, especially when they are more than about three years old, considerable inherent variability may be expected in the data and time trends cannot be firmly established. Aps (1989) showed that the weight-at-age in the northern Baltic increased from the 1950s to the 1980s by about 30% coinciding with a reduction in sprat biomass, thus suggesting density-dependent growth.

Natural mortality

Sparholt (1991) gives a thorough review on natural mortality of Baltic cod, herring, and sprat based on catch-effort data and hydroacoustic stock estimates. This indicated that it was appropriate to use a value of $0.2\,y^{-1}$ for that part of the natural mortality which was not due to predation but due to diseases, spawning stress, damage by fishing gears etc. This value could be applied to both cod, herring, and sprat.

The other part of the natural mortality, the predation mortality, is dealt with by the MSVPA model and considered below.

Interaction between species

A predator–prey relationship between cod and herring in subdivision 22 was first demonstrated by Jensen (1929). He found a significant negative correlation between the catch of cod with the catch in pond-nets of autumn-spawning herring two years later. Using the same procedure, he also found negative correlations between cod and herring in the North Sea, in subdivisions 24-32, and between cod and sprat in Skagerrak and in subdivision 22 (Jensen 1962, 1966). The predator–prey relationship, however, became less pronounced in the 1960s.

Lishev & Uzars (1967) found the same kind of negative relationship between the catch of cod in year n and that of sprat in year $n+2$, $n+1$, n, and $n-1$ and of herring in year $n-1$ and $n-2$ in subdivision 26+28.

These relationships may indicate that cod have a negative influence on herring and sprat through predation. However, large year-classes of herring and sprat might increase the predation mortality on cod eggs and larvae and thus reduce recruitment, which would lead also to an inverse relationship. Köster & Schnack (1994) has presented strong indications that sprat and to a lesser extent herring in some years can eat significant numbers of cod eggs and a few cod larvae.

In the western Baltic (subdivisions 22-24) the diet of cod is diverse but dominated by herring, sprat, the mollusc *Cyprina islandica*, various Polychaeta, the crustaceans *Diastylis rathei* and *Saduria entemon*, and various teleost (mainly Gobiidae) (Arntz 1978, Bagge 1981b, Schulz 1987, Weber & Damm 1992).

In the central Baltic the food consists only of rather few species and is strongly dominated by herring, sprat, *Saduria entemon,* and 'other invertebrates' (Table 4). 'Other invertebrates' are dominated by *Mysis mixta*, and the polychaete *Harmothoë sarsi* (Uzars 1985, Załachowski 1985).

Table 5 briefly reviews the attempts made in the past to quantify the impact of the cod predation on herring, sprat, and other food in the Baltic based on stomach data. The results are very variable, but generally the impact on the prey is substantial.

Several multispecies models of the Baltic Sea have been developed to estimate the natural mortality rates and growth of cod, herring, and sprat for potential use in the management of these stocks.

Mandecki (1976) applied the Andersen & Ursin (1977) type model for the entire Baltic Sea and included zooplankton besides cod, herring, and sprat as a dynamic component in the model. Majkowski (1977) developed a similar model for cod, herring, and sprat stocks in the Baltic proper (approximately subdivisions 25-29). Both Mandecki's and Majkowski's models were fitted to cod stomach data from Chrzan

Table 4. Diet of cod in weight fractions. Values are means over quarters which each are means over years, subdivisions, and countries, weighted by the square root of number of stomachs in the samples.

Length of cod, cm	*Saduria entomon*	Other invertebrates	Sprat	Herring	Clupeids indet.	Cod	Other fish	Total
16-25	0.19	0.84	0.06	0.02	0.01	0.01	0.08	1.00
20-30	0.21	0.51	0.00	0.00	0.27	0.00	0.00	1.00
21-25	0.20	0.65	0.08	0.01	0.00	0.00	0.07	1.00
26-30	0.31	0.48	0.13	0.05	0.01	0.00	0.04	1.00
26-35	0.24	0.24	0.22	0.19	0.05	0.01	0.04	1.00
31-35	0.34	0.33	0.19	0.08	0.01	0.01	0.04	1.00
31-40	0.27	0.33	0.17	0.09	0.09	0.01	0.05	1.00
36-40	0.30	0.23	0.33	0.09	0.00	0.00	0.05	1.00
36-45	0.19	0.14	0.33	0.24	0.04	0.01	0.05	1.00
41-50	0.26	0.17	0.34	0.15	0.03	0.01	0.05	1.01
46-55	0.18	0.06	0.29	0.32	0.03	0.07	0.06	1.00
51-60	0.24	0.06	0.32	0.27	0.04	0.02	0.07	1.01
56-65	0.14	0.02	0.14	0.46	0.02	0.09	0.14	1.00
61-70	0.26	0.02	0.22	0.33	0.04	0.04	0.10	1.00
>65	0.11	0.01	0.13	0.38	0.01	0.19	0.18	1.00
>70	0.19	0.02	0.15	0.40	0.02	0.08	0.15	1.00

Table 5. Review of estimates of cod predation in the Baltic (biomass and consumption in thousands tonnes; SB: stock biomass; C: consumption by cod; n: number of cod stomachs examined).

Author(s)/ Species	SB	C	Σ C/SB	n	Period	Remarks
Lishev & Uzars (1967)						
Cod	30	–	6.0	unknown	1963-1966	Subdivisions 26 + 28
Herring		20				
Sprat		47				
Others		108				
Uzars (1975)						
Cod	233	–	12.9	11 000	1963-1973	Subdivisions not specified
Herring		276				
Sprat		408				
Others		2311				
Załachowski *et al.* (1976)						
Cod	323	47		7106	1971-1974	Central and southern Baltic (approximately subdivisions 25 + 26)
Herring		315				
Sprat		266				
Others		484				
Axell (1982)						
Cod	534	–	4.0	406	1976-1977	Only stomachs from Åland Sea; extrapolated to subdivisions 25-32
Herring		666				
Sprat		851				
Others		617				
Lishev & Uzars (1980)						
Cod	324	–	3.3	unknown	1975-1978	Stomachs from subdivisions 29 + 28; C based on *in situ* evacuation rate
Herring		141				
Sprat		156				
Others		785				
Bagge (1981b)						
Cod	221	–	2.7/5.2	2452	1976-1980	Subdivision 25; lower C-values, Daan (1973); higher C-values, Jones (1974)
Herring		265/539				
Sprat		–				
Others		239/421				
Schultz (1987)						
Cod	79	2117	3.9	7179	1978-1984	Subdivisions 22-24
Herring		26 165				

(1962) from the Gulf of Gdańsk. The obtained predation mortalities are almost identical in the two models.

Lassen (1979) developed a modified VPA for sprat in subdivisions 26+28 which takes into account predation by cod. The formulation of the natural mortality was based on Andersen & Ursin (1977). Although Lassen's model is simpler than the previous two models, the estimation of natural mortality is still rather complicated and it is mathematically not fully valid, because the approximation procedure used is sensitive to large changes in the cod stock.

Horbowy & Kuptel (1980) also applied the Andersen & Ursin (1977) model to the Baltic Sea. They included several stocks of cod, herring, and sprat and two stocks of zooplankton and benthos. Horbowy (1989) developed the above model further for subdivisions 25-29S and verified it for internal consistency.

The same criticism can be applied to all the above models that has been applied to Andersen & Ursin's North Sea model, namely that the models are too complex and a substantial part of the input parameters are unknown or 'guesstimated'.

Table 6 shows the predation mortalities due to cod estimated by some of the above models. The models agree regarding the level of predation mortality on sprat but differ considerably on cod and herring.

Table 6. Estimated predation mortalities (*M*2) due to predation by cod from multispecies models.

Species/ Age	Horbowy (1989) Subdivisions 25-29S	Mandecki (1976) Subdivisions 22-32	Lassen (1979) Subdivisions 26+28
Sprat			
0	0.69	–	
1	0.71	0.6	
2	0.52	0.6	0.52-0.59*
3	0.40	0.5	
4	0.32	0.5	
5	0.28	0.5	
6	0.25	0.5	
Herring			
0	0.28	–	
1	0.24	0.5	
2	0.13	0.4	
3	0.08	0.3	No estimates
4	0.06	0.2	
5	0.04	0.2	
6	0.04	0.2	
7	0.04	0.2	
Cod			
0	0.18	–	
1	0.08	0.6	
2	0.02	0.2	
3	0	0.1	
4	0	0.1	
5+	0		

* Values depending on Lassen's availability index (100 and 25, respectively).

The MSVPA/MSFOR model

The MSVPA model is described by Gislason & Sparre (1987) and by Sparre (1991) and the FORTRAN coding of the model can be found in Sparre (1984). However, the MSVPA has been under constant development and none of the above descriptions are fully up to date. There is no 'standard' version and the versions used for the North Sea and the Baltic Sea differ slightly. For instance in the Baltic Sea version the oldest age groups are regarded as real age groups and not plus groups, weight-at-age differs by year, and the submodel for the predator–prey preference (in the MSVPA context called suitabilities), has been improved.

The MSFOR model (e.g. Sparre 1980, 1991, Gislason & Sparre 1987,) is a simulation model used for forecasting the developments in the fish stocks from the MSVPA. It uses stock numbers at the end of the terminal data year and predator–prey preference parameters, called suitabilities in the following, as estimated by the MSVPA as well as data on expected recruitment and fishing mortalities. Data on weight-at-age, maturity, residual natural mortality etc. are usually the same in the MSVPA and MSFOR. The formulae used are also very similar to the MSVPA formulae.

The MSVPA versus the VPA: The MSVPA model is an extension of the VPA in that the interactions between species are taken into account. In essence, several VPAs are done simultaneously, one for each stock considered, and the stock numbers estimated for one stock are used to calculate the predation from that stock on other stocks. By summing the predation on a given stock from its various predators the total predation mortality is obtained.

The time-steps used in the VPA are usually years. In the MSVPA model quarters are used because the main predation is on the juvenile fish and these grow very much during one year. Thus, in order to avoid problems with large differences in biological parameters between the beginning and the end of the year, quarters as time-steps are more appropriate.

MSVPA input and output data: Figure 4 gives an overview of the data needed to run the MSVPA model and the parameters estimated by it. As with the VPA, catch-at-age by time step and terminal fishing mortalities are needed. In addition, the rela-

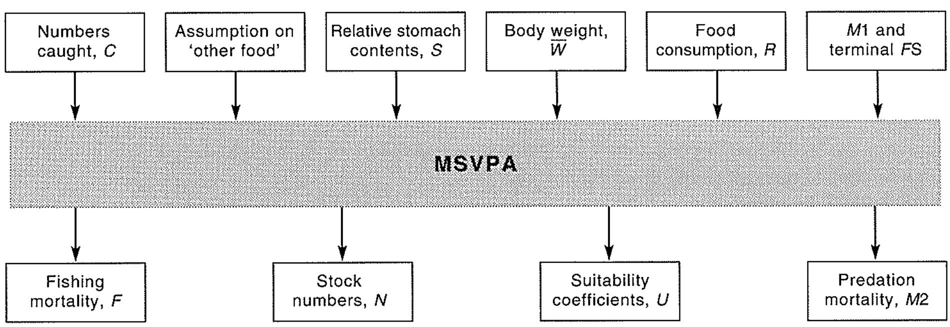

Figure 4. Inputs and outputs to the MSVPA. Modified from Sparre (1991).

tive stomach content for each predator age group is needed and this has to be given by prey age groups. Furthermore, data for all four quarters are needed as the parameters change between quarters but data are not needed for all years, in fact only one set of stomach data for each quarter is needed and these do not have to be from the same year. That is why it was decided for the North Sea to carry out one major stomach sampling program in 1981 as described above. In the Baltic Sea the stomach sampling effort was distributed over the years 1977-1990 with a total sampling size approximately similar to that in the North Sea 1981 program.

Data for the predators' consumption rations by age and quarter are also needed. These have been based on extensive food evacuations experiments at laboratories in various countries. By combining the results of these experiments with the observed mean stomach contents from the stomach sampling the rations have been obtained.

The body weights-at-age of the prey species are needed in order to relate the amounts eaten by predators to numbers of fish. Because the weight-at-age in the Baltic Sea herring has varied significantly during the period 1977-1992 considered in the MSVPA for this area, the weight-at-age data have to be given by year. In the North Sea this is not so important as the changes there have been minor.

A figure for the part of the natural mortality which is not caused by the MSVPA predators, called residual natural mortality or $M1$, has to be given. This mortality can be caused by diseases, spawning stress, damage by fishing gears, senility etc. Usually, it is a small value and will have little influence on the results, although it often is very difficult to estimate precisely.

In some versions of the MSVPA the biomass of 'other' food has to be given. In the North Sea version it has to be specified due to the suitability sub-model used. The suitability sub-model in the Baltic Sea version is different from the North Sea version and the value is not needed.

The output parameters from the MSVPA are like that from the VPA, i.e. fishing mortalities and stock numbers, although they will differ from the VPA values. In addition, the predation mortalities, $M2$, and the suitabilities are estimated. The suitabilities are not in themselves of value in the historical analysis but are needed when forecasting the developments in the fish stocks by the MSFOR model.

Suitability coefficient: The suitability coefficients, U, are central elements in the MSVPA. It is a measure of the suitability or preference, as it is also called in the ecological literature (e.g. Manly 1974, Chesson 1978, 1983) of a prey species for a particular predator. The term was introduced by Andersen & Ursin (1977) as the product of a size-preference coefficient and a vulnerability coefficient. In the MSVPA it is not split into these two components. The suitability coefficients are fractions and total to unity.

The suitabilities may be interpreted as being proportional to the probability of encounter between the prey and the predator multiplied by the probability of the predator eating the prey once encountered. If the suitability is to remain constant the product of these two probabilities should be constant. This means that if the spatial distribution of the predator or the prey changes then the suitability will change given that the probability of the predator eating the prey once encountered remains constant. Thus, the constant suitability assumption in the MSVPA implicitly requires constancy in spatial distribution between years.

Andersen & Ursin (1977) assumes that the relative stomach content, S_{pi}, of a prey p in the stomach of predator i is the ratio of the suitable biomass of prey p to the total suitable biomass available to predator i. The suitable biomass is the product of the suitability coefficient, the stock number, N, and the body weight of the prey, w_j. Thus,

$$S_{pi} = (N_p \cdot w_p \cdot U_{pi}) / \sum_j (N_j \cdot w_j \cdot U_{ji}),$$

where the summation is over prey items. S_{pi} represents a fraction, and the S_{pi}'s summed over prey (index p) add up to 1.0. Thus, U_{pi} reflects the diet composition of the predators relative to the available food.

It can be shown algebraically, that Equation (2) together with $\sum U_{pi} = \sum S_{pi} = 1.0$ implies that (Sparre, 1980):

$$U_{pi} = (S_{pi} / (N_{pi} \cdot w_p)) / \sum_j (S_{ji} / (N_{ji} \cdot w_j)).$$

Thus, if the N's are known the U's can be calculated, as the S's are given by the stomach content data.

It is assumed that for a given predator and a given prey the suitability is specific for the season, i.e. quarter.

Iterative estimation of parameters: The MSVPA estimates or calculates the parameters in an iterative way (see Sparre 1991). It has been shown by Magnus & Magnusson (1983) that the MSVPA produces unique solutions in cases like the Baltic Sea MSVPA where there is no cannibalism between predator and prey of the same age; for instance cod of age 1 are not eating cod of age 1. To date the mathematical 'necessary' conditions for uniqueness of the MSVPA have not been given.

MSFOR: In the ICES routine assessment of fish stocks the VPA which deals with historical catch data has a counterpart. This is the prediction or simulation of development of the fish stock in the near future, most often the next two years, and the estimation of the long-term effects of various management strategies of the fishery on a given stock. These predictions and simulations are then passed to the various fishery management bodies and used for setting quotas and TACs (Total Allowable Catches), and to determine the long-term management strategies.

Thompson & Bell (1934) type models are used for the short-term prediction and the Beverton & Holt (1957) yield-per-recruit (Y/R) type models are used for determining the long-term strategy. As with the VPA the MSVPA also has a counterpart, which can be used instead of the Thompson & Bell model and the Beverton & Holt model. This is the MSFOR model.

The MSFOR is a multispecies extension of the Thompson & Bell model. It is more straightforward than the MSVPA because it uses the parameters estimated by the MSVPA in the simulation and requires only one iterative step.

The MSFOR uses the VPA equations. In the singlespecies prediction the following parameters have to be known: 1) the stock numbers at the beginning of the time period, 2) the recruitment, 3) the fishing mortalities, 4) natural mortalities, and 5) mean weights. In the MSFOR all these also have to be known except the natural mortalities. In the MSFOR the predation mortalities are calculated based on suitability and consumption ration parameters. Sparre (1991) describes the algorithms in the MSFOR.

Because of the interaction between fish predators and their prey, multispecies predictions of yield are not directly proportional to recruitment as in the singlespecies case. Thus, the very convenient feature of the Beverton & Holt Y/R model, namely that the optimal exploitation of a particular fish stock can be estimated without knowing the future recruitment, does not hold for the MSFOR (or for ecosystems where predation is an important feature). Furthermore, the determination of an optimal exploitation of the fish stocks in a multispecies ecosystem becomes much more complex than in the singlespecies case. Economical considerations become much more important because some species are more valuable than others and thus more important to get the maximum yield from than others.

The Central Baltic MSVPA

Cod is included as predator in the MSVPA for the central Baltic and cod, herring, and sprat as prey species. Because the MSVPA is based on the observed stomach content of cod and because food items less than about 5 cm are quickly digested and difficult to identify in stomach samples, the species interactions described in the model only apply to prey specimens larger than 5 cm. There is a natural border line between the western and the central Baltic at longitude 15°E, crossing through the island of Bornholm (see above). The stock units used by ICES in the routine assessment reflect this for cod and herring, but not for sprat. Sprat is assessed as one stock unit in the entire Baltic (subdivisions 22-32). Thus, it is implicitly assumed that there is a significant mixing between sprat concentrations east and west of Bornholm. The actual level of the mixing is, however, unknown. In order to keep simple MSVPA models for the Baltic until the mixing of sprat between western and central Baltic has been quantified, an MSVPA for the western Baltic and another MSVPA for the central Baltic have been established.

Fish stocks specified

The stocks included in the MSVPA model for the central Baltic are one cod stock (subdivisions 25-32), two herring stocks (subdivisions 25-27 and 28+29S) and one sprat stock (subdivisions 25+26+28). Usually, only a few percentage of the cod are found in subdivisions 29N, 30-32 and herring and sprat stocks (or sub-stocks) in these areas are not included. The stock unit used for cod is the same as used in the routine stock assessment (Anon. 1993a). For herring, the stocks used in the MSVPA were previously used in the routine assessment, but in later years they have been aggregated. Due to the rather large difference in size-at-age between the two herring stocks they have been kept separate in the MSVPA because predation seems to be very size dependent. The sprat stock used in the MSVPA has never been used in the routine assessment, but as discussed above this is regarded as an appropriate stock unit in the MSVPA context.

Other predators and prey

The catch of salmon is given by Anon. (1993c) as 2000-5600 t per year in subdivisions 24-29 in 1978-1992. The fishing mortality is high and it is unlikely that the biomass is greater than 10 000 t. The commercial catch of various percomorph fish has been stable over the years and was 3579 t per year in 1980-1984 (Table 1). Although the F values on these probably are lower than on salmon and although there might be a catch by anglers of a few thousand tonnes, the biomass of these are probably not more than, say, 15 000 t in subdivisions 25-29S. Thus, not more than about 25 000 t of other piscivorous fish are present in the central Baltic. As the cod stock in some years has been larger than 1.0 million t, the other fish predators can be ignored in this context.

There are three species of seals in the Baltic: the ringed seal (*Phoca hispida botnica*), the grey seal (*Halichoecus gryptus*), and the harbour seal (*Phoca vitlina*). All species predate on fish.

Anon. (1990) indicates that ringed seals eat about 2000 t herring, 200 t sprat, and 200 t cod per year; grey seals about 4600 t herring, 600 t sprat, and 1530 t cod per year; and harbour seals about 500 t herring, 70 t sprat, and 180 t cod per year. These estimates are mainly based on data from the 1960s and the 1970s. The cod stock was large in that period compared to now, and it is therefore likely that the seals now consume less cod.

A number of seabirds include fish in their diet. Of these the following species probably have the largest impact on the fish stocks: guillemot (*Uria aalge*), cormorant (*Phalacrocorax* c. *sinensis*), goosander (*Mergus merganser*), and red-breasted merganser (*Mergus serrator*). Other species seem to be less important because they are scarcer or not obligate fish eaters. They include black guillemot (*Cepphus grylle*), razorbill (*Alca torda*), smew (*Mergus albellus*), terns (Strenidae), and gulls (Laridae). The total annual consumption of fish by sea birds in the Baltic is of the order of 20 000-25 000 t (Anon. 1990).

As the cod stock in the central Baltic in most years has consumed over 1 million t of food mainly consisting of herring and sprat (see below) the consumption of sea birds and sea mammals can in this context be ignored. Thus the mortality of herring, sprat, and cod due to predation by sea birds and sea mammals can be regarded as a part of the residual mortality, $M1$, of the MSVPA model.

The diet of cod

An international cod stomach database has been established for the Baltic Sea. Almost all cod stomachs sampled and analysed since 1977 in the Baltic have been reported to the database. The data are reported in the form of two types of tables.

One table gives the amount (in weight) of each food item found in the cod stomachs by cod length group, year, quarter, ICES subdivision, country, and gear with which the cod have been sampled. Numbers of empty stomachs are also given. For cod, herring, and sprat the amount is given in two categories: an A category which represents lightly digested food for which lengths can be given with the precision of 1 cm, and a B category which represents heavily digested food items for which lengths can only be roughly estimated. If a herring or a sprat is so digested that it is impossible to determine the species, it will be reported as clupeoid undetermined. Fish other than cod, herring, and sprat are just reported as 'other fish'. *Saduria entemon* and other invertebrates are reported as such. As very few cod in general are reported within a cod length group, year, quarter, ICES subdivision, country, and gear, the mean length of the cod found in the stomach is given in this table.

The other table contain information on the length of the herring and sprat found in the stomachs. This is given in 1 cm units for category A items and by the following length groups for category B items: less than 11 cm, between 11 cm and 19 cm, and greater than 19 cm. Some countries have reported cod found in the stomachs in this way too.

In total, 43 544 cod stomachs have been examined, reported, and compiled in the database for the central Baltic during the period 1977-1990.

The consumption rations of cod

The development of the MSVPA for the central Baltic aimed to revise the figures for consumption rations of cod. This has been done by using basic experimental data for gastric evacuation rates of cod (dos Santos 1990) as well as by using the stomach database for Baltic cod, and data on the temperatures to which the cod are exposed in the central Baltic.

The relation between stomach content of cod and the quarterly consumption rations were found by Anon. (1992) to be:

$$C_q = 2190 \cdot r \cdot 0.8 \cdot (\text{avg}[S])^a,$$

where $a = 0.53$ and $r = 0.00237 \cdot \exp(0.1 \cdot \text{temp.}) \cdot L^{1.17}$. L is the cod length in cm and temp. is temperature in °C.

From the international cod stomach database the average stomach contents (avg[S]) for central Baltic cod for 1977-1990 were calculated for each age group and quarter (see Anon. 1992a). Cod mean length-at-age were taken from Anon. (1990, table 3.3). Temperature for each age group and quarter were calculated according to depth distribution (Sparholt *et al.* 1991). The results in terms of annual consumptions are shown in Table 7.

Table 7. Annual growth and food consumption by age for cod and corresponding food conversion efficiency according to three gastric evacuation models.

Age	Growth g	Food consumption, g New model	Jones' model	Daan's model	Conversion efficiency New model	Jones' model	Daan's model
1	93	227	471	563	0.41	0.20	0.16
2	302	614	1310	976	0.49	0.23	0.31
3	555	1358	2939	1663	0.41	0.19	0.33
4	683	2336	5087	2443	0.29	0.13	0.28
5	713	3665	7983	3507	0.19	0.09	0.20
6	833	5051	10982	4611	0.16	0.08	0.18
7	890	6298	13717	5461	0.14	0.06	0.16
8	555	7569	16619	5932	0.07	0.03	0.09
9+	1534	8290	18354	5932	0.18	0.08	0.26

The above procedure is compared with those of Daan (1973) and Jones (1974) in Table 7. Daan's model is more conservative regarding dependence of consumption ration on cod size compared to the two other models, giving the highest value for small cod and the lowest for large cod. Although almost independent of cod size, the rations based on the new model only amount to about 46% of that given by Jones' model. The ration figures for Daan's and the new model are on the other hand in relatively good accordance except for cod in age groups 1 and 2.

In a further attempt to evaluate the rations based on the three evacuation models, the food conversion efficiency (growth per food unit) for each age group has been calculated (Table 7). The growth calculations are based on mean length-at-age from Anon. (1990, table 3.3) and the relationship $W = 0.01 \cdot L^3$. However, no accurate conclusions can be drawn from this as none of the efficiencies are unrealistic and the basis for these calculations is a rough approximation to real conditions.

The high rations obtained by using Jones' model may be explained by the fact that Jones (1974) used pieces of fillets of the lean fish saithe as prey items. Such a meal is assumed to be evacuated faster than whole herring, which in addition is a fatty fish. The procedure used in the MSVPA seems superior to Daan's model as the gastric evacuation model used is more accurate.

In future works cod bioenergetics should be used as an alternative way of estimating food consumption or at least as a check of the present methods. So far a common evacuation model (herring) has been applied for all prey species. The production of models for other important prey species (e.g. *Saduria entomon*) should be encouraged.

Other input data

The MSVPA run presented here is an update of the run made by Jensen & Sparholt (1992). The update regards the commercial catch data for which 1991 and 1992 data have been included. The MSVPA run covers the period 1977-1992 with cod stomach data of 43 324 cod from the period 1977-1990. The residual natural mortality, M1, have been set to 0.2 per year for all three species. Details about the input stomach data can be found in Sparholt (1993), about the input catch data in Anon. (1994) and the remaining data in Jensen & Sparholt (1992).

Further assumptions

The biomass of the other food items of cod has been assumed to be constant over time. The actual biomass has no influence on the Central Baltic MSVPA results because of the way the suitabilities are calculated in the central Baltic MSVPA (as opposed to the North Sea MSVPA), a given change in the biomass value of other food will be completely counteracted in the suitability values, resulting in unchanged predation mortality and biomass values (see Anon. 1992a).

Results of model run

Table 8 shows the mean predation and fishing mortalities (1978-1988) as estimated by the MSVPA. For 0- and 1-year old cod the predation mortality is very high, 0.80

Table 8. Predation and fishing mortalities as estimated by the central Baltic MSVPA. Mean values for 1978-1988. Mortality rates per year except for age group 0, which are per half year.

	Cod		Herring Subdiv. 25-27		Herring Subdiv. 28-29		Sprat	
Age	*F*	*M2*	*F*	*M2*	*F*	*M2*	*F*	*M2*
0	0.00	0.80	0.00	0.16	0.00	0.27	0.00	0.21
1	0.00	0.43	0.06	0.53	0.01	0.51	0.03	0.62
2	0.09	0.12	0.14	0.15	0.06	0.19	0.14	0.48
3	0.34	0.02	0.18	0.09	0.11	0.25	0.18	0.41
4	0.64	0.00	0.20	0.07	0.15	0.20	0.22	0.32
5	0.81	0.00	0.22	0.07	0.20	0.17	0.25	0.50
6	0.87	0.00	0.23	0.06	0.22	0.15	0.23	0.50
7	0.83	0.00	0.26	0.05	0.25	0.17	0.17	0.55
8	0.73	0.00	0.23	0.04	0.22	0.15	–	–
9	0.62	0.00	0.16	0.03	0.10	0.13	–	–

and 0.43, respectively, while it is almost zero for older cod. For herring and sprat the predation mortality is rather low on 0-year olds, 0.16-0.27, and high, 0.51-0.62, on 1-year olds. For the older herring the subdivisions 25-27 stock has a lower predation mortality than the subdivisions 28-29 stock. For all age groups of sprat the predation mortality is high, around 0.50.

For cod the MSVPA results seem to be in line with the results of Mandecki (1976) but much higher than the results of Horbowy (1989) (see Table 6). The reason for the difference between the MSVPA result and Horbowy's result is unknown but may be caused by the low value for cod vulnerability to cod used by Horbowy . He uses only half the value of the sprat vulnerability to cod predation, which seems peculiar as the spatial overlap between young and adult cod probably is higher than between sprat and cod, being a pelagic and a demersal species, respectively. Horbowy also did not determine the rather low predation mortality on 0 group herring and sprat. The reason for this is likely to be his assumption of equal vulnerability for all age groups of herring and sprat to cod. According to the general knowledge about the spatial distribution of 0-group herring and sprat, i.e. in shallow waters with very few cod, the vulnerability of 0-group herring and sprat must be low. Furthermore, the assumption of a constant optimal ratio between predator and prey sizes as assumed by Horbowy and by Mandecki may be incorrect (Bundgaard & Sparholt 1992). This also explains the relatively high predation mortality estimated by Mandecki on cod of age 2-4. Lassen's (1979) estimate of sprat predation mortality seems to be in good agreement with the MSVPA results.

Table 9 (next page) shows the biomass consumed by cod by prey species as estimated by the MSVPA. In 1979 and 1980 more than 100 000 t of cod was eaten by cod while in the later years only around 1000 t was eaten. This large decrease reflects both the decrease of the cod stock and the presence of poor year classes of cod in the later years. For the two herring stocks and the sprat stock the biomasses consumed by cod per year have exceeded the commercial catches in most years. Only in the most recent years has it been the other way around. The amounts of other

Table 9. Biomasses consumed by cod (in thousands t) as estimated by the central Baltic MSVPA and biomasses taken by the fishery.

Year	Cod		Herring, 25-27		Herring, 28-29		Sprat		Other food	Total
	Catch	Pred.	Catch	Pred.	Catch	Pred.	Catch	Pred.	pred.	pred.
1977	227	46	165	123	28	44	91	164	713	1090
1978	225	64	151	180	30	66	82	192	968	1470
1979	326	104	146	215	32	107	45	214	1109	1749
1980	516	123	123	226	35	161	36	189	1131	1830
1981	474	89	178	330	24	116	30	219	963	1717
1982	447	74	146	264	40	141	35	307	968	1752
1983	442	53	150	232	41	148	17	437	808	1678
1984	561	39	125	210	33	130	39	321	654	1354
1985	379	36	126	135	32	103	56	205	583	1062
1986	356	22	128	93	34	72	59	123	471	781
1987	226	12	120	73	39	66	72	118	398	667
1988	210	7	142	74	39	57	57	119	343	600
1989	221	4	160	71	62	50	66	119	214	458
1990	159	1	119	43	82	42	70	102	129	317
1991	123	1	106	17	69	20	70	78	78	194
1992	53	1	97	12	71	12	109	49	64	138

Table 10. The stock biomass (in thousands t) of cod, herring, and sprat in the central Baltic as estimated by the MSVPA.

Year	Cod	Herring, 25-27	Herring, 28-29	Sprat	Total
1977	678	1004	405	638	2725
1978	829	1069	398	525	2821
1979	1092	1042	591	395	3120
1980	1311	932	506	273	3022
1981	1232	1182	378	445	3237
1982	1197	1019	563	516	3295
1983	1191	1119	426	916	3652
1984	1142	1008	477	953	3580
1985	858	703	570	749	2880
1986	688	845	476	552	2561
1987	508	985	785	628	2906
1988	459	932	705	512	2608
1989	401	888	494	708	2491
1990	276	1266	728	1158	3428
1991	240	983	721	1455	3399
1992	140	1116	715	1753	3724
Mean	765	1006	559	761	3091

food items consumed by cod have in most years been at the same level as the amount of cod, herring, and sprat consumed.

Table 10 shows the stock biomasses by year as estimated by the MSVPA for cod, the two herring stocks and for sprat. All the stocks have varied significantly over the years, cod by a factor of 10, sprat by a factor 7 and the two herring stocks by a factor of about 2. However, the total biomass has been constant between 2.5 and 3.7 million t.

Evaluation

The MSVPA run output cannot easily be validated because independent information of predation mortalities, stock sizes, etc. are scarce. However, it is possible to compare biomass estimates from the MSVPA with biomass estimates from hydroacoustic surveys. As the MSVPA biomass estimates are sensitive to the estimated predation mortalities this evaluation is valid. However, hydroacoustic surveys are usually not very precise. The present MSVPA results for sprat are compared with hydroacoustic estimates in Table 11. As sprat predation mortality is very high compared to fishing mortality, the MSVPA biomass estimate of sprat should be especially sensitive to errors in predation mortality. Taking into account that the hydroacoustic survey under-estimates the amount of 0, 1 and 2 year old sprat (the estimated stock numbers increase from one year to the next for a given cohort for these ages) the MSVPA and hydroacoustic biomass estimates have relatively good agreement.

Table 11. Biomass (in thousands t) estimate of sprat from the MSVPA and from Hydroacoustic surveys.

Year	A VPA 26+28 (Anon. 1991c)	B Acoustic Subdiv. 25	Total (A+B)	MSVPA
1977	417	168	585	638
1978	262	127	389	525
1979	145	49	194	395
1980	107	12	119	273
1981	160	86	246	445
1982	173	96	269	516
1983	355	151	506	916
1984	432	97	529	953
1985	524	108	632	749
1986	394	90	484	552
1987	428	82	510	628
1988	372	87	459	512
1989	498	47	545	708
1990	674	80	754	1158

A trial run with the MSVPA model, where Jones' (1974) consumption rations for cod were used, gave sprat biomasses which in most years were about a factor of 3 larger than the hydroacoustic estimates. Thus, the present evaluation is clearly not in favour of Jones' consumption estimates.

The Central Baltic MSFOR model

Input data

Weight-at-age, fishing mortalities, and recruitment were taken as mean values in 1983-1988 from the MSVPA. Other values are used in some of the MSFOR forecasts (see below). Suitabilities, consumption rations of cod, proportion of mature fish by age, residual natural mortalities, stock sizes at the end of 1992, and biomass of other food items were also taken from the MSVPA.

Optimal exploitation

The MSFOR model can be used to indicate, e.g. the optimal exploitation level of cod in the central Baltic given an unchanged fishery on herring and sprat. Given the assumption implicit in the above input data, it is necessary to carry out several MSFOR runs each time changing the fishing mortality for cod. By plotting the steady-state yield and spawning-stock biomass against *F*, the optimal exploitation level can be found as the point giving the maximum yield as in the Beverton & Holt (1957) singlespecies yield per recruit (Y/R) curve. Figure 5 shows that there is no MSFOR maximum *F*, i.e. the steady-state yield will increase with an increase in *F* even at very high *F* values. This is clearly at variance with the singlespecies Y/R which has a maximum at $F = 0.25$ (Figure 5). The present fishing mortality for cod in the central Baltic is about 1.0 and the MSFOR calculations indicate that by reducing *F* to 0.25 the yield will be reduced by about 50%.

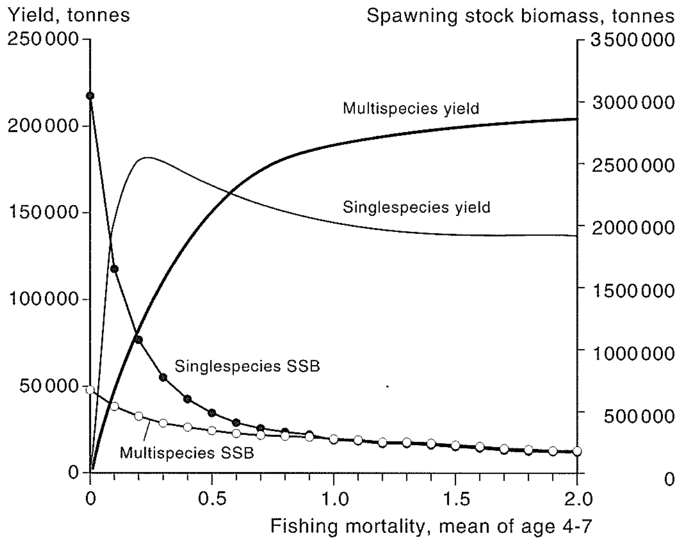

Figure 5. The long-term steady-state yield and SSB from singlespecies and multispecies models as a function of fishing mortality.

The discrepancy between the singlespecies and the multispecies forecasts is the result of the fact that an increase in the cod stock will mean an increase in cod cannibalism and thus fewer cod will reach the commercial size.

However, in order to minimize cannibalism, the stock of large cod has to be exploited to a low stock level and the spawning-stock biomass (SSB) will then be very small and probably not able to produce year classes of average size. Thus, in the multispecies context the management problem becomes a balance between reducing cannibalism and securing sufficient spawners to produce average recruitment. The need to establish an SSB-recruitment relation is thus important, which it was not in the classic Y/R and F_{max} context.

The forecasts of the fisheries and stock developments of herring and sprat are also dependent of the stock size of cod. Thus, the forecasts of herring and sprat catches is dependent on the management of the cod stock. If the cod stock is allowed

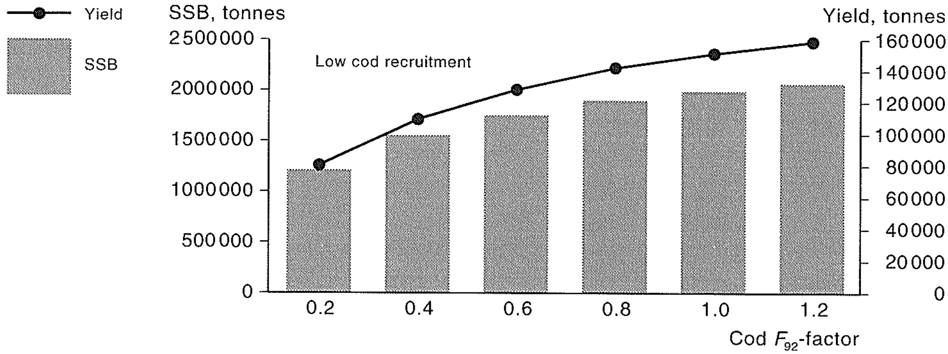

Figure 6. Sprat spawning stock biomass (SSB) and yield in year 2001 plotted against the fishing mortality (given as a multiplier of the 1992 fishing mortality) on cod in 1993-2001, based on MSVPA/MSFOR forecasts. Low cod recruitment (mean over 1985-1990) was assumed.

to increase in size, the predation on herring and sprat will increase and the catches will decrease. The magnitude of this interaction can be seen for sprat in Figure 6. Here the spawning-stock size (SSB) and yield in year 2001 are plotted against the fishing mortality on cod in the period 1993-2001 (see Anon. 1994). If the fishing mortality on cod is reduced to 20% of the 1992 level the sprat SSB will be about 1.2 million t and the annual yield around 80 000 t while if F is kept at the 1992 level the SSB will be about 2.0 million t and the yield around 160 000 t.

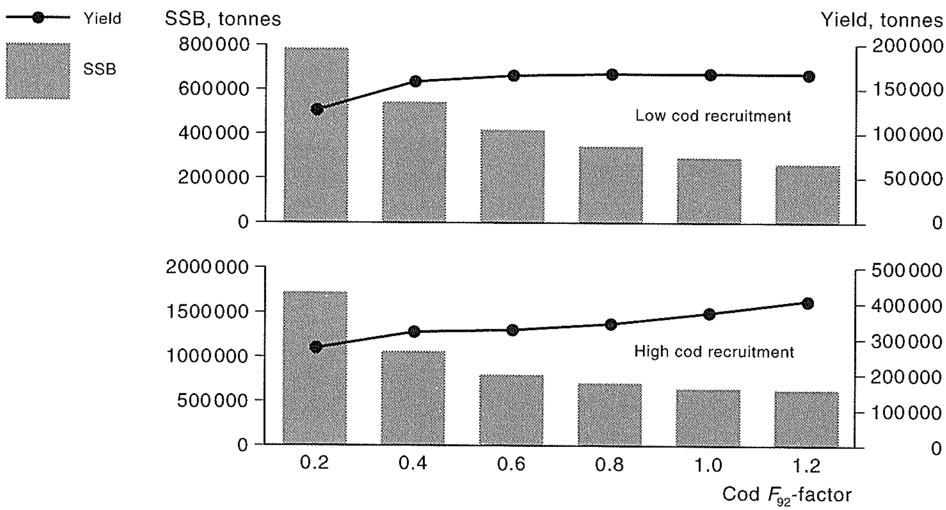

Figure 7. Cod SSB and yield in year 2001 plotted against the fishing mortality (given as a multiplier of the 1992 fishing mortality) on cod in 1993-2001, based on MSVPA/MSFOR forecasts. Low cod recruitment (mean over 1985-1990) was assumed in the upper plot and high cod recruitment (mean over 1977-1990) was assumed in the lower plot.

As the SSB–recruitment relationship is not known for Baltic cod, as for most other fish stocks, such a relationship cannot be included in the MSVPA/MSFOR models. If the relationship becomes known in the future it can easily be incorporated. However, prior to this the MSVPA/MSFOR can be used in the management of Baltic cod, e.g. see Figure 7. These plots are similar to Figure 6 except that they show the SSB and yield of cod instead of sprat. It can be seen that in the case of low recruitment of cod in 1993-2001 (in this case the mean value for 1985-1990) there are no large gains in yield from having *F* higher than 40% of the 1992 level, but an almost doubling in SSB. Thus with low recruitment, the recommendation of *F* being 40% of the 1992 level would be necessary to keep the SSB high and safeguard the recruitment. However, the recruitment cannot be predicted and if the recruitment is high (the 1977-1990 mean) the loss in yield by reducing *F* to 40% of the 1992 level will produce a greater reduction in yield than if cod recruitment is low. Conversely it will mean a significant higher SSB which may be preferable instead of keeping *F* at

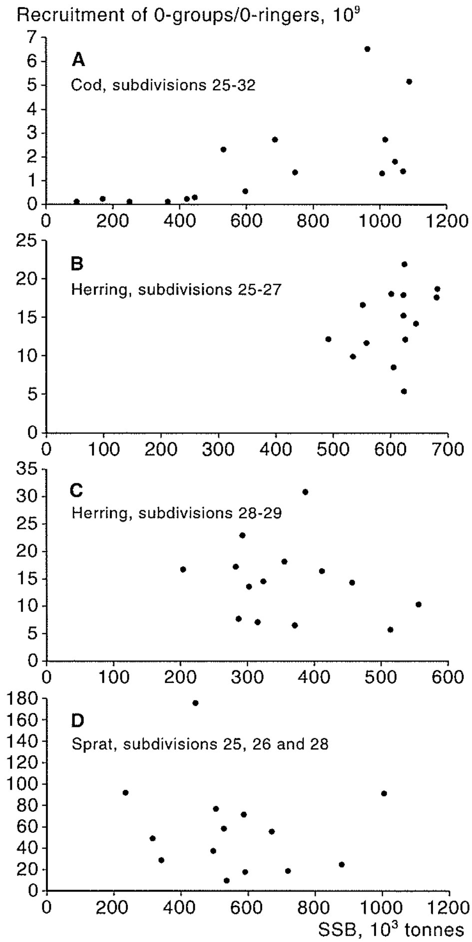

Figure 8A-D. Plots of recruitment of 0-groups against spawning stock biomass (SSB). Data from 1977-1990 from the MSVPA.

the 1992 level. Thus, even though it is not possible to predict the recruitment a sensible long-term management strategy would be to reduce F to, say 40% of the 1992-level.

Considerations similar to those above including stochasticity on cod recruitment and probability profiles of the risk of depleting the SSB to levels below a certain limit, seem worthwhile pursuing in the future.

Stock–recruitment relationships

As stated above, establishment of SSB-R relationships is very important for the future fisheries management of the Baltic fish stocks although the nature of the relationships is unclear. Figure 8A-D shows the SSB-R relationships for cod, the two herring stocks, and sprat in the MSVPA. The data are from the MSVPA for the years 1977-1990 and the figure indicates an SSB-R relationship only for cod. Although the relationship for cod is not mainly causal but due to auto-correlation in recruitment between years. This can be deduced from Figure 9, where it is seen that the recruitment decreased before the SSB decreased. Thus, a more probable hypothesis is that recruitment is more related to some unknown environmental factors than to SSB.

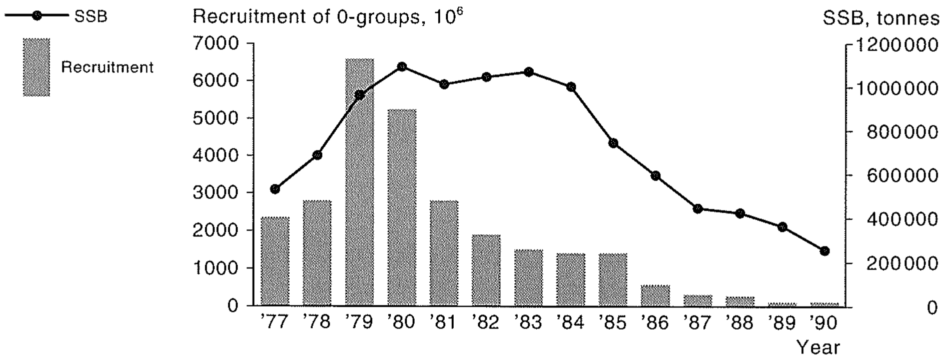

Figure 9. Recruitment of 0-group cod and SSB plotted against year. Data from the MSVPA.

Cod in the central Baltic live at their salinity tolerance limit. It has been shown that cod eggs need salinity levels above about 10 psu in order to float. If the salinity is lower they will sink to the bottom and probably die. Furthermore, if the water oxygen concentration is less than about 2 $ml \cdot l^{-1}$ O_2, the cod eggs will not survive. Thus, salinity level and oxygen concentration at the spawning grounds may be related to the size of the cod year classes. However, it has been very difficult to obtain clear correlations between cod year-class strength and these two hydrographical parameters.; see e.g. Bagge (1993) and Plikshs *et al.* (1993) for more details.

Köster & Schnack (1994) has shown that sprat and to a lesser extent herring predate heavily on cod eggs. In some years and in some areas the predation is sufficiently high to potentially be an important factor in the regulation of cod recruit-

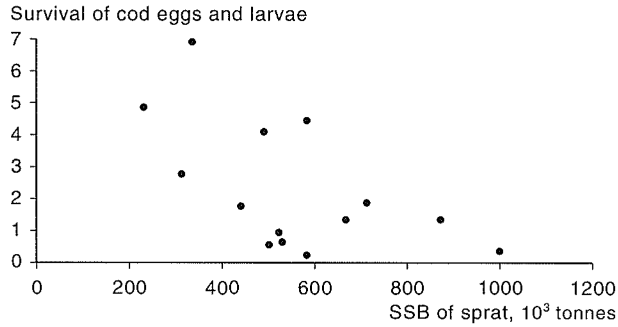

Figure 10. Survival of cod eggs and larvae measured as production of 0-group recruits per unit spawning stock biomass, plotted against SSB of sprat. Data from the MSVPA, 1977-1990.

ment. Although Köster & Schnack use large samples compared to most other similar studies, the inherent variability in the data and the lack of spatial and temporal coverage are still substantial. This makes it difficult to reach firm conclusions although it is encouraging that the survival of cod eggs and larvae until the 0-group stage (here measured as the production of 0-groups per biomass of SSB) appears to be negatively correlated to the SSB of sprat (Figure 10). Caution is, however, needed when interpreting the correlation because, as with the cod SSB-R plot, the correlation might not be causal. For example, if cod recruitment is only related to hydrographical conditions, then the cod SSB will be affected and, subsequently, the sprat SSB will be affected through changed predation mortality.

Investigations of stock–recruitment relationships on pre-recruit stages, of hydrographical effects on cod egg survival and on sprat and herring predation on cod eggs are clearly important fields of research, which deserve much attention in the future.

Conclusions

Fish species interactions in the central Baltic Sea have been very significant in the past. When defining long-term management strategies for the Baltic fisheries it is very important that managers take fish species interactions into account. Ignoring these in the biological advice about fisheries management to the International Baltic Sea Fishery Commission, can be very misleading.

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I have been a member of the ICES Working Group on Multispecies Assessment of Baltic Fish in the period 1984-1992. From 1988 to 1992, I was the chairman of the Working Group and the manager of the international Baltic cod stomach database. The latter has involved the creation, maintenance and updating of the database as well as accomplishing the compilation of the data for input to the MSVPA. However, without the dedicated assistance of my colleagues, Mr B. Gloerfeldt-Tarp, Mr H. Jensen, and Mr I. Bundgaard as well as of the national coordinators of the cod stomach sampling, Mr E. Aro (Finland), Dr O. Bagge (Denmark), Mr J. Modin (Sweden), Mrs D. Uzars (Latvia), and Dr W. Załachowski (Poland), I would not have been able to fulfill my tasks. To sample and process the data have been a tremendous task. It has involved extra crew on cruises with research vessels in the period 1977-1992, extra cruises in areas and at times of the year where it could not by combined with already existing cruises, major efforts in the laboratories when working up the stomachs sampled, and in reporting, computerizing, testing, and compiling the data. Furthermore, thanks to the Nordic Council and the EU for financial support.

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