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The Eastern Baltic cod stock in the 20th century: Resolving impacts of fishing, human-induced trophic changes and climate

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Abstract

The Baltic Sea has experienced large human-induced changes in the 20th century, including eradication of marine mammals, eutrophication and increased fishing pressure. In addition, major variations have occurred in hydrographic conditions related to large scale climatic variability. Due to long time series of data and large contrasts in the stock size and in forcing factors, cod (*Gadus morhua*) in the Baltic Sea provides a unique opportunity to investigate the relative impacts of top-down and bottom-up forces on a decadal-scale dynamics of a predator fish population in a large marine ecosystem. We show how various human activities interacted with a cod population and demonstrate that a combination of both top-down and bottom-up processes have determined the dynamics of the eastern Baltic cod stock in the 20th century.

Introduction

Several fish populations at higher trophic levels have declined over the past decades or centuries (Jackson et al. 2001; Myers and Worm 2003). This has in many cases resulted in large-scale changes in lower trophic levels influencing the structure and functioning of the ecosystems (Frank et al. 2005; Daskalov et al. 2007). Changes in the abundances of predator fish species are often believed to be largely related to fishing, however climate, predation and resource-mediated bottom-up processes have been shown to play important roles in the dynamics of fish populations at higher trophic levels (Cushing 1982; Harwood and Croxall 1988; Frank et al. 2007). An integrated view on the relative roles of top-down and bottom-up forcings in marine ecosystems is emerging (Frank et al. 2007) and is of great importance in order to improve the knowledge of functioning of the ecosystems. Understanding the magnitude of human impacts compared to natural variability is of particular importance in order to recover depleted fish stocks and sustainably manage fisheries and ecosystems. Separating the effects of different factors on fish populations is however often difficult, partly related to the shortness of available time series and to co-varying driving forces.

The Baltic Sea is an example of an ecosystem where a drastic reduction in the main predator fish, i.e. cod, in the late 1980s apparently resulted in a multi-level trophic cascade (Casini et al. 2008). The Baltic case provides a unique opportunity to evaluate the potential effects of top-down and bottom-up forcings on a predator population, in a historically much longer time scale than usually possible to consider. For the Baltic Sea, information on stock dynamics of cod and on several ecosystem and environmental parameters are available since the early decades of the 20th century and large contrasts in top-down pressures on cod as well as in climate and in resource- driven bottom up forcing have occurred since then. These changes in the Baltic ecosystem resulted from different human perturbations at a multi-decadal scale that can be seen as a large-scale eco-engineering experiment. During the period from the early 1900s to the 1940s the abundance of top predators (i.e. seals) was reduced more than five-fold by intensive hunting (Harding and Härkönen 1999). Nutrient inputs to the Baltic increased three to five-fold during the 1940s-1980s as a consequence of increased use of fertilizers and intensified industrialization after the Second World War (Larsson et al. 1985; Jansson and Dahlberg 1999). The fishing mortality on eastern Baltic cod was below 0.2 until the late 1930s and increased to above 1.0 by the 1960s (Eero et al. 2008). In addition, climate-driven hydrographic conditions influencing cod recruitment (e.g., Köster et al. 2005) varied widely in the past century (Matthäus 2006).

In this paper we compare changes in these key forcing factors: climate, predation, nutrient load and fishing with changes in the eastern Baltic cod population since 1925. We do not attempt to resolve or quantify the mechanisms behind inter-annual variations in the cod stock, but focus on constructing and interpreting the historically observed patterns to elucidate the potential relative impacts of anthropogenic disturbances compared to climate forcing on multi-decadal changes in a cod population. The study is a contribution towards better understanding of the Baltic ecosystem functioning and sustainable management of the fisheries and the ecosystem.

Material and methods

Cod stock size and fishing mortality

The eastern Baltic cod (ICES Subdivisions 25-32, *http://www.ices.dk/aboutus/icesareas/ICES_areas_Arc9_Baltic_300.pdf*) spawning stock biomass (SSB), stock numbers and fishing mortalities for the entire management area and by Subdivisions (SD) were available from ICES assessments from 1966 and 1976 onwards, respectively (ICES 2006; 2007). The estimates back to 1946 were taken from Eero et al. (2007a).

The SSB and fishing mortality rates in 1925-1944 were based on the estimates for specific years and periods (Eero et al. 2008), combined with annual catch per unit of effort (CPUE) data as an indicator of inter-annual developments in stock size. We utilized the national CPUE data for hook and line fisheries by Sweden in SDs 25 and 28 and by Latvia in the central Baltic in 1925-1938 (Eero et al. 2007b). The effort represented total numbers of motorboats and fishing days in the Swedish and Latvian fisheries in the particular areas, respectively. SSBs estimated from different methods by Eero et al. (2008) were averaged. The SSB and the standardized average CPUE in 1925-1938 were significantly correlated ($r^2 = 0.695$, $p<0.01$), however the SSB estimates indicated an increase in the stock size a few years earlier in the 1930s compared to the development of CPUE. As the annual variability was considered to be better represented by CPUE data, we used the relationship between CPUE and SSB in 1925-1929 when major deviations in the trends between the two were not observed to adjust the SSB values in 1930-1938. The fishing mortalities were adjusted accordingly as estimated based on the ratio between the landings and the SSB.

Comparing anomalies of cod recruitment with changes in intensity of major Baltic inflows

Earlier investigations covering the period of recent decades have shown that the recruitment of eastern Baltic cod is related to hydrographic conditions (e.g., Köster et al. 2005), largely determined by major inflows of saline and oxygen-rich water from the North Sea (Matthäus 2006). We compared the occurrence of anomalies in inflow intensity with cod recruitment to detect the potential major impact of inflow activity on cod reproduction in earlier decades of the 20th century.

Indices of major inflow events (Matthäus 2006) between September 1 (*t*-1) and April 30 (*t*) were summed up to obtain an annual index, potentially influencing cod reproduction in a year *t* (Hinrichsen et al. 2002b). Because we focused on decadal scale changes rather than inter-annual variability, time series of inflow data ($\ln(x + 1)$) and corresponding recruitment (age 2, lagged for 2 years) from 1948 onwards were smoothed by taking five-year running means. Anomalies in the inflow index were presented as deviations from the long-term average over the years 1898-2003.

Due to incomplete data coverage for SD 25 in the period before the 1970s (Eero et al. 2007a) the combined recruitment estimates for cod subpopulations in ICES SDs 26 and 28 were used to represent relative trends in recruitment of the total stock (SD 25-32). In 1976-2003, recruitment estimates for the total stock and for SDs 26 and 28 were highly correlated (r^2=0.939, $p<0.01$).

In the years before the 1940s, no recruitment estimates were available. Variability in SSB in this period was assumed to follow trends in recruitment with respective time lag. Based on size composition data (Eero et al. 2008), age-groups 3-7 were considered to form a major part of the spawning stock. Therefore, the SSB was compared with the average inflow index 3-7 years earlier, corresponding to the birth-years of the five respective year-classes that is consistent with the time interval for the average recruitment applied in the later period.

Comparing cod stock developments with changes in top-down and bottom-up drivers

1920s -1950s

The level of cod SSB in selected years (1926, 1938, and 1957) during the periods of peaks in the stock size was compared with changes in top-down forcing, i.e. fishing mortality and abundance of seals, in the period from the 1920s to 1950s. Additionally, changes in nutrient regime in this period (Österblom et al. 2007) were considered. The average inflow conditions for development of cod year-classes forming the stock in the compared years were all favourable, i.e. the average inflow index was above long-term mean. The years 1926 and 1938 were selected because multiple estimates (three and five, respectively) of SSB from different analyses were available for these years, increasing the credibility of the estimates. The year 1957 refers to the peak in SSB in the mid-1950s.

The developments in cod SSB (considered to be represented by age-groups 3-7) were compared with changes in the average abundance of predators, i.e. grey seals (*Halichoerus grypus*) over the preceding 1-6 years, corresponding to the time interval back to when the oldest age-group contributing significantly to the spawning stock biomass (age 7) recruited to the stock as 1-year-old. The fishing mortalities were averaged over the preceding four years.

1950s-1990

Cod stock numbers and fishing mortalities by age for SDs 26 and 28 were used to investigate temporal changes in adult survival and in recruitment (age 2) production per unit of SSB. Survival was estimated as the fraction of stock numbers at age 2 surviving to a given age. As natural mortality for ages 2+ in this period is assumed constant (Eero et al. 2007a; ICES 2007), the differences in survival represent changes in fishing mortality.

In order to demonstrate the effect of reduced fishing mortality on the spawning stock in 1975-1987, we simulated cod spawning stock numbers by modifying the fishing mortalities by age and year that influenced the stock (SD 25-32, ages 3-7) in 1975-1987 (e.g. the stock in 1975 was affected by fishing mortalities on ages 2-6 in 1974, on ages 2-5 in 1973 etc.). The fishing mortalities by age in this period were set equal to the average values experienced by year-classes forming the stock in 1960-1974 (e.g. mortality on age 2 in all the years influencing stock numbers in 1975-1987 was set equal to the average mortality on age 2 in the years influencing the stock in 1960-1974 etc.).

The simulated stock numbers were calculated based on the standard stock numbers equation (e.g., Hilborn and Walter 1992) applying the modified fishing mortalities. The recruitment in respective years was modified according to the difference between the simulated and observed SSB. The ratio of the number of recruits produced per unit of spawning stock biomass in each year was kept equal to the original value and the recruitment was adjusted accordingly.

Results

Changes in cod recruitment and major Baltic inflows

Since the 1920s, periods of low average cod recruitment and stock size generally coincided with relatively poor inflow conditions (Fig. 2a-d). Since the mid-1980s, the average inflow intensity has been far below the long-term mean. Concurrent with a dramatic decline in the inflow index, the average cod recruitment declined to very low levels after a peak in the late 1970s. Shorter periods with weak or lacking inflow events in the late 1920s and 1950s corresponded to reduced stock size and relatively low average recruitment in the early and mid-1930s and in the late 1950s-early 1960s, respectively. The average recruitment was relatively low also in the late 1960s-early 1970s coinciding with reduced inflow intensity.

Consequently, the relatively high stock size in the mid-1920s and in the late 1930s-early 1940s and relatively high average recruitment in the late 1940s-mid 1950s, in the mid-1960s and from the mid- 1970s to the early 1980s occurred in the periods when the corresponding average inflow index was above the long-term mean (Fig. 2a-d). The differences in the level of recruitment at peaks however do not appear to be explained by inflow conditions: for example recruitment was twice as high in the late 1970s-early 1980s as in the 1950s or mid-1960s, though the average inflow indices were similar.

Cod SSB and major changes in forcing factors from the 1920s to 1950s

The cod SSB in the late 1930s (1938) was estimated about 35 % higher compared to the mid-1920s (1926) (Fig. 3a). Mean SSB in the late 1930s (1938) was relatively similar to the level in the mid-1950s (1957), however the range of different estimates for 1938 suggests that the stock in this period might have been larger than in the 1950s (Fig. 3a).

During the period from the 1920s to 1950s, a major shift occurred in the top-down pressures on cod. The abundance of predators, i.e. grey seals declined from about 67,000 individuals in the first half of the 1920s to 39,000 and 22,000 individuals in the mid-1930s and 1950s, respectively (Fig. 3b; Harding and Härkönen 1999). In contrast, the average fishing mortality during this period increased sharply from 0.04 to 0.16 and further to 0.74, influencing the stock size in 1926, 1938 and 1957, respectively (Fig. 3b). This substantial increase in fishing mortality to relatively high levels however does not appear to have lead to a corresponding large reduction in SSB in the 1950s compared to the 1930s.

In the 1950s, the Baltic apparently changed from an oligotrophic to a more eutrophic sea, triggered by hydrographic processes (Österblom et al. 2007). In addition, anthropogenic nutrient input to the Baltic started to increase after the Second World War (Elmgren 1989) and the load in the 1950s has correspondingly been estimated somewhat higher compared to the previous decades (Fig. 3c). The increased nutrient availability potentially enhanced cod production in the 1950s via bottom-up mechanisms, counteracting the increased fishing pressure.

Major changes in the cod stock and in forcing factors from the 1950s to 1990

The anthropogenic nutrient inputs to the Baltic increased continuously during the 1950s - 1980s. Consequently, the concentration of nitrogen is estimated to have increased from about 15 mmol/m^3 in 1950 to approximately 27 mmol/m^3 in the late 1970s (Wulff et al. 1990). An even larger increase is estimated to have occurred with respect to phosphorus, from 0.3 to 0.9 mmol/m^3.

The increase in nutrient concentrations, especially in the 1970s, did not appear to have had a major positive impact on cod recruitment. The number of recruits per SSB showed large variability during 1948-1990, but did not exhibit an increasing trend (Fig. 4). The high values of recruits per SSB observed around 1950, in the mid-1960s and in late 1970s were all at a similar level (Fig. 4) and coincided with favourable (i.e. above- average) inflow conditions (Fig. 2).

The substantially higher recruitment observed in the late 1970s - early 1980s (Fig. 1) must therefore be due to a higher SSB. The high SSB in the late 1970s was related to higher survival of a number of year-classes in the post-recruitment phase. The survival of year-classes from age 2 until reaching ages 3 - 6 was 10-25 percent higher in the late 1970s compared to the previous and subsequent time periods (Fig. 4). The effect of reduced fishing mortality in the late 1970s on the stock was further illustrated by a simulation exercise. Applying similar fishing mortalities as exerted on the stock in the 1960s - early 1970s on the year-classes contributing to the stock in the late 1970s - early 1980s resulted in nearly 50 percent lower spawning stock numbers in the early 1980s compared to the observed level (Fig. 5).

Summary of major changes in the cod stock and forcing factors

Major trends in the cod stock in the 20th century coincided with changes in the intensity of major Baltic inflows. The stock size was additionally modified concurrent to the human-induced trophic changes and exploitation intensity. Before the 1940s, the level of cod biomass was likely restricted by high abundance of predators and low nutrient availability (Fig. 6). By the 1950s-1960s, these limiting factors were replaced by fishing. The drastic decline in the stock from the late 1980s to the present coincided with heavy fishing pressure, combined with unfavourable salinity and oxygen conditions. The period corresponding to the record high cod biomass in the late 1970s - early 1980s stands out as representing a combination of milder pressures on the cod stock compared to the other periods in the 20th century, i.e. a prolonged period with favourable climate, low predation, high ecosystem productivity and reduced fishing pressure (Fig. 6).

Discussion

The cod stock in the Baltic in recent decades is known to be influenced by salinity and oxygen conditions as well as heavy fishing pressure (Bagge et al. 1994; Köster et al. 2003). Historically, changes in the abundance of top-predators, i.e. seals and eutrophication have been suggested to have influenced the cod stock in the Baltic as well (Hansson and Rudstam 1990; Thurow 1997b; Österblom et al. 2007). However, none of the earlier analyses has simultaneously considered the long-term developments in all four key factors, i.e. climate, fishing, eutrophication and marine mammals, as potentially influencing the cod stock dynamic in the past century, at a sufficiently high time resolution. Also, the historical stock size has been poorly known as only recently major effort has been made to improve the knowledge of stock dynamics of the eastern Baltic cod in the first half of the 20th century (Eero et al. 2008).

Is this paper we evaluate the potential effects of top-down and bottom-up forces on the main predator fish in the central Baltic ecosystem in a historically much longer time scale than is generally possible to cover by detailed analyses of respective mechanisms. Our study demonstrates the importance of considering multiple changes in an ecosystem in parallel, at a long-term perspective and at a sufficient time resolution in order to understand major changes in fish populations and the relative impacts of human-induced and environmental drivers. These issues are highly relevant for managing the ecosystems and fish populations worldwide, however in a few cases possible to address and the effects of different factors are often difficult to separate. Cod in the Baltic Sea provides an unusual case where long time series of data and large changes in both natural and human impacts on the ecosystem allow demonstrating the cumulative and compensatory effects of different top-down and bottom-up forces influencing a century scale dynamics of a fish population in a large marine ecosystem.

Influence of climate and resource-driven bottom-up forcing on the cod stock

During the entire analysed time period since the 1920s, changes in the intensity of major Baltic inflows driven by large scale climatic processes (Schinke and Matthaus 1998) were followed by respective trends in the average cod year-class strength and the stock size. This suggests that climate forcing influencing cod reproduction is a major driver for cod stock dynamics in the Baltic Sea. Major Baltic inflows favour cod recruitment through several processes while cumulative negative effects occur at stagnation periods. Reduced salinity and oxygen concentrations have a direct negative effect on egg survival (e.g., Kosior and Netzel 1989; Lablaika et al. 1989), low inflow situations increase predation on cod eggs by sprat and herring (Köster and Möllmann 2000; Köster et al. 2005), and low salinity reduces cod larval survival by reducing their prey abundance (Möllmann et al. 2000; Voss et al. 2003; Hinrichsen et al. 2002a).

Availability of nutrients for biological production in the Baltic is also related to major Baltic inflows that force nutrients from the bottom to the euphotic layer (e.g., Nehring 1982). The exceptionally strong inflow in 1951 embedded in a cluster of 12 major inflows between 1948-1952 (Matthäus et al. 2008) has been suggested to have triggered a change in nutrient regime in the Baltic from oligotrophic to a more eutrophic sea (Österblom et al. 2007). Anthropogenic nutrient load also started to increase after the Second World War, and from the 1950s onwards the nutrient regime in the Baltic can be considered to be a combination of hydrographic and anthropogenic effects (e.g., Nehring et al. 1984; Matthäus et al. 2008; Nausch et al. 2008). However, the open Baltic is not considered to have been strongly affected by eutrophication before the 1960s-1970s (Nausch et al. 2008).

Given that long-term levels of fish production in marine ecosystems are functionally related to primary production (e.g., Ware and Thompson 2005), one might hypothesize that resource-driven bottom up processes have influenced the cod stock in the Baltic in the past century. Due to lack of comparable datasets it has been difficult to demonstrate the effect of increased nutrient inputs on different trophic levels in the Baltic (Larsson et al. 1985 and references therein). However, indirect measures of biological production such as Secchi depth indicated lower water transparency and higher chlorophyll values in 1969-1991 compared to 1919-1939 (Sandén and Håkansson 1996). Also, the benthic biomass above the halocline increased significantly from 1920-1923 to 1976-1977 (Cederwall and Elmgren 1980).

We suggest that the apparent change in nutrient regime in the 1950s (Österblom et al. 2007) had a positive effect on cod biomass, partly compensating for the substantial increase in fishing mortality. The mechanisms can however not be investigated with available data and both increased recruitment and/or enhanced individual growth could have contributed to the relatively high cod biomass in the 1950s. Improved growth in the 1950s is indicated by Fulton's condition factor, being estimated at 0.8 in Bornholm Basin in the early 1940s (Eero et al. 2008) and at about 1.0 in the same area and season in 1955-1960 (Stanek 1964). Higher growth rates of young cod in the 1950s compared to the 1930s are also indicated (Thurow 1974).

The continuous increase in nutrient concentrations during the 1960s-1980s is however not indicated to have further enhanced cod recruitment production compared to the 1950s (Fig. 4). Also the growth of cod during the 1950s-1970s was stable (Eero et al. 2007a). It is more likely that eutrophication had a negative impact on cod recruitment in this period due to increased occurrence and duration of hypoxia and anoxia, especially during the periods of low inflow activity (Elmgren 1989).

Influence of top-down forcing on the cod stock

During the first half of the 20th century, the dominant top-down pressure on the cod stock in the Baltic apparently shifted from seal predation to fishing. In the early decades of the past century the consumption of cod by seals likely exceeded the removals by the fishery.

This is indicated by higher SSB in the late 1930s compared to the mid-1920s after about forty percent reduction in seal population, despite the nearly fourfold increase in fishing mortality during this period (Fig. 3). Elmgren (1989) suggested average daily fish consumption of grey seals to be 3.2 $kg \cdot day^{-1} \cdot ind^{-1}$ that corresponds approximately to 75,000 tonnes of fish at the level of grey seal abundance in the mid-1920s. In the investigations of grey seal diet in the late 1960s - early 1970s, cod was found in about 20 percent of stomachs (Söderberg 1975). Assuming similar proportion also back in time would suggest a consumption of 15,000 tonnes of cod in the mid-1920s, likely concentrated on younger age groups (Thurow 1997a). For comparison, the eastern Baltic cod landings in this period were below 10,000 tonnes (Sparholt 1994). Cod has also been found in the stomachs of ringed seals (*Phoca hispida*), however due to limited spatial overlap, their predation on cod is expected to have been much lower compared to grey seals (Söderberg 1975). The population dynamics of the two seal species were similar (Harding and Härkönen 1999).

The abundance of seals declined to a third from the 1920s to 1940s (Harding and Härkönen 1999). Assuming similar reduction in the predation mortality on cod would indicate 5,000 tonnes of cod consumed annually by grey seals at their population level in the 1940s-1960s. Their influence on cod population dynamics in this period can be expected to have been minor, considering that the biomass for only the recruiting age-group (age 2) was at least 50,000 tonnes in the 1940s-1960s. Consequently, seals were not considered as a major factor influencing cod population dynamics from the 1940s onwards. If the higher seal abundances in the 1940s-1960s compared to the later period (Harding and Härkönen 1999) had a measurable influence on the natural mortality of cod, resulting in underestimation of recruitment and overestimation of fishing mortality, this would have a minor influence on our conclusions. R/SSB in the 1950s-1960s would then be even higher compared to the later period and survival of recruits would be indicated even lower, although a fraction of it could be due to higher predation mortality.

By the end of the first half of the 20th century, the role of natural top-predators in the Baltic ecosystem was taken over by the fishery. The impact of fishing on the cod stock was first apparent during the Second World War and intensive fishery at this time was likely a major factor contributing to the stock decline in the first half of the 1940s (Eero et al. 2008). Unfortunately, data on hydrographic conditions for the war years are not available to fully test this hypothesis. Nevertheless, the strong inflows in 1938 and 1939 (Matthäus 2006) likely favoured at least these two year-classes contributing to the spawning stock in the first half of the 1940s.

After a period with high fishing intensity in the 1950s-1960s, fishing pressure was gradually reduced. This was first apparent for younger cod (Fig. 4) that was partly due to technical measures introduced to protect the stock (e.g., Kosior 1974). The overall reduction in cod fisheries in the 1970s was partly related to the development of more profitable fishing possibilities for other species, i.e. the pelagic fishery for sprat and herring (Lablaika et al. 1991). The cod fishery intensified again in the 1980s, stimulated by the observed large increase in stock size. Our results show that higher survival of cod caused by reduced fishing mortality was a major factor contributing to the record high stock size in the late 1970s-early 1980s, twice as high compared to the simulated scenario assuming the previous high exploitation rates (Fig. 5).

Top-down vs. bottom-up forcing and the role of human impacts in the cod stock dynamics

Frank et al. (2007) has analysed bottom-up and top-down mechanisms in different marine ecosystems in the north Atlantic and concluded that in the areas of low species diversity and simple food-webs as characteristic also for the Baltic Sea, top-down forcing generally dominates. This is supported by a top-down trophic cascade that has been shown to have occurred in the central Baltic in recent decades after a drastic reduction in cod abundance (Casini et al. 2008; Möllmann et al. 2008). Our results suggest that top-down pressures, i.e. predation by seals and fishing, have had major impacts on cod population dynamics in the 20th century, that combined with the findings by Casini et al. and Möllmann et al. (2008) indicate a strong top-down control of the entire central Baltic ecosystem.

In addition to top-down effects, changes in hydrographic forcing throughout the past century led to major changes in the cod population. This response indicates a central importance of climate-driven hydrographic conditions for determining the reproductive success of the main predator fish and therefore, also the structure and functioning of the entire Baltic food web. Resource-driven bottom up mechanisms are suggested to have additionally promoted the cod stock earlier in the 20th century, however despite the large increase in nutrient concentrations in 1960s-1980s, no positive effect on cod production in this period is detectable. This could be due to data uncertainties and the complexity of food web responses to eutrophication, or alternatively due to temporal changes in trophic dynamics. The latter has been observed in other ecosystems, e.g. in Scotian Shelf where a transition from bottom-up to top-down control is suggested to have occurred as a consequence of overfishing the top-predators (Frank et al. 2007).

Consequently, a combination of both top-down and bottom-up forcing is suggested to determine the dynamics of the main predator fish population in the central Baltic. This is best illustrated by the period in the late 1970s early 1980s when a favourable combination of both bottom-up and top-down controls (i.e. favourable climate, low predation, high ecosystem productivity and reduced fishing pressure) led to the highest recorded cod biomass in the Baltic. A similar combination of driving forces has not occurred in other time periods in the 20th century. Reduced exploitation especially on young cod in the late 1960s-early 1970s, combined with relatively high reproductive success in the early 1970s allowed to build up a larger spawning stock whose offspring subsequently benefited from the major inflows in the late in the late 1970s and from the relatively low fishing mortality.

The large scale changes in the upper and lower trophic level in the Baltic resulted from human activities. The Baltic cod provides a contrasting example to many other marine fish stocks that showed much higher abundances in pre-industrialized time periods compared to their present levels (e.g., Jackson et al. 2001; Myers and Worm 2003; Rosenberg et al. 2005). The cod stock in the Baltic was lower in the earlier decades of the 20th century compared to the level in the late 1970s - early 1980s, demonstrating an enhancement of a fish population in a marine ecosystem as a consequence of human perturbations. The decadal-scale changes in the cod biomass in the Baltic during the past century reflect the developments in the society influencing the Baltic environment, i.e. hunting of marine mammals, developments in industry and agriculture leading to eutrophication of the Baltic and developments in fishing technology. These anthropogenic influences with opposite effects on the cod population have historically counteracted each other, implying that despite the large scale changes in each forcing factor, the cod stock fluctuated at a relatively constant level during the 1920s-1960s, the trends being mainly driven by climate variations.

In conclusion, our results demonstrate the impacts of both bottom-up and top-down forcing and highlight the potential and limitations of human manipulations for influencing a predator fish population in a marine ecosystem, using the Eastern Baltic cod as an example. During the past ca 80 years, major trends in the eastern Baltic cod stock coincided with climate variations. This indicates that in cases where fish populations are sensitive to climate, recovering depleted stocks under unfavourable climatic conditions by fisheries management measures has limitations. This emphasizes the need for taking climate variability into account in defining the target levels for fisheries management. However, at similar climatic conditions the level of stock size was largely determined by different human impacts. Our results provide new understanding of the relative influences of fishing and human-induced changes in upper and lower trophic levels on cod stock dynamics and can potentially help to define limit and target reference levels for biomass and fishing mortality as well as other ecosystem parameters that can be modified by management actions.

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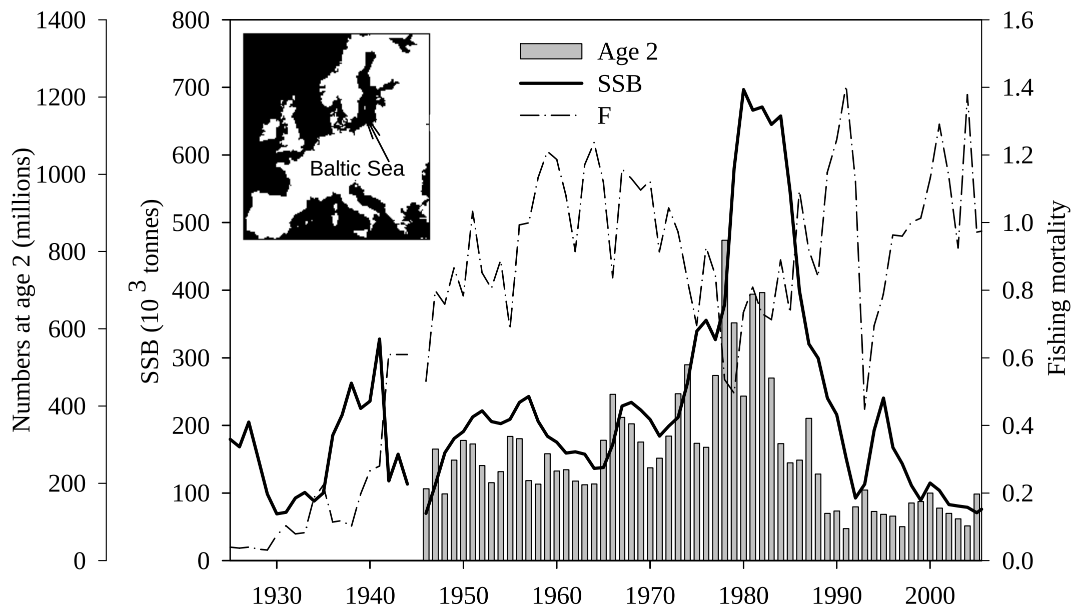

Figure 1. Eastern Baltic cod spawning stock biomass (SSB), recruitment (age 2) and fishing mortality (for 1925-1944 the level of F on SSB, from 1946 onwards average F on ages 4-7) in 1925-2005 (ICES 2007; Eero et al. 2007a; and modifications from Eero et al. 2008).

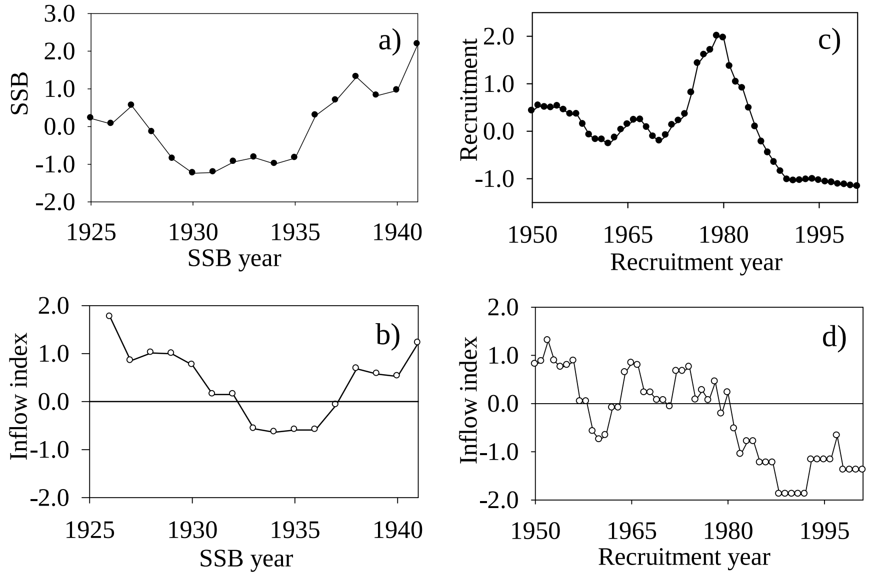

Figure 2. a) Standardized spawning stock biomass (SSB) and b) anomalies of average inflow index (ln (x + 1) transformed) lagged for 3-7 years in relation to SSB. c) Standardized recruitment (age 2; a running mean of 5 years; the years on the x-axis correspond to the middle of a 5-year period) and d) anomalies of inflow index (running mean of 5 years) lagged for 2 years in relation to the recruitment.

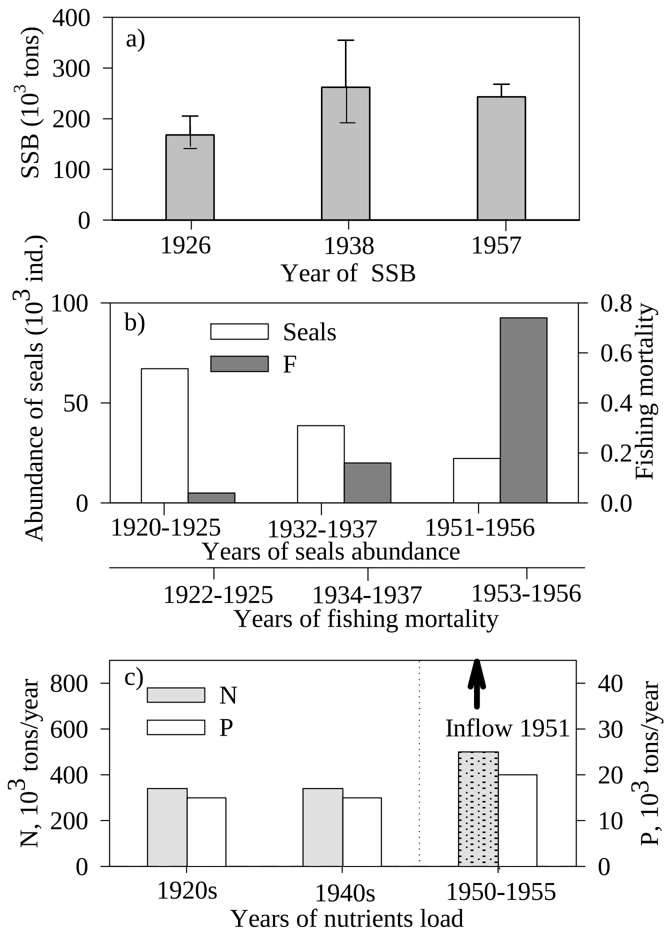

Figure 3. a) The average spawning stock biomass (SSB) of cod in 1926, 1938 and 1957 and b) the average abundance of grey seals (Harding and Härkönen 1999) and fishing mortality (F) in the preceding 1-6 and 1-4 years, respectively. Panel c) indicates the suggested change in nutrient regime in the 1950s, triggered by the inflow in 1951 (Österblom et al. 2007) and potentially contributed by the increased annual loads of nitrogen (N) and phosphorus (P) in 1950-1956 (Wulff et al. 1990) compared to the 1920s - 1940s (Jansson and Dahlberg 1999). The error bars for cod SSB in 1926 and 1938 represent the range of estimates by Eero et al. (2008). For 1957, the error bar indicates the SSB obtained when applying by 0.2 lower F on the subpopulation in SD 25, as the F in this area and period was considered as possibly overestimated by this level (Eero et al. 2008).

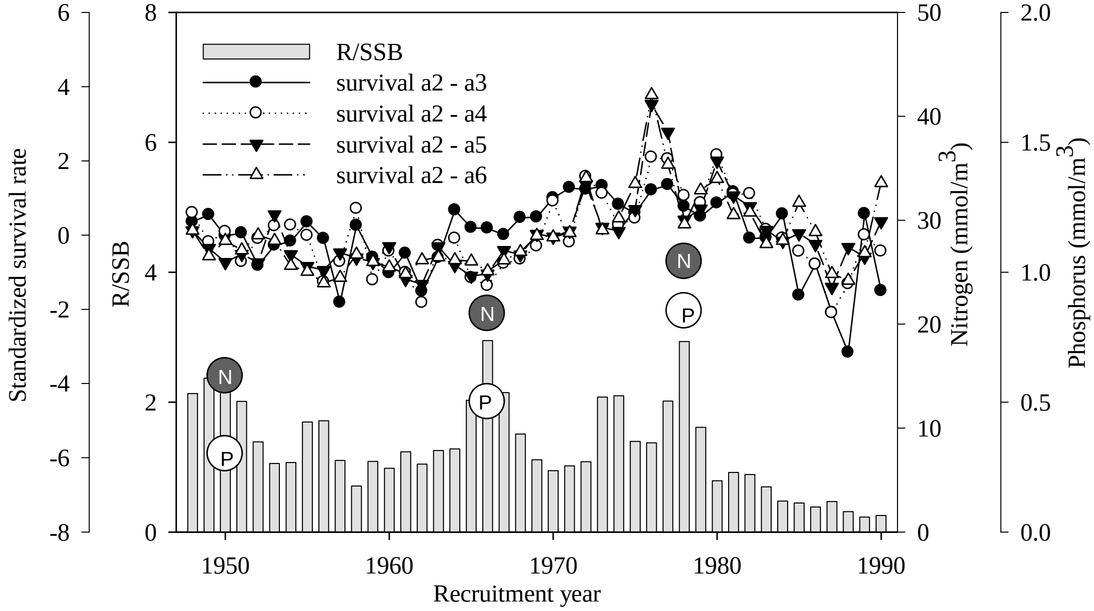

Figure 4. Numbers of recruits (age 2) produced per unit of spawning stock biomass (R/SSB) and the standardized survival rates (z-scores) of the year- classes from age 2 (in the years indicated on the x-axis) to ages 3-6. The concentrations of nitrogen and phosphorus that exhibited increasing trends from 1950s to 1980s (Wulff et al. 1990) are shown for the years corresponding to the peaks in R/SSB.

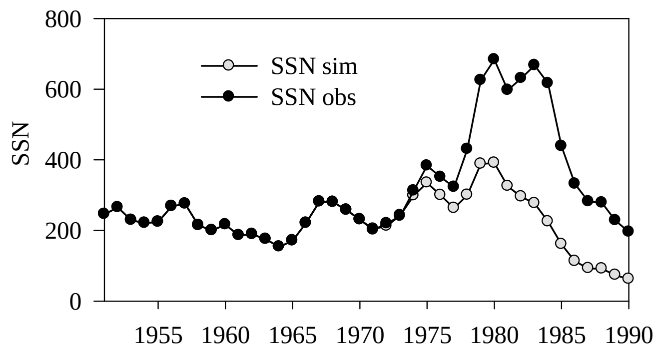

Figure 5. Observed and simulated cod spawning stock numbers (SSN, age 2-8+, SD 25-32). SSNs were simulated from 1975 onwards by applying the average age-based fishing mortalities that influenced the stock in 1960-1974 on the year-classes contributing to the SSNs in 1975-1987 (see Material and Methods for details).

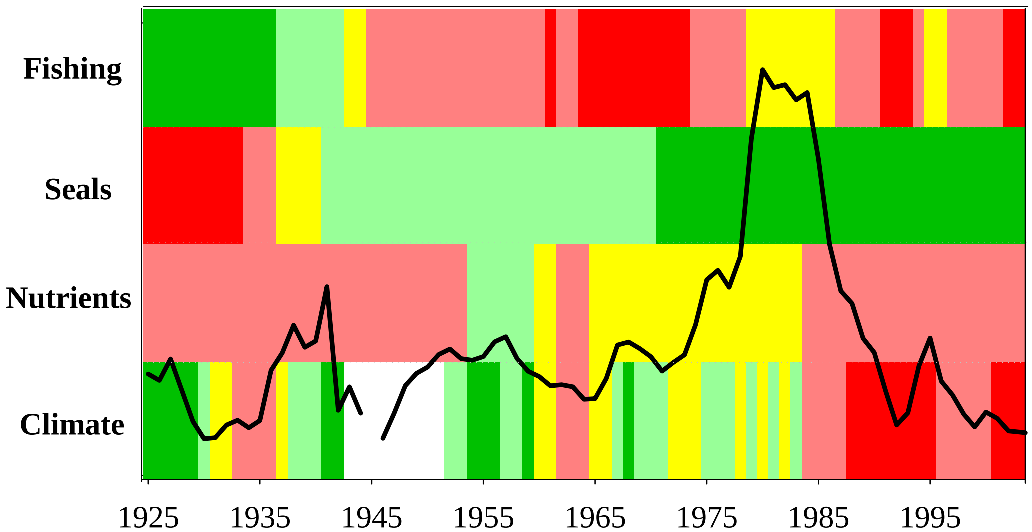

Figure 6. Major changes in the impact of climate (inflow index), nutrients, seal abundance and fishing on the SSB of eastern Baltic cod (represented by the line) in 1925-2005. The years on the x-axis refer to the cod SSB. The values for inflow index, seals and fishing mortality influencing cod SSB in a given year (see Material and Methods for time lags and averaging procedures) were grouped into five categories as 20 percent intervals from the maximum observed value in the period corresponding to the SSB in 1925-2005. The colours represent beneficial and detrimental effects, coded from red (detrimental) to yellow (neutral or moderate) to green (beneficial). The nutrients are suggested to have limited cod production until the apparent shift in nutrient regime in the 1950s (Österblom et al. 2007); from the 1960s onwards the impact on nutrients is considered to be neutral at favourable hydrographic conditions and turn to negative at stagnation periods.