Ecological Applications, 21(1), 2011, pp. 214–226

Multi-decadal responses of a cod (*Gadus morhua*) population to human-induced trophic changes, fishing, and climate

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Abstract. Understanding how human impacts have interacted with natural variability to affect populations and ecosystems is required for sustainable management and conservation. The Baltic Sea is one of the few large marine ecosystems worldwide where the relative contribution of several key forcings to changes in fish populations can be analyzed with empirical data. In this study we investigate how climate variability and multiple human impacts (fishing, marine mammal hunting, eutrophication) have affected multi-decadal scale dynamics of cod in the Baltic Sea during the 20th century.

We document significant climate-driven variations in cod recruitment production at multi-annual timescales, which had major impacts on population dynamics and the yields to commercial fisheries. We also quantify the roles of marine mammal predation, eutrophication, and exploitation on the development of the cod population using simulation analyses, and show how the intensity of these forcings differed over time. In the early decades of the 20th century, marine mammal predation and nutrient availability were the main limiting factors; exploitation of cod was still relatively low. During the 1940s and subsequent decades, exploitation increased and became a dominant forcing on the population. Eutrophication had a relatively minor positive influence on cod biomass until the 1980s. The largest increase in cod biomass occurred during the late 1970s, following a long period of hydrographically related above-average cod productivity coupled to a temporary reduction in fishing pressure. The Baltic cod example demonstrates how combinations of different forcings can have synergistic effects and consequently dramatic impacts on population dynamics. Our results highlight the potential and limitations of human manipulations to influence predator species and show that sustainable management can only be achieved by considering both anthropogenic and naturally varying processes in a common framework.

Key words: Baltic Sea; climate; cod; eutrophication; Gadus morhua; *historical development of the cod population; human impacts; seal predation.*

INTRODUCTION

Global studies of the impacts of human activities on marine populations and ecosystems have demonstrated that humans have altered the biodiversity, structure, and functioning of ecosystems and food webs for centuries if not millennia (Jackson et al. 2001, Lotze et al. 2006, Rick and Erlandson 2008, Lotze and Worm 2009). Moreover, the increasing intensity and number of human pressures interact with ongoing climate–hydrographic variability to further destabilize fish populations and ecosystems (Cury et al. 2008, Perry et al. 2009, Planque et al. 2009). In general, there is agreement about the global causes of declines and degradations, and that reducing or eliminating the human impacts would allow many populations and food webs to recover to ecologically more sustainable configurations; it is less clear how the recovery and restorative policies might be developed and implemented at local levels of individual ecosystems. The number, intensity, and chronology of human impacts differ widely among systems, as do the dynamics of interactions between species (including humans) within the systems, and how those dynamics have been (and will be) influenced by climatic–hydrographic forcings.

In this study, we consider a case ecosystem which in many ways illustrates the challenges faced by many coastal areas throughout the world. The Baltic Sea is a large, brackish ecosystem, which has during the last century been subjected to many of the most serious human impacts that a society can inflict, including near-extirpation of marine mammal top predators, unsustainable levels of exploitation, eutrophication, manipulation of watershed properties (e.g., land use, river runoff regulation), anoxia, contamination, and introduction of nonnative species (Helcom 2007).

The impacts of different human-induced changes on the Baltic ecosystem in the 20th century have been addressed in some earlier studies (e.g., Hansson and Rudstam 1990, Thurow 1997, Österblom et al. 2007). However, the long-term effects of changes in multiple key forcings such as fishing, eutrophication, and marine

Manuscript received 13 October 2009; revised 16 February 2010; accepted 10 March 2010. Corresponding Editor: K. Stokesbury.

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mammals in combination with climate variability have previously not been analyzed in an integrated way, including consideration of their cumulative and counteracting effects on the Baltic fish populations. Earlier investigations on influences of these forcings have also been restricted by poor knowledge of fish biomasses before the 1970s. Recent research efforts have extended the time series of biomass analyses of the eastern Baltic cod back to the 1920s (Eero et al. 2007, 2008), which provides new opportunities for elucidating the influences of multi-decadal variations in top-down and bottom-up processes that are due to both human (eutrophication, exploitation of both cod and its predators, i.e., seals) and natural impacts (climate variations affecting cod reproductive success). Thus, we focus in this paper on the eastern Baltic cod, which has important structuring roles in the Baltic food web (Casini et al. 2009) and is commercially one of the most important species in the central Baltic. The newly reconstructed time-series of cod stock dynamics extends to the period when the Baltic was still considered oligotrophic and contained large seal populations. Moreover, due to relatively late developments in fishing technology compared to other areas in the North Atlantic, exploitation of cod in the Baltic was low until the 1940s–1950s (Eero et al. 2008, Hammer et al. 2008). This combination of long ecological data sets transcending the historical development of key human impacts is relatively rare in marine ecology, and enables us to investigate in a chronological and process-oriented fashion how the onset of those impacts affected the population dynamics and productivity of a large piscivorous predator species.

Material and Methods

Data

Cod stock size and biological parameters.—The eastern Baltic cod (ICES Subdivisions [SD] 25–32) stock numbers at age, spawning stock biomass (SSB), mass at age, and maturity ogives were available from 1946 onward (Eero et al. 2007, ICES 2009). Average masses at age and maturity ogives in 1946–1960 (Eero et al. 2007) were applied for 1925–1945. The SSB in 1925–1944 was based on the average of different estimates available for specific years and periods (Eero et al. 2008), combined with annual catch per unit of effort data (see Appendix A for details).

Fishing mortality.—Fishing mortalities by age for 1925–1945 were calculated based on average fishing mortality on ages 3–7 in this period (Eero et al. 2008) and the average selection pattern in 1946–2007 (Eero et al. 2007, ICES 2009). For 1940–1944, we assumed fishing mortality on age 2 to be 1.0, in order to account for the intensive fishery with small-meshed trawls during the Second World War (Alander 1946).

Seal predation.—During the period from the early 1900s to the 1940s, the numbers of grey seals (*Halichoerus grypus*) and ringed seals (*Phoca hispida*) were reduced more than fivefold by intensive hunting (Harding and Härkönen 1999). In the late 1960s–early 1970s the abundances of seals continued to decline and in the 1980s–1990s the abundance of grey seals was <10% of the level in the first half of the 1920s.

Based on numbers and average daily food requirement of the seals (Appendix A and Elmgren 1989), we calculated their total annual fish consumption. The proportion of cod in seal diet during the entire period from 1925 to 1990 was assumed to be similar to that observed in the 1960s–1970s, i.e., 20% in grey seal and 7% in ringed seal diet (Söderberg 1975). In recent investigations of grey seal diet in the Baltic Sea, the majority of all consumed fish were between 10 and 25 cm in length (Lundström et al. 2007). In the North Sea, grey seals prey mostly on fish below 30 cm (Hammond and Grellier 2006), though the average cod in their diet was at 35 cm in length. Dietary studies of grey seals in Atlantic Canada also show that seals are mainly consuming juvenile stages of cod (Chouinard et al. 2005). To calculate the numbers of cod in seal diet in the Baltic in 1925–1990, we assumed the average mass of cod consumed by seals to be 0.2 kg, which corresponds to a 1-year-old cod below 30 cm in length.

Nutrient loading (eutrophication).—Nutrient inputs to the Baltic increased 3–5 fold during the 1940s–1980s as a consequence of increased use of fertilizers and intensified industrialization after the Second World War (Wulff et al. 1990). Direct measurements of the concentrations of dissolved phosphorous and nitrogen compounds in the Baltic Sea began only in the mid-late 1960s and 1970s. Concentrations prior to this period can only be estimated indirectly (e.g., via. nutrient loads, paleological methods). Consequently, time series of measured nutrient concentrations are too short for the purpose of our analyses. As an alternative, we used a time series of model-based estimates (Wulff et al. 1990) as a proxy for representing the increase in nutrient concentrations in the Baltic Sea from the 1950s to the 1980s. In the analyses we only utilized the concentration of nitrogen. Nitrogen and phosphorus concentrations show similar trends during this period, though the increase in phosphorus concentration is indicated to have been larger than that of nitrogen.

Hydrographic index.—Hydrographic conditions for cod recruitment in the Baltic Sea are generally defined by the "reproductive volume" (RV), i.e., is the volume of water with salinity and oxygen above the thresholds needed for successful fertilization and development of cod eggs (MacKenzie et al. 2000). In this study, we have focused on a much longer time period for which the estimates of RV based on direct salinity and oxygen measurements are available, and therefore used changes in water regime as a proxy for hydrographic conditions.

The salinity and oxygen conditions in the Baltic Sea are controlled by occasional intrusions of saline water from the North Sea and by the amount of freshwater discharge (Schinke and Matthäus 1998). Indices of major saline water inflow events (Matthäus 2006) between 1 September ($t - 1$) and 30 April (t) were summed to obtain an annual time series of inflow, potentially influencing cod reproduction in year t (Hinrichsen et al. 2002). The resulting time series of saline water inflow and time series of annual river runoff to the total Baltic Sea (Meier and Kauker 2003, Andersson 2009) were standardized (by subtracting the mean and dividing by the standard deviation) and subsequently summed within years. Because high saline and low freshwater inflow correspond to good hydrographic conditions and vice versa, we multiplied the standardized river runoff time series by -1 prior to summation. The combined time series of saline and freshwater inflow is referred to as the hydrographic index (HI). In 1974–2007, the constructed HI correlated significantly with cod reproductive volume (Appendix B: Fig. B1; $R^2 = 0.58$, $P < 0.001$).

All the data sets used in the analyses of this paper and respective data sources are listed in Appendix A.

DATA ANALYSES

Our overall objective was to identify and understand which major ecological processes have regulated the dynamics of cod, how their chronologies evolved over time, and the extent to which they were under human control. The analyses cover the entire time period from the 1920s. However, we focus particular attention on the 1920s–1930s and the 1970s to mid-1980s. The 1920s–1930s represents a period prior to the intensification of major human impacts, i.e., increased exploitation of cod and eutrophication of the Baltic Sea (Eero et al. 2008, Nausch et al. 2008), and when abundance of seals was still relatively high (Harding and Härkönen 1999). The period from the 1970s to mid-1980s is of particular interest because cod biomass increased to record high levels during this period (ICES 2009). Some specific questions we focused on were:

1) Can the relatively low cod biomass in the 1920s–1940s be explained by high abundances of marine mammal predators?

2) What were the relative contributions of changes in fishing and climate to an increase in the cod stock to record high levels in the late 1970s–early 1980s? and,

3) Did eutrophication have a major role in this population expansion?

First, we explore the evidence for multi-annual changes in overall stock productivity and in production of juveniles (age 2; hereafter referred to as recruitment) and visually relate these to observed trends in climate forcing and fishing mortality. In a second step, we conduct simulations of population dynamics to quantify the effects of climate variability, exploitation, and eutrophication on stock development from the 1950s to the 1980s and to investigate the potential contribution of seal predation to cod mortality, with focus on the 1920s–1930s. In order to obtain recruitment values for these simulations, we conduct multiple regression analyses to develop relationships between cod recruitment and major forcing variables. Further details on the analyses and simulations are given below.

Analyses of stock productivity.—In an unexploited population, surplus production is the net sum of recruitment, growth, and survival from natural mortality, and thus defines the change in stock size over time (Walters et al. 2008):

$$\mathrm{SP}_t = B_{t+1} - B_t \qquad (1)$$

where SP_t is the surplus production in a given year t, and B is the total stock biomass. Exploitation of fish populations removes some of the surplus production:

$$\mathrm{SP}_t = B_{t+1} - B_t + C_t \qquad (2)$$

where the proportion of surplus production retained in the sea is represented by $\mathrm{SP}_t - C_t$, where C_t represents the catch.

SP_t depends at least partly on B (Hilborn and Litzinger 2009); thus we also calculated the mass-specific surplus production:

$$\mathrm{SSP}_t = \mathrm{SP}_t / B_t.$$

We used General Additive Modeling (GAM) to evaluate the hypothesis that SSP remained stable throughout the time period for which total biomass estimates were available (1946–2007). The GAM analysis was conducted using locally weighted least squares regression (LOESS), an identity link function and a Gaussian error distribution with degrees of freedom selected objectively using a generalized cross-validation (GCV) procedure (Swartzman et al. 1992, SAS 2000, MacKenzie and Schiedek 2007). Significance of the fitted GAM was assessed using the pseudo-R^2 goodness-of-fit criterion (see MacKenzie and Schiedek 2007 for details).

Cod recruitment models.—Reproductive success of the eastern Baltic cod is related to salinity and oxygen conditions in the Baltic deep basins (e.g., Köster et al. 2005). Major Baltic inflows favor cod recruitment through several processes, while cumulative negative effects occur during intervening stagnation periods when both salinity and oxygen concentrations fall (Köster et al. 2005). Under favorable environmental conditions, recruitment success is significantly impacted by the size of the spawning stock (Köster et al. 2009). Köster et al. (2009) suggested that the SSB in ICES Subdivisions (SD) 25 has been the only reproductive part of the cod stock since 1981. Therefore, we used the SSB only in SD 25 (Eero et al. 2007) as a predictor variable for cod recruitment from 1981 onward.

The potential positive effect of eutrophication on cod recruitment was explored using only the data until 1983, because during the subsequent period when major inflows were less frequent, the high concentration of nutrients contributed to increased occurrence and duration of hypoxia and anoxia, deteriorating conditions for cod reproduction (Elmgren 1989, Österblom et al. 2007).

TABLE 1. Summary statistics of multiple linear regression models for predicting cod recruitment from hydrographic index (HI), spawning stock biomass (SSB), and nutrient concentration (NUTR), fitted for 1946–1983 and 1946–2005.

Model number	Period	R^2 adjusted	Variables	Estimate	SE	*t*	*P*
1	1946–2005	0.64	HI	3.09×10^4	7.79×10^3	3.97	<0.001
			SSB	0.967	0.0991	9.76	<0.001
			Intercept	8.80×10^4	2.30×10^4	3.83	<0.001
2	1946–1983	0.58	HI	2.88×10^4	1.11×10^4	2.597	<0.05
			SSB	1.02	0.140	7.278	<0.001
			Intercept	9.42×10^4	3.74×10^4	2.522	<0.05
3	1946–1983	0.65	HI	2.60×10^4	1.02×10^4	2.554	<0.05
			SSB	0.690	0.174	3.969	<0.001
			NUTR	1.43×10^4	5.05×10^3	2.83	<0.01
			Intercept	-1.24×10^5	8.43×10^4	−1.471	>0.05

We used three multiple regression models to predict cod recruitment, fitted for different time periods and including different variables.

Model 1: HI and SSB included as predictor variables, fitted for 1946–2005.

Model 2: HI and SSB included as predictor variables, fitted for 1946–1983.

Model 3: HI and SSB and nitrogen concentration (N) included as predictor variables, fitted for 1946–1983.

The included variables explained significant amounts of variation in all three models (Table 1).

Adding an extra variable to *Model 2* to represent the increase in nutrient concentration significantly improved the overall fit of *Model 3*, relative to *Model 2* (Table 1). *Model 3* explained 65% of recruitment variability during 1946–1983; all variables had significant, positive effects on cod recruitment (Table 1). The residuals from *Model 3* were not significantly autocorrelated ($P < 0.05$).

Simulations of cod stock dynamics.—

1. *Effects of climate, fishing and eutrophication.—* Four simulations of cod SSB during 1946–1985 were conducted to investigate the effects of changes in fishing mortality, hydrographic conditions, and nutrient availability on cod dynamics in this period. Recruitment for each year was predicted from the regression models developed above, using the simulated SSB two years earlier as a predictor variable in the regression. The recruits were projected forward in time using the standard stock numbers at age equation (e.g., Hilborn and Walters 1992). The simulations were structured to investigate the population response to one variable at a time. Thus, if not stated otherwise, the values for variables were kept as observed. Initial stock numbers by age in 1946 and recruitment in 1947 in all simulations were used as observed. In order to obtain confidence intervals for simulated SSB, recruitment for each year was selected randomly from the 95% confidence intervals of predicted recruitment, and 1000 iterations of the stock projection were run.

Sim 1: Recruitment (R) estimated based on simulated SSB and observed HI and N (*Model 3*).

Sim 2: R estimated based on simulated SSB and observed HI (*Model 2*).

Sim 3: R estimated based on simulated SSB and HI (*Model 2*); HI for the entire period set to the average level observed during 1982–2003.

We used *Model 2* (excluding the positive effect of eutrophication) in this simulation, because at poor hydrographic conditions, high nutrient concentration reduces oxygen level and is thus not likely to enhance cod recruitment.

Sim 4: R estimated based on simulated SSB, observed HI and N (*Model 3*). Fishing mortalities by age for the entire period set to the average level observed in 1957–1972.

2. *Effect of seal predation.—*Two simulated time series of SSB were derived under assumptions of natural mortality, which either excluded or included assumed predation mortality by seals, and compared with the observed SSB. Our hypothesis was that if seal predation was the main factor responsible for relatively low cod stock before the 1940s, the simulation incorporating seal predation should yield stock estimates close to the observed level.

Annual recruitment for 1925–1983 was predicted from *Model 3*. For the years 1984–2005, when effects of eutrophication on cod reproduction are more difficult to resolve, we only used SSB and HI to predict recruitment (*Model 1*). Differently from the simulations that investigated the effects of climate, fishing, and eutrophication on the cod population, recruitment for each year was predicted using the observed SSB two years earlier as a predictor variable in the regression, instead of the simulated SSB. Natural mortality (due to all other causes except seal predation) at 0.2 was applied for all ages (2–8+) and years. In the simulation incorporating seal predation, the numbers of cod assumed to have been consumed annually by seals were subtracted from the recruitment. The initial age structure of the population (i. e., numbers at age) was not known and was chosen to correspond to the SSB in 1925.

RESULTS

Multi-annual variations in surplus and recruitment production

Total surplus production (SP) of cod varied substantially over time, but has always been positive in the

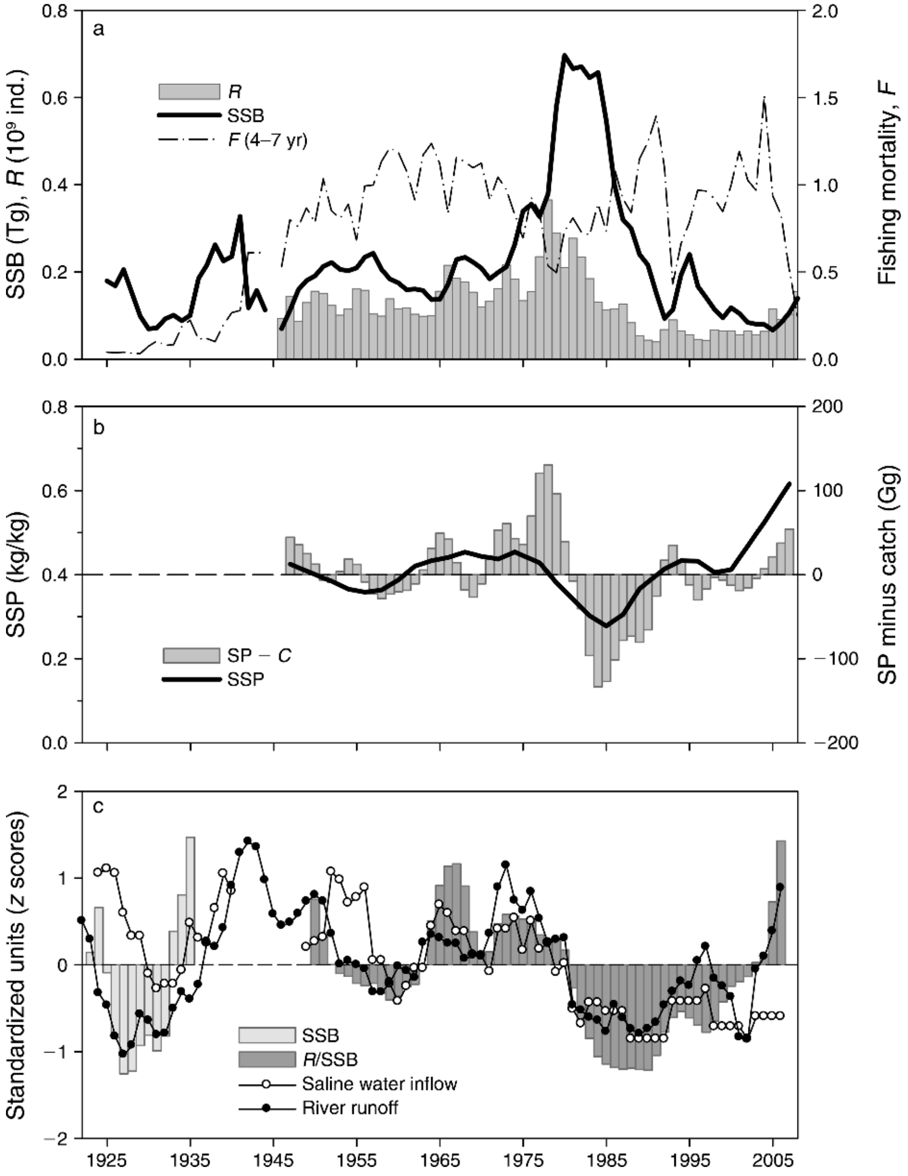

FIG. 1. (a) Eastern Baltic cod spawning stock biomass (SSB), recruitment (*R*; age 2), and fishing mortality (Eero et al. 2007; modifications from Eero et al. [2008] and ICES [2009]). (b) Cod surplus production per biomass (SSP), and total surplus production (SP) minus catch (*C*), both shown as GAM (general additive modeling) fit. (c) Anomalies of saline water inflow and river runoff (shown in reversed scale, i.e., high values correspond to low runoff) in comparison with cod recruitment (*R*) per unit of SSB in 1948–2005 and cod SSB in 1925–1938 (as *R* data for this period are not available). Hydrographic data and *R*/SSB are shown as running means over five years. Hydrographic data are lagged in relation to *R*/SSB and SSB to correspond to the hatching years of respective year classes (age 2 for *R* and ages 3–7 for SSB). Years on the *x*-axis correspond to the midpoints of five-year averaging periods of cod recruitment.

assessment history of the stock (Appendix C). Highest surplus has been observed in the late 1970s–early 1980s, in the period of a record high stock size (Fig. 1a; Appendix C). Visual and statistical inspection of the time series of surplus production per biomass (SSP) identified significant multi-annual variations: the GAM fit explained 51% of the deviance of the original series ($P < 0.001$; Fig. 1b). In the period from the mid 1960s to the late 1970s, SSP was above the long-term mean (0.4); thereafter it declined to the lowest observed level in the mid 1980s, and recovered to near average levels in the 1990s. In the early 2000s, the SSP increased to its current record high level. The longest observed time period with continuously high productivity of the stock from the mid 1960s to the late 1970s (Fig. 1b) coincided with a reduction in fishing mortality (Fig. 1a). Consequently, a large proportion of the high surplus biomass produced in this period was retained in the sea to build up a record

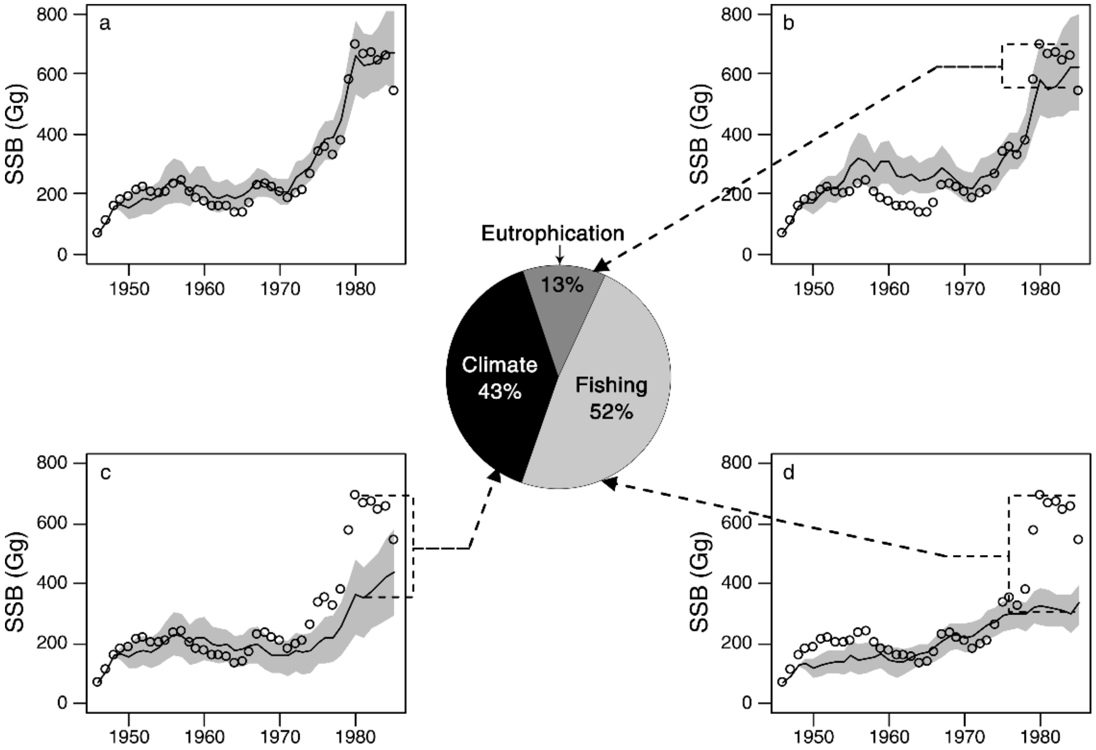

FIG. 2. The four panels show simulated cod spawning stock biomass (SSB, shown as a line; gray area represents 95% confidence intervals) using recruitment predicted from (a) hydrographic index, SSB, and nutrient concentration; (b) hydrographic index and SSB; (c) SSB and hydrographic index at the average level as observed in 1982–2003; (d) hydrographic index, SSB, and nutrient concentration; fishing mortality was applied at the average level observed in 1957–1972. Data points (open circles) in each panel denote the SSB estimated from analytical assessments (Eero et al. 2007, ICES 2009). The central pie chart illustrates the relative impacts (percentage difference between simulated and observed SSB) of eutrophication, climate, and fishing on the average cod SSB during the peak in 1980–1984, based on the three scenarios.

high stock (Fig. 1a, b). In contrast, the period of low stock productivity in the 1980s coincided with high fishing mortality, implying that the amounts annually removed by the fishery considerably exceeded the surplus production in these years, resulting in drastic stock decline.

The trends in SSP are similar to changes in recruitment production per unit of SSB (Fig. 1b, c). Major trends in average recruitment production coincided with changes in the hydrographic regime from the late 1940s to the 1990s, with relatively higher numbers per unit of spawner biomass produced during periods of high saline and low freshwater inflow (Fig. 1c). In the period from the 1920s to 1940s, recruitment similarly followed trends in the hydrographic index (Fig. 1c), assuming that changes in SSB represent changes in recruit production given the time lag between recruit age (2 years) and maturity (SSB assumed to represent ages 3–7 [Eero et al. 2008]). In recent years (2000s), cod recruit production per SSB shows a pronounced increase, concurrent with reduced river runoff (Fig. 1c).

Simulations of cod population dynamics

1. *Effects of climate, eutrophication and fishing.*—The simulation of cod SSB with recruitment predicted from the hydrographic index, SSB, and nutrient concentration produced a similar stock development to that estimated from the analytical stock assessment for 1946–1985 (Fig. 2a). The simulation using recruitment from the regression model that excluded eutrophication as an input was also able to reproduce observed cod dynamics reasonably well, although it slightly overestimated SSB in the late 1950s–early 1960s and underestimated SSB in the early 1980s by ~10% (Fig. 2b).

The scenario with relatively poor hydrographic conditions (i.e., similar to the average observed in 1982–2003) applied to the entire period from 1946 to 1983 produced a peak SSB during 1980–1984 at 370 Gg, which is ~40% lower than the observed level. An even lower SSB in this period was produced in the scenario where the average fishing mortalities observed in 1957–1972 were applied to the entire period from 1946 to1985 (Fig. 2d). In this simulation, the SSB in 1980–1984 was only 315 Gg, which is less than half the observed spawner biomass in these years.

2. *Effect of seal predation.*—Modeled recruitment, in combination with estimated fishing mortalities and natural mortality at a 0.2 level produced SSBs similar to the observed values from the 1940s onward. In the period before 1940, the simulation resulted in consider-

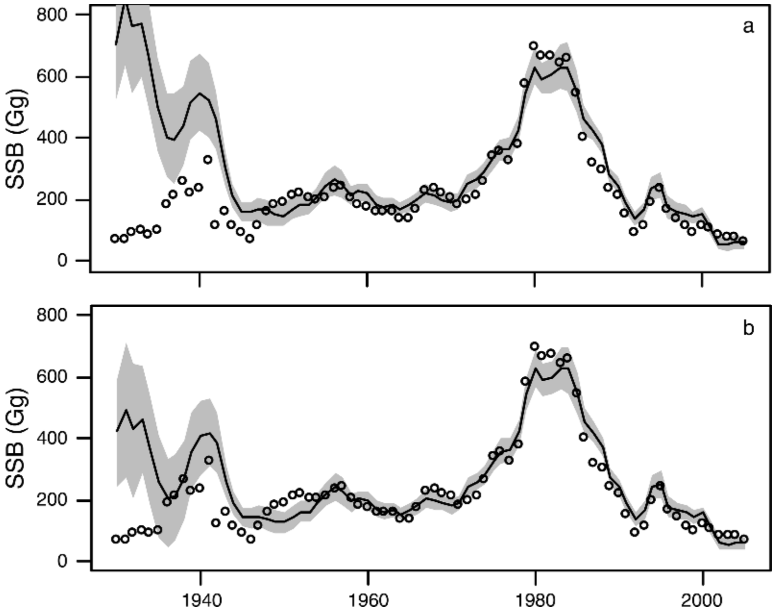

FIG. 3. Simulated cod spawning stock biomass (SSB, shown as a line) for 1925–2003 based on recruitment from multiple linear regression model, compared to SSB from analytical assessments (shown as open circles; Eero et al. 2007, 2008, ICES 2009). The gray area shows 95% confidence intervals for simulated SSB. (a) Natural mortality of 0.2 was applied for all years and ages; (b) in addition to natural mortality of 0.2, seal predation was taken into account.

ably higher SSB than previously estimated. This result indicates that either natural mortality in this period must have been higher than assumed ($M > 0.2$) or the real recruitment was lower than predicted from the regression model (Fig. 3a). Taking into account predation by seals resulted in SSB in the late 1930s close to the previously estimated level (Fig. 3b), i.e., ~150 Gg lower than estimated without considering seal predation (Fig. 3a). In earlier years, the simulated SSB was still considerably higher, showing that seal predation at the presumed level cannot fully explain the low stock size in this period (Fig. 3b).

Chronology of changes in the key forcings compared to trends in cod biomass

Chronology of changes in the four key forcing factors on cod addressed in this study are summarized and visualized as a traffic light diagram (Fig. 4). The purposes of this diagram are to illustrate how the pressures on cod alternated over time and highlight the time periods when different drivers had cumulative or opposite effects on the population dynamics. The major trends in the cod stock in the 20th century coincided with changes in climate-driven hydrographic conditions. The stock size was additionally modified due to the trophic changes and exploitation intensity. Before the 1940s, the cod biomass was partly restricted by a high abundance of seal predators and presumably also by low nutrient availability. 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 unfavorable climate conditions, which led to reduced productivity of the stock (Fig. 1b). 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 stock, i.e., a prolonged period with favorable climate, low predation, increasing ecosystem productivity, and reduced fishing pressure (Fig. 4); this situation has not occurred at other time periods during the past century.

DISCUSSION

The recovery of marine animal populations and ecosystems to earlier configurations or at least promoting sustainable developments is widely recognized as an objective of marine conservation and fisheries and ecosystem management (e.g., Jackson and Hobbs 2009). Restoring and recovering populations and ecosystems requires knowledge of their responses to perturbations, both natural and human induced, so that realistic recovery objectives can be set and the environmental framework under which they can be achieved and maintained can be identified.

The various historical human impacts on the Baltic ecosystem could, with 21st century hindsight, be considered as a series of (unplanned) large-scale experiments on population- and ecosystem-level responses to anthropogenic forcing. Here we show how the productivity and abundance of a top predator fish species has varied during the 20th century due to interactions of humans with the natural forcing of the system: the controls on the Baltic cod population have

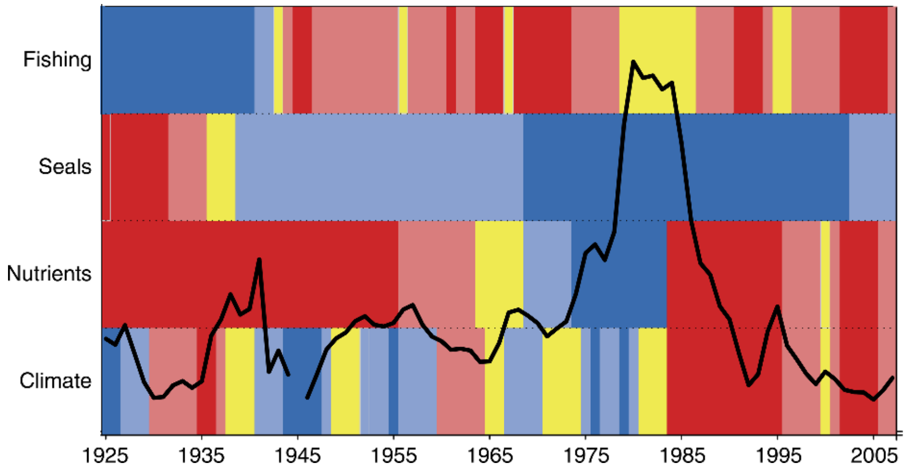

FIG. 4. Changes in climate-driven hydrographic conditions, nutrient concentration, seal abundance, and fishing mortality compared to trends in SSB of the eastern Baltic cod (shown as a line) during 1925–2007. The data for climate and fishing variables are lagged in relation to SSB to represent their potential impacts on age groups 3–7 in SSB in a given year. The values of the parameters shown by the five color categories represent 20th percentiles of the range of observed values (from minimum to maximum) for each variable during the analyzed period. The colors represent beneficial and detrimental effects on cod, coded from red (detrimental) to yellow (neutral or moderate) to blue (beneficial).

changed as different forcings have weakened and strengthened over time.

Climate variations

The Baltic Sea is situated at the transition zone of the continental Euro-Asiatic and maritime Atlantic climate systems. Periodic climatic fluctuations cause considerable changes in living conditions (e.g., temperature, salinity, oxygen concentration) for fish and other taxa in the Baltic Sea (Kalejs and Ojaveer 1989, Möllmann et al. 2009). We found that major variations in cod recruitment production were associated with changes in hydrographic conditions during the entire analyzed period since the 1920s, which is consistent with earlier analyses for shorter, more recent time periods (Jarre-Teichmann et al. 2000, Köster et al. 2005). These results indicate strong climatic control on the top-predator fish species and thereby on the configuration of the entire Baltic ecosystem (Casini et al. 2009). Since 2005, the cod recruitment per spawner has been high, which is partly explained by the latest major inflow in 2003. The high recruitment production in most recent years (2006–2008) was not associated with a major inflow event, and may be due to other hydrographic processes, possibly related to intensity of freshwater discharge and mixing processes in the Belt Sea and western Baltic Sea. Hence, hydrographic processes in addition to major saline inflow events may be partly responsible for variations in salinity and oxygen conditions in the deeper parts of the Baltic Sea (Meier et al. 2006), and potentially influence cod recruitment.

Fishing

The impact of fishing on the cod stock was first apparent during the Second World War when the intensive cod fishery in the Baltic Sea began (Meyer 1952, Eero et al. 2008) and continued to develop during the 1950s–1960s. Thereafter, the exploitation rates gradually declined, although landings remained relatively stable (Hammer et al. 2008). The decline in fishing mortality was first apparent for younger cod (Eero et al. 2007), which was partly due to new technical measures (minimum landings size, mesh size) introduced to protect the stock (e.g., Kosior 1974). The decline in overall exploitation rate was due to a combination of two factors. An increase in productivity of the stock, as observed in the 1960s–1970s, alone would lead to an increase in stock size and consequently to a reduction in fishing mortality rate, even if fishing effort remained stable or increased at a rate which was lower than the increase in productivity. In the case of the Baltic cod, in fact there is qualitative evidence that fishing effort declined in this period. This reduction was due to reallocation of fishing effort from cod to pelagic species that became more profitable at the time (Lablaika et al. 1991). As a result, the fishing mortality rate declined due both to an increase in stock productivity and a reduction in fishing effort. The increase in productivity temporarily exceeded the losses in biomass due to exploitation. In other words, due to attractive alternative fishing possibilities the fishery did not remove the increasing cod surplus becoming available in the 1960s–1970s due to a favorable environment. This situation allowed the population to accumulate its high surplus production and build up a record high biomass.

The cod fishery intensified again in the 1980s (Hammer et al. 2008), stimulated by the observed large increase in stock size and simultaneous decline in pelagic stocks (ICES 2009). The period of a large cod fishery, however, did not last long, as it coincided with the onset of a period of low stock productivity due to deteriorated environmental conditions, which in combination with intensified fishing, drove the stock rapidly down to low levels.

In hindsight, the period of high productivity in the 1960s–1970s and relatively low interest in the cod fishery in this period was extremely fortunate for the population and the fishery in the following years. Had the fishery kept up with increasing stock abundance from the start and maintained the fishing mortality at the same level as during 1957–1972, the increase in spawner biomass and the subsequent peak in the early 1980s would have been much lower (Fig. 3d). This situation would have made the population more vulnerable to the imminent major change in hydrographic conditions (Perry et al. 2009, Planque et al. 2009), which occurred in the 1980s and during much of the 1990s (Fig. 1c).

Seal predation

Investigating the effect of seal predation on the cod stock is limited by the fact that seals were most abundant in the Baltic in the early decades of the 20th century when information on their dietary preferences is limited, and information on the abundance of their other important prey items, such as clupeids (Lundström et al. 2007), is not available. Thus, the share and size composition of cod in seal diets is uncertain. Consequently, instead of attempting to estimate the amount of cod annually consumed by seals, we focused on whether seal predation alone could possibly explain the relatively low cod stock before the 1940s. To do so, we assumed that the proportion of cod consumed by seals in the period back to the 1920s was similar to the maximum proportion found in the available studies, i.e., 20% for grey seals. This share is consistent with the annual average share of gadoids in seal diets in the North Sea (Hammond and Grellier 2006), Skagerrak (Härkönen and Heide-Jørgensen 1991), and parts of Atlantic Canada (Chouinard et al. 2005).

Our results show that reduced seal abundances did not contribute to the cod stock increase in the late 1970s. Seal predation on the cod juveniles at the assumed level can, however, explain the relatively low cod biomass in the late 1930s, given that recruitment production in this period is explained by SSB and hydrographic conditions. In the early 1930s, the cod SSB was considerably lower than could be explained by seal consumption. We conclude that with current knowledge of historical seal diets and prey abundances, seal predation on the juveniles is unlikely to be the main factor responsible for the low cod spawner biomass in the early 1930s and late 1920s, and that other processes in the ecosystem were involved.

Eutrophication

Anthropogenic nutrient loading into the Baltic Sea probably started during the industrial revolution and accelerated after the Second World War (Conley et al. 2009). The open Baltic is not considered to have been strongly affected by eutrophication before the 1960s–1970s (Nausch et al. 2008). Estimates of cod biomass were until recently only available for a period when nutrient loading had already reached high levels, which have limited the possibility for evaluating eutrophication effects on fish production in the Baltic Sea in earlier studies (e.g., Österblom et al. 2007). Our study therefore provides new insights into how nutrient loading has affected the upper trophic level in the Baltic Sea.

We have shown that increased nutrient loading to the Baltic Sea was associated with higher cod recruitment from the 1940s to 1980s. This result is consistent with the positive influence of primary production on fish production seen in many marine ecosystems (Ware and Thomson 2005, Frank et al. 2006), at least up to a level of eutrophication beyond which negative impacts begin to dominate. However, the positive effect of eutrophication on cod stock dynamics in the Baltic appeared to be relatively minor (Fig. 2a, b). Our analyses and interpretations of the influence of eutrophication on Baltic cod are centered on its role in recruit production, which is presumably related to an improvement of feeding, growth, and survival conditions for larvae and juvenile stages. Although eutrophication can be hypothesized to have also benefited older cod stages, available growth data for adult cod show that growth was relatively stable during the 1950s–1980 (Eero et al. 2007). Cod condition improved during the period from the 1940s to 1960s; Fulton's condition factor was estimated at 0.8 in Bornholm Basin in the first quarter in the early 1940s (Eero et al. 2008) and at about 1.0 in the same area and season in 1955–1960 (Stanek 1964). Also, qualitative information from the fisheries suggests that the cod in the catches before the late 1940s was extremely thin and of bad quality (Alander 1949).

Our results suggest that low nutrient availability may have been a factor that restricted the cod stock in the 1920s–1930s. The availability of nutrients for biological production in the Baltic Sea is partly related to hydrographical processes, which force nutrients from the bottom to the euphotic layer (Conley et al. 2009). In the first half of the 1930s, vast amounts of accumulated nutrients were liberated from the sediments (Meyer and Kalle 1950), which may have promoted fish production. In addition, in the 1920s–1930s young cod were likely competing with large stocks of flatfish for benthic food resources, which were at this time about fourfold less abundant than in the 1970s (Cederwall and Elmgren 1980). Flatfish (plaice *Pleuronectes platessa*, flounder *Platichthys flesus*, and dab *Limanda limanda*) provided the largest contribution to the Baltic fish catches in the 1920s–1930s (Hammer et al. 2008), which indicates that flatfish species were abundant in this period, although the biomasses are not known. In the 1940s, the flatfish fisheries collapsed and never regained their former importance (Hammer et al. 2008). Benthic organisms (e.g., Mollusca, Polychaeta) are important prey items both for flatfish and young cod in the Baltic Sea (Hüssy et al. 1997, Karlson et al. 2007). Thus, we suggest that nutrient availability, via its influence on structure of the food web, had an important role on cod stock dynamics before the 1940s.

Human-induced changes in ecosystem forcing: implications for management

Integrating available knowledge of past developments in an ecosystem into decision-making advice is increasingly recognized as being essential for setting meaningful targets for management, restoration and recovery (e.g., Jackson and Hobbs 2009, Lotze and Worm 2009). The internationally agreed Baltic Sea Action Plan (BSAP) for ecosystem management and protection (Helcom 2007) has defined management goals for the Baltic Sea, which include among others reduction in nutrient concentrations and recovery of populations of marine mammals (Helcom 2007). Cod in the Baltic Sea is subject to an EU management plan aiming at sustainable fisheries and recovery of the population. Achieving these goals will be challenging, partly because climate change, which will likely have negative consequences for cod in the Baltic Sea (MacKenzie et al. 2007*b*) is expected to intensify in the future (BACC 2007). The ecosystem structure and food web present in the early decades of the 20th century correspond roughly to the type of ecosystem that the BSAP is aiming to achieve during the 21st century (Helcom 2007). Thus, knowledge of historically observed effects of respective drivers and their interactions with each other and with climate variability is useful for developing and implementing restorative ecological policies such as the BSAP.

If nutrient loads are reduced in the future, then in principle, a reduction in overall ecosystem productivity might be expected ("oligotrophication"). However, due to a large accumulation of nutrients in the sediments and the surrounding watershed, and the slow flushing time of the Baltic Sea, nutrient levels and primary production will likely remain high for several decades following a reduction in nutrient loading (Conley et al. 2009). Hence, the theoretical detrimental impact of a reduction in nutrient concentrations on cod recruitment will likely be relatively small, and undetectable for many decades, given that the fivefold increase in nutrient loads during the 1940s–1980s (Wulff et al. 1990) resulted only in a minor enhancement of cod biomass. In contrast, a reduction in nutrient loading would likely have positive benefits on cod recruitment via improved oxygen conditions in cod spawning areas. There is strong evidence that the extent of anoxia has increased, especially during the last decades (Conley et al. 2009), which is due at least partly to the ongoing eutrophication, but also to a reduction in the intensity and frequency of the major Baltic inflows, which renew oxygen conditions in cod spawning areas.

The abundance of grey seals in the Baltic Sea is increasing (ICES 2008) and is presently similar to that observed in the 1940s–1960s (Harding and Härkönen 1999). At the present low level of cod abundance, the proportion of cod in seal diet is $<5\%$ (Lundström et al. 2007), indicating an insignificant impact of seal predation on the cod stock. This situation may, however, change in the future if the seal population continues to grow and the cod stock also increases in abundance, and consequently expands its distribution area northwards (Aro and Sjöblom 1982, 1984), where densities of grey seals are highest. From the time series for the 20th century it is apparent that in the period when seals were abundant, the cod stock was relatively low, which suggests that there may be limitations to restoration of both populations to high levels. There is some evidence that the cod stock might have been larger than at present in the late 1500s and early 1600s (MacKenzie et al. 2007*a*), when the Baltic presumably contained larger seal populations than their present levels (Harding and Härkönen 1999), but fishing mortality in this period was likely low (MacKenzie et al. 2007*a*).

In contrast to many other marine fish populations that were much more abundant in preindustrialized time periods compared to their present levels (Lotze and Worm 2009), the cod biomass in the Baltic Sea was lower in the earlier decades of the 20th century compared to the late 1970s–early 1980s. The Baltic cod example, along with others in the recent literature (e.g., Dutil and Brander 2003, Rothschild 2007, Swain and Chouinard 2008) demonstrates that multi-decadal variations in cod productivity occur, and often do so for reasons not directly connected to exploitation of the particular species. Consequently, the exploitation levels that a fish population can sustain may be different depending on environmental and ecosystem parameters that can change over time. In addition, the sensitivity of a fish population to certain types of pressures may not be constant but depend on the level of other forcings. One example is the effect of hydrographic conditions and eutrophication on cod in the Baltic Sea; at good hydrographic conditions, increased nutrient availability appeared to have supported cod production (Fig. 2b), whereas the effect likely turned negative at subsequent poor environmental conditions (Elmgren 1989, Österblom et al. 2007). Moreover, the vulnerability of fish populations to environmental variability may depend on the population structure and life history traits, which can be modified by fishing (Brander 2007, Perry et al. 2009).

Avoiding stock collapses therefore requires monitoring of indicators of population and ecosystem status so that fishing regulations can be adjusted as conditions change (Mohn and Chouinard 2007). We believe that the Baltic example is a contribution to general ecological understanding of bottom-up and top-down factors affecting multi-annual changes in fish productivity and of the potential and limitations of human actions to influence these.

Acknowledgments

The study was supported by the History of Marine Animal Populations project of the Census of Marine Life and by FP6 Specific Targeted Research Projects of the Commission of the European Communities addressing mechanisms of stock decline and recovery (022717, UNCOVER), climatic impact on stock dynamics (044133, RECLAIM), and indicators of fish stock and ecosystem status (044227, IMAGE).

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APPENDIX A

List of data sets used in the analyses and calculation of cod spawning stock biomass in 1925–1944 (*Ecological Archives* A021-012-A1).

APPENDIX B

Hydrographic index compared to cod reproductive volume (*Ecological Archives* A021-012-A2).

APPENDIX C

Cod surplus production vs. total biomass (*Ecological Archives* A021-012-A3).