International Council for the
Exploration of the Sea

C.M. 2001/U:06
Theme Session on Ecosystem
Changes in the Baltic

Fish stock development and environmental variability in the Central Baltic Sea

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Abstract

Cod (*Gadus morhua*), sprat (*Sprattus sprattus*) and herring (*Clupea harengus*) are the dominating commercially important fish species in the Central Baltic Sea. In the present study, stock developments of these species were reconstructed using Multispecies Virtual Population Analysis. The cod stock declined from historic high during the early 1980's to lowest levels on record in the beginning of the 1990's, showing no sign of recovery afterwards. The sprat stock size increased to historic high level concurrently, whereas herring abundance remained relatively stable. A review of recruitment processes influenced by the variable physical environment leading to observed dynamics was performed for cod and sprat, being the species most intensively studied and showing most contrast in stock development. Identified important processes are i) egg production in dependence of ambient hydrographic conditions and food availability, ii) egg developmental success in relation to oxygen concentration and temperature at depths of incubation, iii) egg predation by clupeids dependent on predator-prey overlap, iv) larval development in relation to hydrographic processes and food availability, and v) predation on juveniles. Basically, all above processes negatively affected the cod population, while the sprat stock benefited from them, despite a developing industrial fishery, resulting in a regime shift from a cod to a sprat dominated system in the Central Baltic.

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Introduction

The Baltic Sea is characterized by specific pattern of horizontal and vertical hydrographic gradients, which have significant influence on the spatial distribution and regional community structure of the fish species as well as their zooplanktonic and benthic prey organisms (Arndt, 1989). As typical for estuaries, marine and freshwater organisms are found in a regional succession with species specific ranges of distribution. Depending on their specific preferences and tolerances for salinity, oxygen and temperature, most species in the Baltic approach the border of their general distribution. Hence, they show an increased vulnerability and stock size variability related to changes in the environment and potentially also to the fishery.

The fish community in the open sea areas of the Baltic can be characterized by three species dominating in abundance and production, i.e. cod (*Gadus morhua*), sprat (*Sprattus sprattus*) and herring (*Clupea harengus*), sustaining more than 95% of the commercial catch (Sparholt, 1994). Throughout the last two decades, the cod stock declined from historic high (early 1980's) to lowest levels on record in (beginning of the 1990's), hardly recovering afterwards (ICES, 2001/ACFM:18). This stock development was caused by a combination of recruitment failure and high fishing intensity (Bagge et al., 1994). The decline of the top predator in the system resulted in a release in predation pressure on sprat (Sparholt, 1994), and in combination with high reproductive success and relatively low fishing mortalities in a pronounced increase in sprat stock size (Parmanne et al., 1994; Köster et al., 2001a). Both cod and sprat aggregate in deep Baltic basins to spawn, having historically also largely overlapping spawning times (Bagge et al., 1994; Parmanne et al., 1994). Nevertheless, their reproductive success appears to be out of phase and additionally largely independent of their spawning stock size, suggesting environmental processes to affect recruitment success significantly (e.g. Köster et al., 2000b). The population development of the other abundant clupeid species in the Baltic, herring, seems to be relatively stable, independent of the cod stock development, as only juvenile herring are preyed upon intensively (Parmanne et al., 1994).

In the present study, we reconstructed the stock development of cod, sprat and herring in the Central Baltic Sea using Multispecies Virtual Population Analysis (MSVPA). Further we reviewed recruitment processes influenced by the variable physical environment leading to observed dynamics. In this review we concentrated on cod and sprat as both species show high contrast in stock development and detailed information on processes affecting their reproductive success has accumulated throughout the 1990's.

We identified the following important processes: i) egg production in dependence of ambient hydrographic conditions and food availability, ii) egg developmental success in relation to oxygen concentration and temperature at depths of incubation, iii) egg predation by clupeids dependent on predator-prey overlap, iv) larval feeding success in relation to hydrographic processes and food availability, and v) predation on juveniles. Although not all processes are completely understood and quantified yet, they explain most recent cod and sprat stock trends. Based on this information, we describe how these processes resulted in a regime shift from a cod to a sprat dominated system in the Central Baltic.

As fisheries has as well a pronounced impact on the population dynamics of both species, information on the development of the fishing intensity is given. However, the present study does not intend to give a comprehensive overview of interrelationships between hydrographic conditions, fisheries actions and ultimately stock dynamics, although being a potentially rewarding research area.

Material and methods

The MSVPA incorporates cod as the top-predator in the system and cod, sprat and herring as prey (Sparholt, 1994). This set-up allows to quantify predation on juveniles and the determination of pre-recruit abundance not available from standard assessment (ICES, 2001/ACFM:18; Köster et al. 2001a).

The stock units utilized in the present MSVPA for the Central Baltic are: cod in ICES Sub-divisions 25-29 & 32, sprat in Sub-divisions 25-32 and herring in Sub-divisions 25-29 & 32 including the Gulf of Riga (Fig. 1). As the sprat population in Sub-divisions 30 and 31 is rather low (ICES, 1999/H:5), the MSVPA derived stock estimates refer basically also to Sub-divisions 25-29 & 32. To estimate the predation mortality on these stocks, the cod assessment unit was adjusted accordingly, thus not considering the part of the stock in Sub-divisions 30 and 31. Landings reported in these Sub-divisions are in general less than 1% and in maximum 3.5% of the total catch from the Central Baltic (ICES, 1997/J:2).

The stocks are composed of age-groups 0 to 7 for cod, 0 to 9 for herring and 0 to 7 for sprat with the oldest age-groups handled as plus-groups in cod and herring. Quarterly catch at age in numbers and weight at age in the catch were revised by ICES (1999/H:5) for the years 1977-1997 and updated for the period 1976 and 1998-2000 by ICES (2001/ACFM:18). Weight at age in the catch was assumed to be equal to weight at age in the stock, exceptions being age-groups 0 to 2 for cod. Here, due to size selection by commercial gears, period specific (before 1989 and after 1990) average weights derived from trawl surveys and compiled by ICES (1999/H:5) were applied.

To identify the spawning component of the cod stock, existing maturity estimates were employed as averages over the periods 1980-84 (applied also before 1980), 1985-89 and 1990-94, year specific data for 1995-97 for combined sexes as presented in ICES (1999/H:5), updated with data for 1998 and 1999 according to ICES (1999/ACFM:15 and 2000/ACFM:14). For 2000 an average over the years 1997-1999 was utilized. Maturity ogives of sprat and herring were used as given in ICES (1996/Assess:2), being constant over time and areas.

Quarterly relative diet compositions and individual food rations are based on cod stomach content data covering the period 1977-1993 according to Sub-division (ICES, 1997/J:2). The Sub-division specific data were averaged applying relative distribution pattern obtained from trawl surveys as spatial weights (ICES, 1997/J:2), kept constant for 1996-2000. The quarterly consumption rates were revised based on re-calculated ambient temperatures (ICES, 2001/H:4), according to the procedure outlined by ICES (1999/H:5). The consumption model in use, corresponds to the model applied in the North Sea (ICES, 1997/Assess:16), based on a general model of gastric evacuation, considering actual environmental temperatures and predator weights as additional variables (Temming and Herrmann, 2001). As stomach content data are available for most of the quarters and years covered by the present MSVPA, consumption rates were computed for every predator age-group, quarter and year. Missing quarters/years, i.e. also the years 1974-1977 and 1994-2000 were substituted according to ICES (1999/H:5).

The residual natural mortality rate was assumed to be 0.2 per year, equally distributed over quarters, corresponding to standard MSVPA runs in the Baltic (Sparholt, 1991). Suitability coefficients of prey species age-groups as food of specific predator age-groups (Sparre, 1991) were estimated according to the standard suitability sub-model implemented in the Baltic MSVPA, with the biomass of other food set constant over time, corresponding to earlier MSVPA runs (ICES, 1997/J:2).

The tuning of the MSVPAs was performed with the new 4M-programme routine iteratively running XSAs (Extended Survivor Analysis) and MSVPAs (Vinther, 2001). Abundance indices utilized for tuning originated from the international bottom trawl survey directed to cod, performed annually in February/March (Sparholt and Tomkiewicz, 2000) and the international hydroacoustic survey directed to herring and sprat, conducted annually in September/October (ICES, 2001/ACFM:18). XSA settings were identical to those used in the standard assessment (ICES, 2001/ACFM:18). Fishing mortalities in the terminal year for the 0-groups and for 1-group cod were not estimated in the XSA tuning and values were tuned to reach abundances close to the average values estimated in period 1995 to 1999.

Results

Stock abundance

The stock abundance of cod in the Central Baltic is characterized by a pronounced increase from 1976 to 1980, remaining on a high level until 1983, afterwards steadily declining to lowest level on record in 1991, being since then close to the historic minimum (Fig. 2). The estimated stock size of sprat shows a reverse trend, with a decline from 1975 to 1980, low levels until 1988, followed by a pronounced increase to the highest stock size on record in 1996 and a decline in most recent years. In contrast, the herring stock appeared to be rather stable, with deviations of less than 25% around the long-term mean and a slight downward trend in most recent years.

Spawning stock biomass

Spawning stock biomass (SSB) of cod and sprat follow approximately same time trends as the abundance, however, some deviations are apparent (Fig. 3a). Cod SSB remained longer on a high level until 1985 and recovered to a certain degree after the minimum in early 1990's, which is hardly obvious from abundance estimates. Sprat SSB was relatively stable also in most recent years (Fig. 3b), while the abundance showed a decline from maximum levels by nearly 40%. In contrast, SSB of herring declined by around 50% since the early 1980's (Fig. 3c), a trend which is far less pronounced in stock abundance.

Recruitment

Inspecting the recruitment originated by the spawning stocks, revealed a high reproductive success in cod at intermediate SSB values in the 1970's and declining reproductive success at historically high spawning stocks from 1981 to 1985 (Fig. 3a). Sprat recruitment showed a positive development from mid 1980's to mid 1990's, with high fluctuations in most recent years, virtually independent of the SSB (Fig. 3b). For herring an overall trend of a declining recruitment with declining SSB is indicated, however, with considerable inter-annual variability (Fig. 3c).

Weight at age

Concurrently to the decline in stock size of cod an increase in weight at age is obvious (Fig. 4a). Average weight at age of sprat showed a substantial decline from 1990 to 1997 and a reverse trend in most recent years (Fig. 4b) concurrently to the increase and subsequent decline in stock abundance. Independent of stock size, the weight at age of especially older herring declined from 1983 to 1996 by more than 50% (Fig. 4c).

Predation mortality

A pronounced time trend in cod cannibalism is apparent (Fig. 5a), with increasing predation mortalities until 1983 and a decline until 1991, being stable low afterwards. Age-specific differences in predation mortality are obvious, with cannibalism rates on 0-group being considerably higher (reaching maximum values >1.0) than on 1-group cod (maximum 0.61), especially when considering that the mortality rates on 0-group refer only to a half year period. Predation on 2-group cod was in general low, i.e. less than 50% of the applied residual mortality of 0.2. Sprat 0-group do not suffer from high predation pressure, while age-group 1 (maximum around 1.1) and also to a lesser degree adult sprat do (maximum 0.51). Intense pressure on sprat occurred in 1979-1983, with a subsequent decrease until 1991 driven by the decline in predator population size (Fig. 5b). The time trend in predation mortality of herring is very similar to sprat, however, the absolute values are lower for age-group 1 (in maximum 0.66) and especially for adult herring (in maximum 0.17), while 0-group mortality rates are similar in both species (Fig. 5c).

Fishing mortality

The average fishing mortality of cod age-groups 4-7 increased from 0.4 in 1979 to 1.4 in 1991 and decreased sharply to lowest level on record in the two following years (Fig. 6a). This reduction is caused by rigid enforcement of management measures, i.e. a TAC reduction by 40% and 60% in 1992 and 1993. Afterwards a pronounced increase in fishing mortalities to original high level is indicated. The fishing mortality of sprat and herring were substantially lower throughout the entire time period, i.e. ranging from 0.09 to 0.48 with an increasing trend since early 1990’s.

The corresponding yield to biomass ratios followed in general the development of the fishing mortality, with a less steep decline for cod in the beginning of the 1990’s (Fig. 6b). On average 41% of the cod biomass available in the beginning of the year was removed by the fishery, ranging between 22% in 1978 and 64% in 1991. In sprat and herring the corresponding removals are on average 11% and 16% respectively, with somewhat higher variability in the more short-lived species.

Discussion

Validation of stock trends

Stock development trends derived by the multispecies and the standard stock assessment (ICES, 2001/ACFM:18) are rather similar, with the MSVPA additionally covering younger age-groups (i.e. age-group 0 and for cod additionally age-group 1). Revision of the quarterly consumption rates of cod did not change this feature. The reconstructed stock developments are furthermore in accordance with trawl and hydroacoustic surveys utilized for tuning of the XSA (ICES, 2001/ACFM:18) as well as the

MSVPA (Köster et al., 2001a). Deviations in the dynamics of stock abundance and spawning stock biomass in our analysis can be explained in all three species by changes in weight at age, and in cod additionally by an earlier maturation in the 1990’s compared to 1980's (Tomkiewicz et al., 1997).

Egg production in dependence of hydrographic conditions and food availability

An association between stock structure, timing and duration of spawning is potentially an important source of variability in the reproductive success of the Baltic fish stocks due to seasonal changes in environmental parameters (MacKenzie et al., 1996), but also temporal overlap of early life stages with predators (Köster and Möllmann, 2000a) and transport into areas with sufficient food supply for larvae (Hinrichsen et al., 2001a,b). The duration of the spawning activity of the cod stock depends on its size structure and sex composition, however the timing of peak spawning is hardly affected (Tomkiewicz and Köster, 1999). Consequently, the observed shift in the main spawning time of cod from May/June to July/August in the beginning of the 1990’s is likely to be caused by other processes as well (Wieland et al., 2000). Potential candidates are removal of early spawners by the fishery mainly directed to pre-spawning and early spawning concentrations (ICES 1999/ACFM:15) and a coupling to ambient temperature (Wieland et al., 2000), which were on average higher in the 1990’s then before.

Age-specific sex ratios and maturity ogives of cod derived from the International Baltic Trawl Survey (Tomkiewicz et al., 1997; STORE 2001) showed: i) a dominance of females with increasing age, ii) that males generally mature at a younger age than females, iii) that the age at which sexual maturation occurs, increases with distance from Kattegat and the Danish Straits independent of sex and iv) that maturity at age shows significant variability between different time periods. Thus, the quantity of the egg production of Baltic cod depends on the age structure of the stock, as well as the location and the time period. Variability in maturation appears to be coupled to growth rates, reflected in concurrently increasing weight at age and decreasing age at attaining sexual maturity (STORE, 2001).

An analysis of individual Baltic cod fecundity revealed that the relative fecundity is independent of body size (Kraus et al., 2000). Relative fecundity varied significantly between years, but neither between spawning areas nor between different months within one spawning season (Kraus et al., 2000). On individual level a weak impact of the nutritional status of the female on the relative fecundity was detected, while on population level a clear dependence on food availability was resolved (Kraus et al., 2001). Inclusion of temperature improved the relationship further, but had overall a limited influence on relative fecundity. In conclusion, an increase in weight at age, a decline in size/age of attaining maturity and an increasing fecundity with decreasing stock size and increasing prey availability has had a compensating effect on reproductive success, stabilizing recruitment since late 1980’s, however, on a low level.

In Baltic cod a significant relationship exists between the potential egg production by the spawning stock and the realized egg production (Köster et al., 2001b). Apart from problems in parametrization of each of the input data series, remaining variability may be related to atresia due to unfavourable environmental conditions during spawning (Kjesbu et al., 1991), variable fertilization success in relation to salinity changes (Westin and Nissling, 1991) and differences in egg mortality already in the first developmental stage.

A number of investigations on different species, including cod, suggest that egg and larval viability is positively related to egg size (see Trippel et al., 1997 for review), and that egg size vary according to female age/size and condition as well as spawning experience. For Baltic cod relationships between i) egg size and female size, ii) egg size and larval size/growth, iii) egg size and survival during the yolk sac stage, and iv) egg size and egg buoyancy, have been established (Nissling et al., 1998; Vallin and Nissling, 2000). This implies higher egg and larval survival for offspring originating from large females, especially as larger and more buoyant eggs have higher chances to avoid oxygen depleted bottom water layers. Consequently the reduction in the share of older females in the spawning stock from mid 1980's to early 1990's (Wieland et al., 2000), caused by heavy fishing pressure, has had a negative affect on the reproductive success of the Central Baltic cod stock (Vallin and Nissling, 2000).

The temporal pattern of sprat spawning with peak spawning activity in May has remained relatively stable throughout the 1990's (STORE, 2001). In consequence sprat spawned in the 1990's significantly earlier than cod, thus encountering different environmental conditions and reducing the temporal overlap with their predator in spawning areas. This may explain deviations in reproductive success of both species and indicates a release in sprat predation pressure on spawning grounds.

Available data on sexual maturity at age indicate significant inter-annual variability in proportions of sprat being sexually mature at an age of 1, which has earlier been related to winter temperature (Elwertowski, 1960). Furthermore, the relative batch fecundity shows a significant intra- and inter-annual variability (Alekseeva et al., 1997; STORE, 2001). An existing significant relationship between SSB and realized egg production can be improved by incorporating temperature in the intermediate water in May and growth anomaly through the preceding three quarters as a measure of the nutritional status of the adults (Köster et al., 2001b). The effect of temperature on the realized egg production may have several reasons: i) low winter temperature, reflected in low intermediate water temperature in May, may in fact be responsible for changes in the nutritional condition and growth of sprat (e.g. Elwertowski, 1960) and by this reduce the individual egg production, ii) low temperature in pre-spawning periods may reduce the batch fecundity and number of batches spawned (Petrowa 1960), and iii) low temperatures before and during spawning season may cause a delay in the onset and the peak of spawning activity (e.g. Grimm and Herra, 1984) resulting in a mis-match of peak spawning activity and ichthyoplankton surveys.

A coupling of growth and sexual maturation or individual egg production has not yet been demonstrated for Baltic sprat, but appears to be possible similar to cod, especially as the average weight at age showed a substantial decline throughout the 1990's. The decline appears to be related to a reduced food availability of calanoid copepods per individual sprat (Möllmann, unpublished), mainly caused by a reduction in abundance of the largest copepod species *Pseudocalanus elongatus* in the Baltic (Möllmann et al, 2001) and a concurrent increase in stock size of sprat. This limitation in food availability may have acted as a compensatory mechanism in reproductive success via a decrease in individual egg production and potentially an increased age of attaining sexual maturation. However, given the high inter-annual variability in recruitment success in the 2nd half of the 1990's, other variability generating processes appear to be of higher importance for the reproductive success.

Egg developmental success in relation to oxygen concentration and temperature at depths of incubation

In the Baltic, early life stage survival is known to be highly influenced by hydrographic conditions in the spawning areas (e.g. Bagge et al., 1994; Grauman and Yula, 1989; Plikshs et al., 1993; Parmanne et al., 1994). The observation that alive cod eggs are encountered in water layers with oxygen concentrations >2ml/l and temperature >1.5°C and that a salinity of 11 psu is necessary for successful fertilization lead to the definition of the so called reproductive volume (RV), i.e. the water volume sustaining cod egg development (Plikshs et al., 1993). Processes affecting the RV are: i) the magnitude of inflows of saline oxygenated water from the western Baltic (MacKenzie et al., 2000), ii) temperature regimes in the western Baltic during winter affecting the oxygen solubility prior to advection and iii) river runoff (Hinrichsen et al., 2001c) as well as iv) oxygen consumption by biological processes (Hansson and Rudstam, 1990). A linkage of atmospheric conditions and RV has been demonstrated by an analysis of changes in the NAO indices and/or local atmospheric conditions (Hinrichsen et al., 2001c). Resolving the potential egg production by cod spatially, showed that in some years a substantial fraction of the total annual egg production has been unsuccessful (in terms of recruit production), because eggs were exposed to sub-optimal oxygen concentrations in eastern spawning areas (Köster et al., 2001c). This mis-match in egg production and suitable environmental conditions for egg development explains the drastic decline in reproductive success of cod from 1981 to 1985 despite high egg production.

Due to differences in egg specific gravity, egg development of cod and sprat occurs at different depths. Whereas cod eggs are neutrally buoyant at salinities of 12-17 psu (Nissling et al., 1994), the range for sprat eggs is 7-13 psu (Grauman, 1965), i.e. the majority of sprat eggs occur at lower depths than cod. This implies that sprat egg survival is less affected by poor oxygen conditions than the survival of cod eggs. As sprat eggs occur at depths where the water temperature is affected by winter cooling (Wieland and Zuzarte, 1991), egg and larval development may be influenced by extreme water temperatures. In fact, weak year classes of Baltic sprat have been associated to severe winters accompanied with low water temperatures during peak spawning (e.g. Kalejs and Ojaveer, 1989; Grauman and Yula, 1989). A significant impact of temperature on egg developmental success has been resolved in the North Sea (Thompson et al., 1981) and confirmed for the Baltic (Nissling, unpublished), with temperatures below 4°C significantly affecting the egg survival success. As these temperatures occur regularly in the intermediate water layer, originating from winter cooling, an effect on egg survival especially after severe winter situations has to be expected. In this respect, the absence of severe winters situations since 1986/1987 indicate overall favourable thermal conditions for sprat egg survival most likely contributing to the in general high recruitment success.

Egg predation by clupeids dependent on predator-prey overlap

A substantial predation on cod eggs by clupeids has been described for the major spawning area of the cod stock, i.e. the Bornholm Basin. Egg predation is most intense at the beginning of the cod spawning season, with sprat being the major predator (Köster and Möllmann, 2000a). At this time of the year spring spawning herring concentrate in their coastal spawning areas not contributing to the predation-induced egg mortality. Sprat spawn in the Bornholm Basin from March to July, thus concentrating in cod spawning areas in times of high cod egg abundance. After ceased spawning activity sprat population leave their spawning area, resulting in a reduced predation pressure (Köster and Schnack, 1994). With the return of the herring from the coastal areas to their feeding grounds in the Bornholm Basin, the predation on cod eggs by herring increases to considerable levels. The shift of cod peak spawning time from spring to summer (Wieland et al., 2000) resulted in a decreasing predation pressure on cod eggs by sprat, due to a reduced temporal overlap between predator and prey. Additionally a decline in individual sprat predation on cod eggs was observed from 1993-1996, despite of relatively high cod egg abundance in the plankton. This is partly explainable by a reduced vertical overlap between predator and prey. Due to the increased salinity after the 1993 major Baltic inflow, cod eggs were floating in shallower water layers, while clupeids were deeper distributed, due to enhanced oxygen concentration in the bottom water (Köster and Möllmann, 2000a) Thus, predation pressure on cod eggs appears to be higher in stagnation periods when the vertical overlap between predator and prey is enhanced, meaning that cod eggs suffer in these periods from adverse hydrographic conditions and predation.

Egg cannibalism was found to be an important source of sprat egg mortality in the Bornholm Basin (Köster and Möllmann, 2000b). In contrast, the process appears to be of less importance in the more eastern spawning areas. This has been explained by a more limited vertical overlap between predator and prey in these areas, also responsible for a significant reduction in predation pressure in the Bornholm Basin after the last major Baltic inflow in 1993 (see above). The intensive egg cannibalism prior to the last major inflow contributed to the stable sprat stock size in the Bornholm Basin, concurrently to a significant increase in other areas of the Baltic monitored by international hydroacoustic surveys (Köster et al., 2001a). When egg cannibalism was reduced, reproductive success in the area increased and resulted in highest 0-group recruitment on record in 1994 and 1995.

Larval development in relation to hydrography and food availability

Behaviour studies conducted with cod larvae demonstrated that low oxygen concentration has an impact on larval mortality (Nissling, 1994) and that egg incubation at low oxygen impacts on larval activity as well (Rohlf, 1999). Furthermore, these experiments revealed that vertical migration into upper water layers is not started before day 4 after hatch. Hence, a significant impact of the environment within and below the halocline on larval survival can be expected. In an attempt to explain the variability of late cod egg production and larval abundance in the Bornholm Basin, Köster et al. (2001c) tested various environmental variables, i.e. the oxygen concentration in and below the halocline, temperature in the intermediate water and wind driven transport, for their explanatory power. However, the authors were unable to explain the major part of the variability in larval abundance. This lead to the conclusion that either other factors influence the survival until the larval stage, or the variability in larval abundance (integrated over all developmental stages) is too high to detect a major impact of tested factors.

For sprat larvae, an impact of the temperature in the intermediate water on larval survival has been detected by Köster et al. (2001c). This positive effect of higher spring temperature on sprat larval abundance has been explained earlier by the positive effect of higher temperature on the dynamics of the copepod *Temora longicornis*, being the main food item of sprat (Grauman and Yula, 1989; Kalejs and Ojaveer, 1989). In consequence, warm winters since the late 1980´s favoured not only sprat egg production and survival, but also larval growth and survival.

The effect of food availability on growth and survival of cod larvae has been investigated by a coupled hydro/trophodynamic individual-based model (IBM) (Hinrichsen et al., 2001b). Model results suggest the necessity of co-occurrence of peak prey and larval abundances as well as favourable oceanographic conditions for high survival rates. Especially the strong decline of the *Pseudocalanus elongatus* stock during the last two decades as a result of low salinities (Möllmann et al., 2000), has the consequence that early cod larvae changed from a non-food limited to a food limited state. If *P. elongatus* nauplii are present, high survival rates occurred during spring and early summer, whereas omitting *P. elongatus* from the prey field resulted in high mortality rates at this time of the year and only late hatched larvae had chances to survive (Hinrichsen et al., 2001b). Thus, low *P. elongatus* availability may have contributed to the low recruitment of cod since the late 1980s.

Also sprat larvae may face food limitations, however, they are usually drifted out of the spawning areas more rapidly than cod larvae due to their shallower occurrence in the water column (e.g. Wieland and Zuzarte, 1991). Thus, drift in more shallow water areas with higher abundance of *Acartia* spp. and *Temora longicornis* nauplii, being their preferred food items (Voss and Köster, 2001) appears to be the normal case.

Predation on juveniles

Beside predation on cod eggs, juvenile cod suffer from substantial cannibalism (Sparholt, 1994; Neuenfeldt and Köster, 2000). As in other cod stocks, the intensity of cannibalism is related to predator abundance , but also to the area occupied by the juveniles depending on their abundance (Anderson and Gregory, 2000). Apart from medium- to long-term distribution changes, inter-annual variability in cannibalism may be influenced by changing hydrographic conditions as well (Uzars and Plikshs, 2000). For example, low oxygen concentration in the deep Baltic basins may force the adults into shallower slope areas and low temperature in shallow waters may force juveniles into deeper water, by this increasing the spatial overlap between predator and prey and hence cannibalism. This suggests that the process is most pronounced in stagnation periods, especially after cold winters.

Predation on 0-group sprat by cod regularly happens, although predation mortality rates from MSVPA are significantly lower than for 1-group sprat. The intensity of the predation is most likely modulated as well by hydrographic conditions and species specific preferences and tolerance levels to hydrographic variables, resulting in variable potential predator/prey encounter volumes (Neuenfeldt, 2001).

Regime shift from a cod to a sprat dominated system

As seen from the results of the MSVPA, the upper trophic levels of the Central Baltic changed during the last 20 years from a cod- to a sprat-dominated system (Fig. 7). The decline of the cod stock was caused by a recruitment failure, which according to our review was mainly driven by: i) anoxic conditions in deep water layers of spawning sites causing high egg mortalities, ii) high egg predation by clupeid predators, iii) reduced larval survival due to the decrease in abundance of the main food item *P. elongatus*, and iv) high juvenile cannibalism at high stock size. The intensity and significance of all these processes are in one way or the other steered by the hydrographic conditions, which were in the 1990´s characterized by low salinity due to lacking inflow of highly saline water from the North Sea and increased run off, but as well by warmer thermal conditions. A increasing fishing pressure accelerated the decline of the cod stock, with current exploitation levels being still on a very high level. The decline of the cod stock released sprat from predation pressure, which in combination with high reproductive success, due to in general favourable temperature conditions enhancing egg and larval survival, resulted in exceptionally high sprat stock sizes in the 1990s. Indications for compensatory processes in growth, maturation and individual egg production exist for both species, however, appear to be of limited impact on the stock dynamics.

As a result of these processes, a dominance of one of either predator may stabilize a cod-dominated or a sprat-dominated system. Destabilization of the sprat dominated system may be caused either by unfavourable hydrographic conditions for reproduction, e.g. low water temperatures in spring following severe winter situations and subsequent recruitment failures of sprat, or high mortalities caused by the fishery, with concurrent low fishing pressure on cod and North Sea inflow events.

Acknowledgement

All participants of the Baltic STORE project have contributed their experience and knowledge to the present review and this is gratefully acknowledged. The present study has been carried out with financial support from the Commission of the European Communities, Agriculture and Fisheries (FAIR) specific RTD programme: CT98-3959 “STORE”. It does not necessarily reflect the view of the Commission and in no way anticipates the Commission’s future policy in this area.

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Figure captions

Figure 1. Study area of the Baltic with ICES Sub-divisions (numbers).

Figure 2. Population sizes of cod, sprat and herring (age-group 1+, beginning of the year) in the Central Baltic.

Figure 3. Spawning stock biomass (SSB) (2nd quarter) and recruitment (age-group 0) of cod (a), sprat (b) and herring (c) in the Central Baltic.

Figure 4. Average weight at age (beginning of the year) of cod (a), herring (b) and sprat (c) in the Central Baltic.

Figure 5. Annual predation mortality rates of cod age-group 0, 1 and 2 (a), sprat age-group 0, 1 and 2-5 (b), herring 0, 1 and 2-7 (c) in the Central Baltic. Note predation mortality of 0-group refer to 3rd and 4th quarter.

Figure 6. Annual average fishing mortality rates of sprat and herring age-group 3-5 and cod age-group 4-7 (a) and yield per biomass ratio of the three species in the Central Baltic (b).

Figure 7. Schematic presentation of processes stabilizing a cod or sprat dominated system in the Central Baltic. Note the vertical line represents the situation in the 2nd half of the 1990’s with the regime shift taking place in late 1980’s and early 1990’s.

Fig. 1

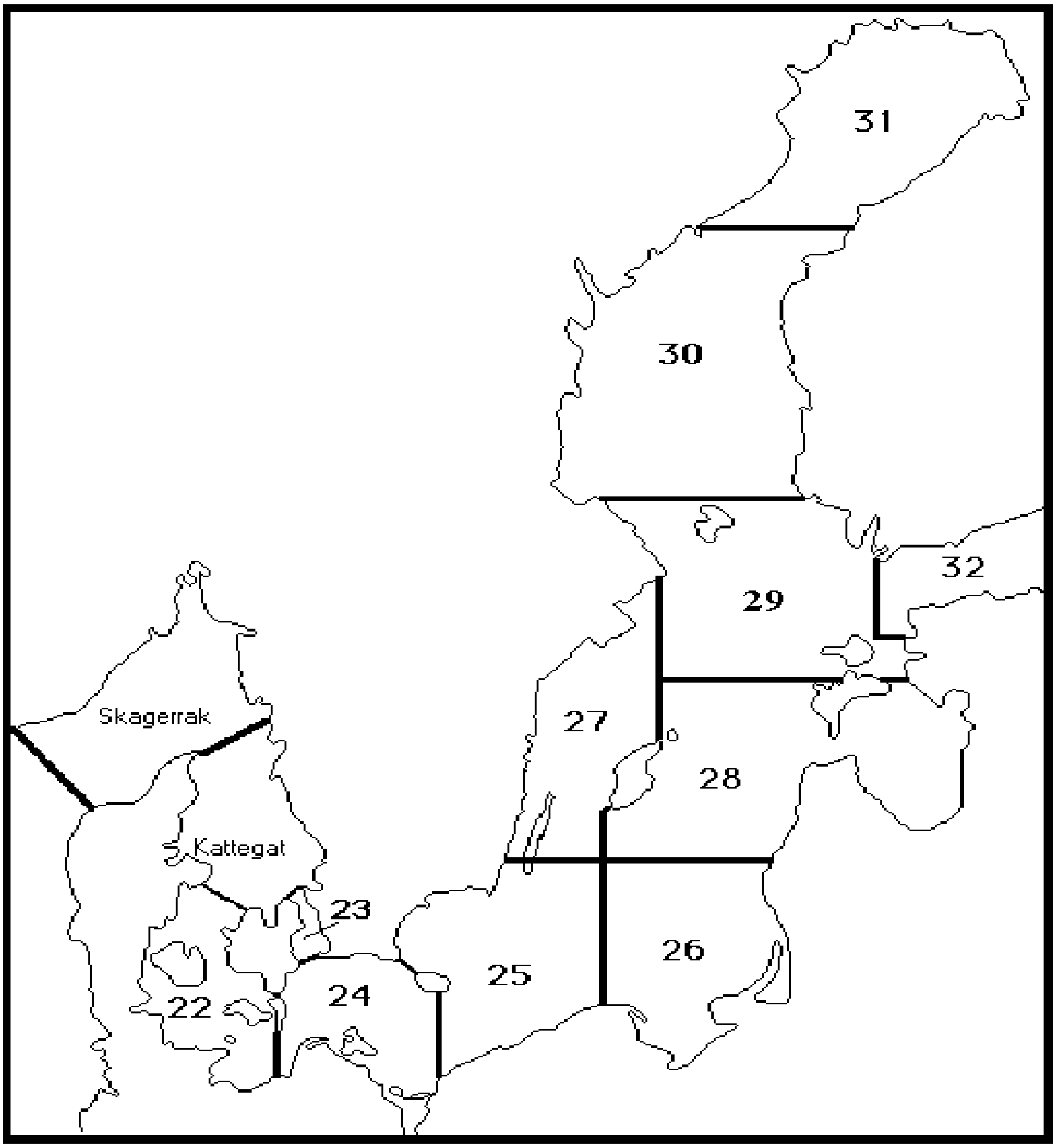


Fig. 2

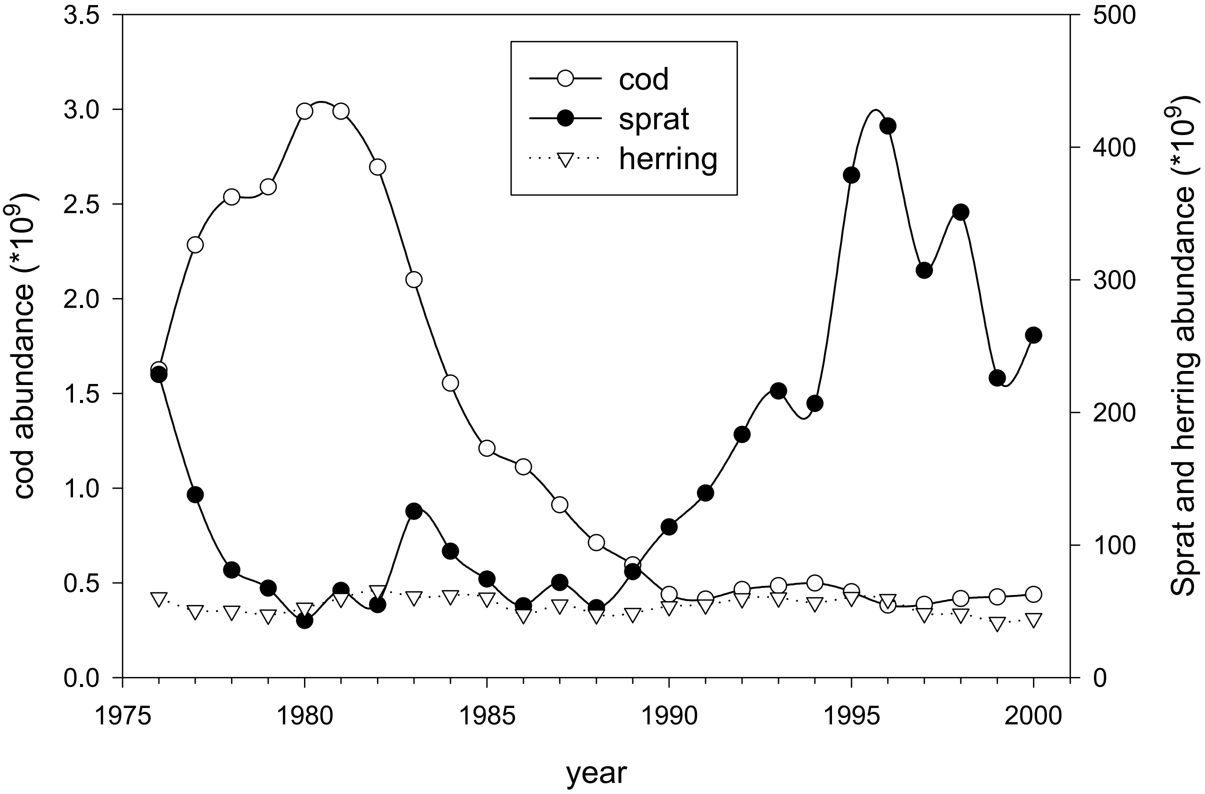

cod
sprat
herring
cod abundance (*10^9)
Sprat and herring abundance (*10^9)
year
0.0
0.5
1.0
1.5
2.0
2.5
3.0
3.5
0
100
200
300
400
500
1975
1980
1985
1990
1995
2000

Fig. 3

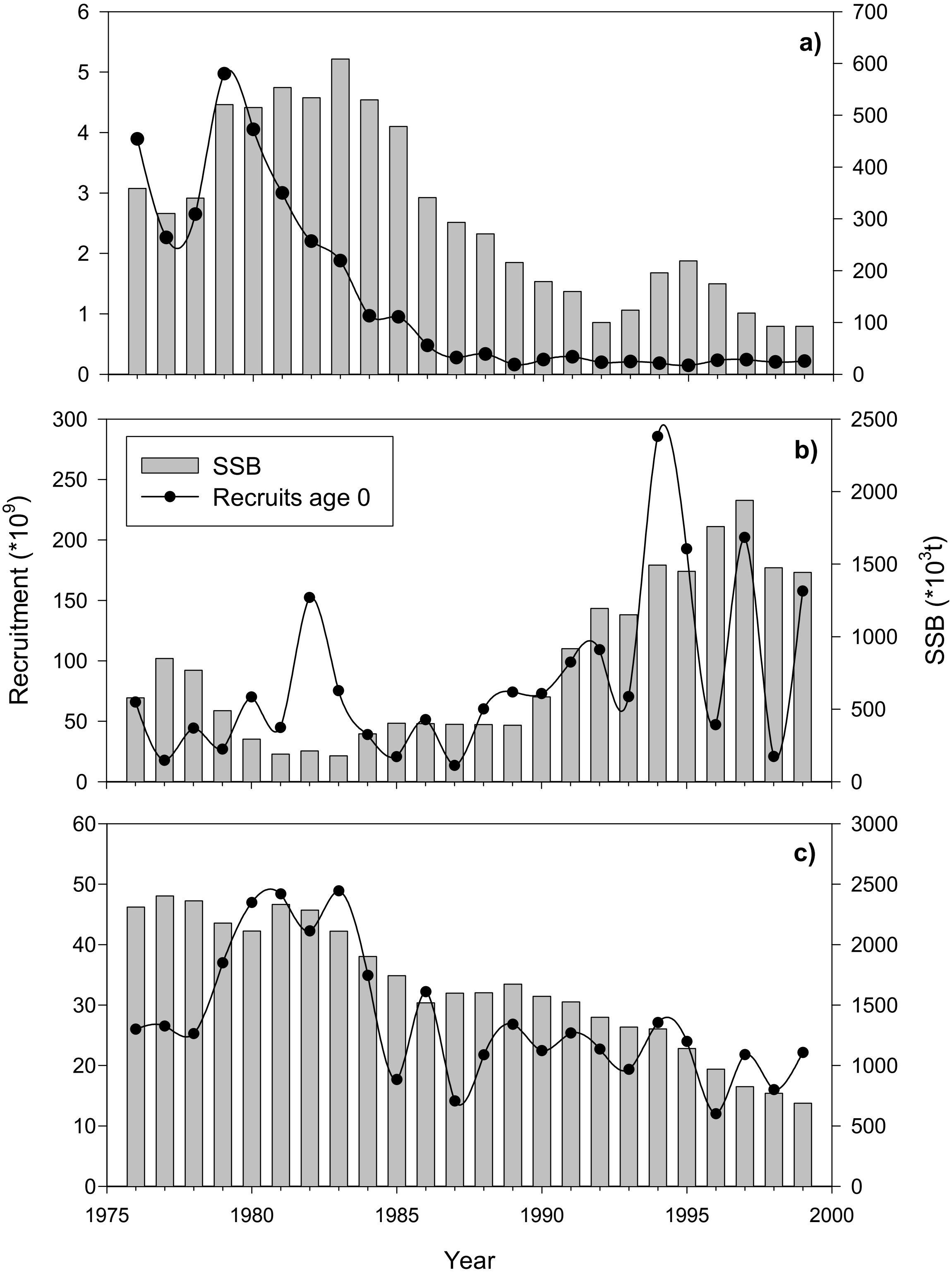

a)
b)
c)
SSB
Recruits age 0
Recruitment (*10^9)
SSB (*10^{3}t)
Year
0
1
2
3
4
5
6
0
100
200
300
400
500
600
700
0
50
100
150
200
250
300
0
500
1000
1500
2000
2500
0
10
20
30
40
50
60
0
500
1000
1500
2000
2500
3000
1975
1980
1985
1990
1995
2000

Fig. 4

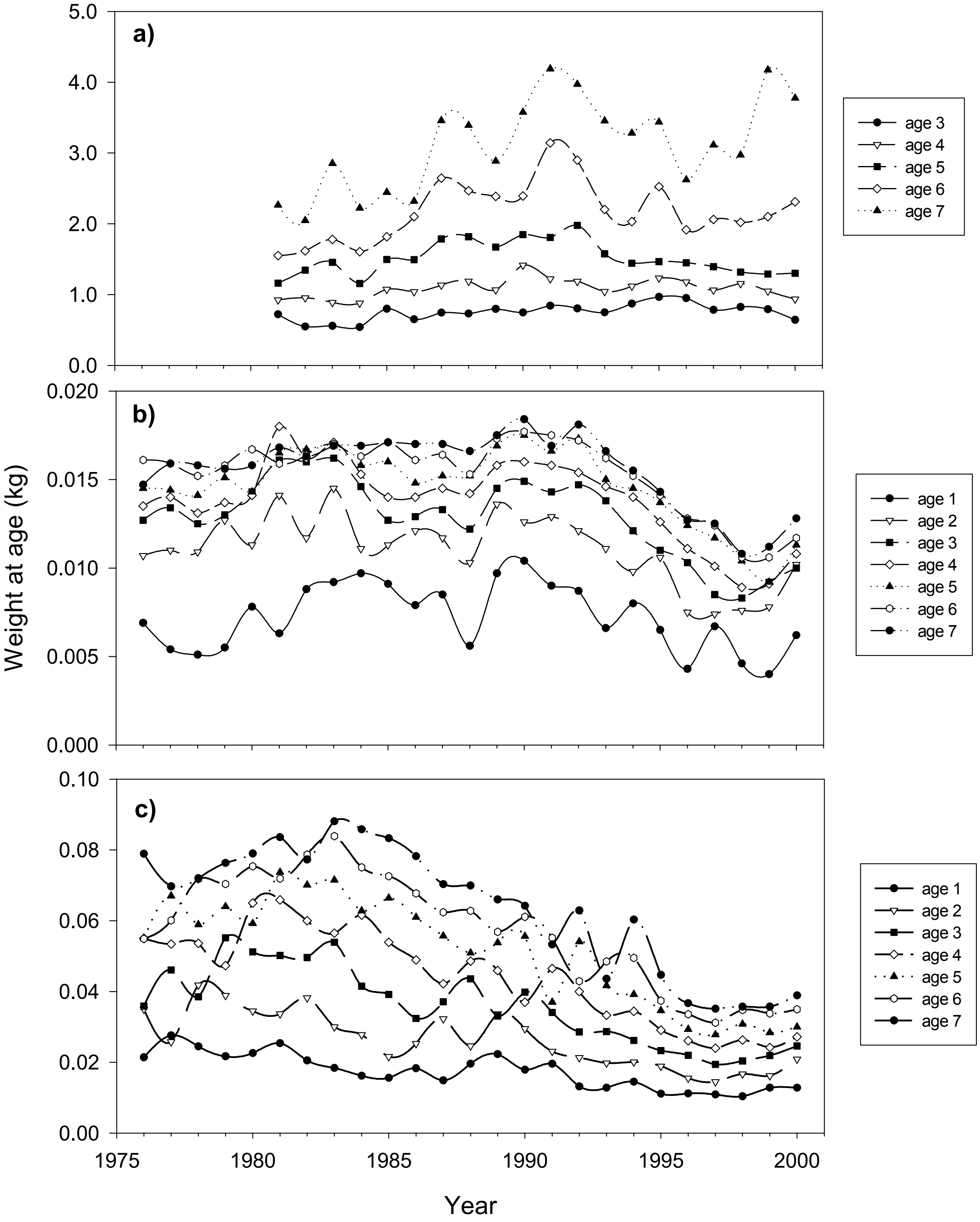

a)
b)
c)
Weight at age (kg)
Year
5.0
4.0
3.0
2.0
1.0
0.0
0.020
0.015
0.010
0.005
0.000
0.10
0.08
0.06
0.04
0.02
0.00
1975
1980
1985
1990
1995
2000
age 1
age 2
age 3
age 4
age 5
age 6
age 7

Fig. 5

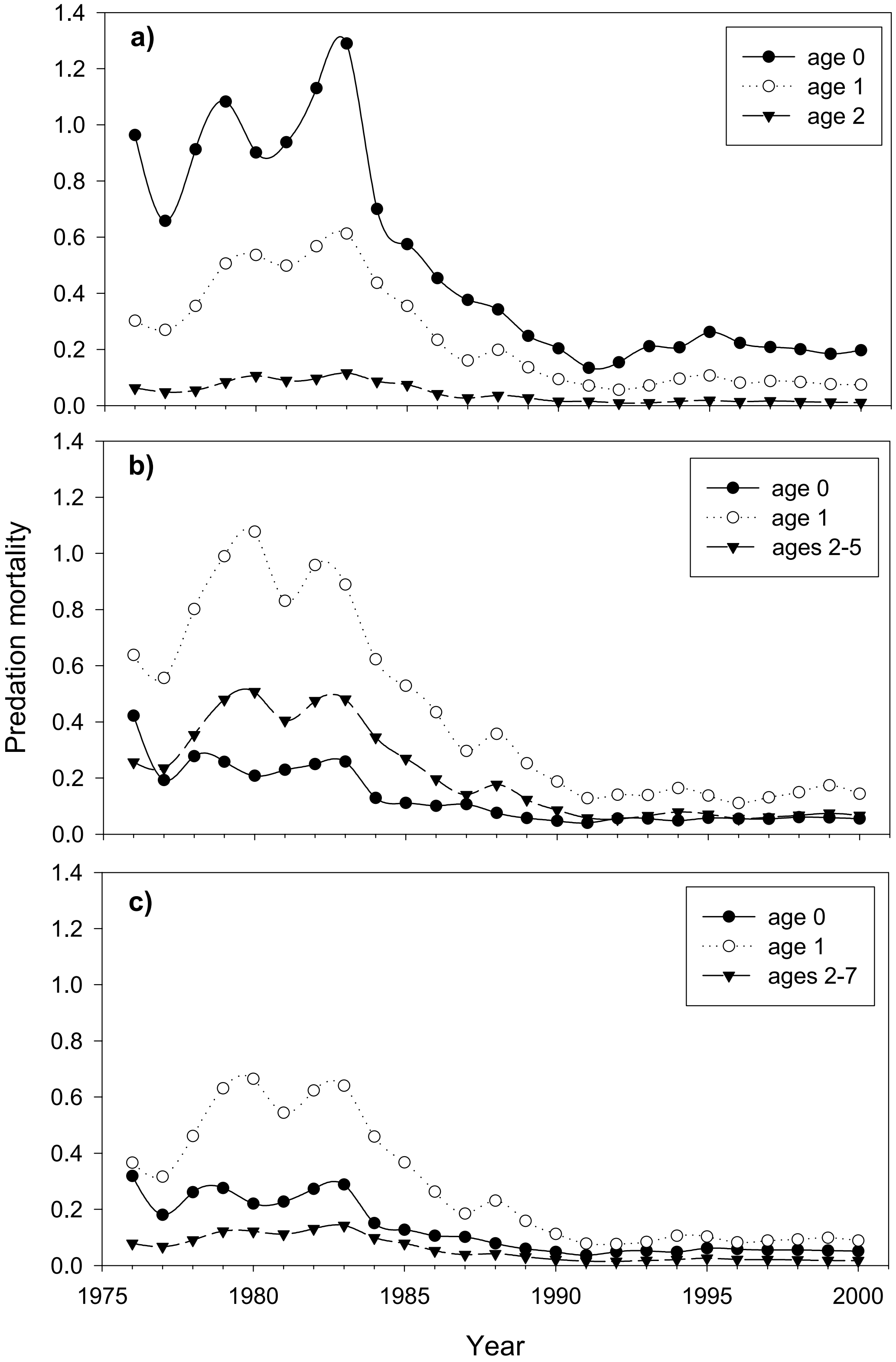

a)
age 0
age 1
age 2
b)
age 0
age 1
ages 2-5
c)
age 0
age 1
ages 2-7
Predation mortality
0.0
0.2
0.4
0.6
0.8
1.0
1.2
1.4
1975
1980
1985
1990
1995
2000
Year

Fig. 6

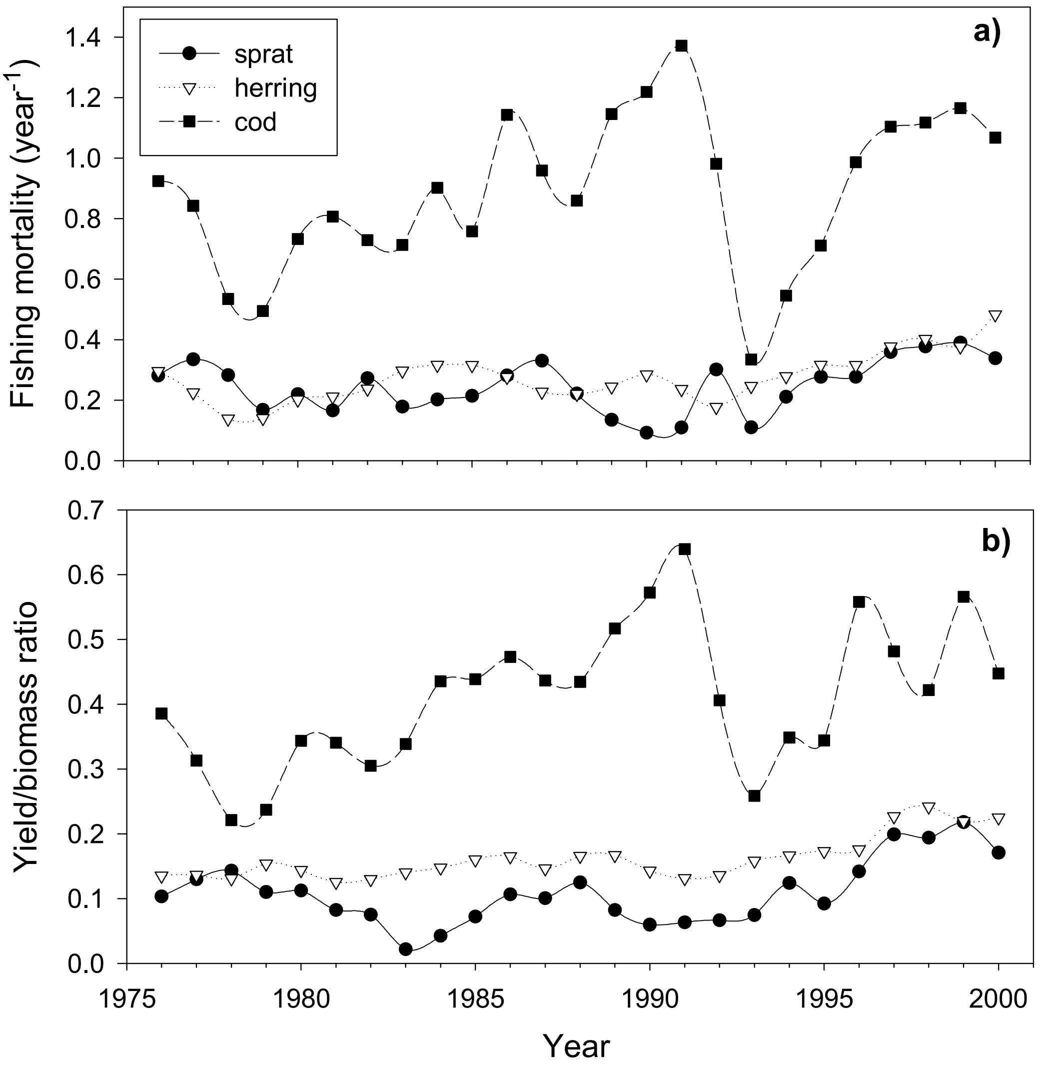
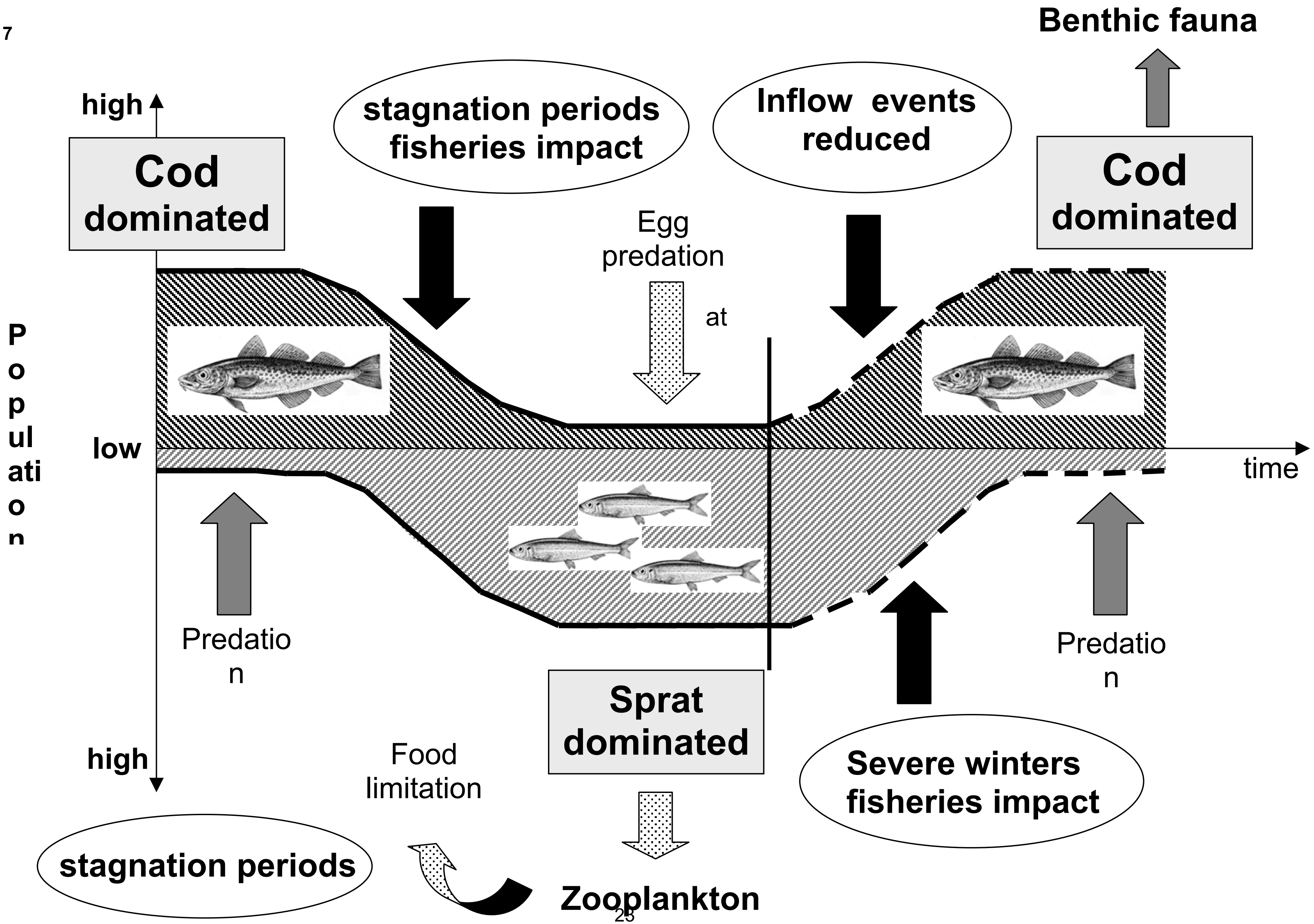

a)
b)
sprat
herring
cod
Fishing mortality (year^{-1})
Yield/biomass ratio
Year
0.0
0.2
0.4
0.6
0.8
1.0
1.2
1.4
0.0
0.1
0.2
0.3
0.4
0.5
0.6
0.7
1975
1980
1985
1990
1995
2000

Fig. 7


Benthic fauna
high
Cod dominated
stagnation periods fisheries impact
Inflow events reduced
Cod dominated
Egg predation
at
P o p ul ati o n
low
time
Predatio n
Predatio n
high
Food limitation
Sprat dominated
Severe winters fisheries impact
stagnation periods
Zooplankton