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Abstract

Cod stocks in the North West Atlantic and the Baltic Sea have shown similar dynamics in recent decades with a rapid decline in abundance and a lack of stock recovery following a period of large biomass. We explore whether the lack of recovery can be ascribed to an emergent Allee effect, which is a mechanism intrinsic to the community in contrast to explanations involving environmental factors. We formulate a stage-structured biomass model for the cod–sprat interaction in the Baltic Sea, paying special attention to the size-dependent prey preference of differently sized cod. The model predicts that alternative community states can occur under the same environmental conditions, in which cod is either present or absent. In a stable equilibrium with its main prey cod has a strong effect on the prey size distribution, resulting in larger densities of preferred prey sizes for cod than in the absence of any predation. Cod thus shapes its food environment to its own benefit. Furthermore, in response to increased exploitation cod biomass and yield tend to increase unless a stock collapse is imminent. After a cod stock collapse and the consequent drop in predation the prey size distribution becomes stunted and offers insufficient food for cod to grow and recover. These results are consequences of the indirect effects of predation and harvesting, whereby increased mortality relaxes competition among surviving individuals, leading to an increase in food intake and hence increased somatic growth and reproduction. We review observed community changes following the collapse of the cod stocks in the North West Atlantic and the Baltic Sea in the light of model predictions. In line with our model predictions growth in body size of cod has slowed down after the collapse, despite high densities of prey biomass. Furthermore, estimates of total prey population fecundity in the Baltic Sea identify the emergent Allee effect as a potentially important mechanism contributing to the lack of cod recovery.
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1. Introduction

Increases in both fishing intensity as well as fishing capacity in the last century have led to the present rapid decline of commercially exploited fish populations. Worldwide, cases of depleted fish stocks cause concern about the sustainability of these populations (e.g. Myers et al., 1997; Jackson et al., 2001; Myers and Worm, 2003; Hutchings and Reynolds, 2004; Reynolds et al., 2005). More than 50% of all the world's fisheries resources are fully exploited and another 24% is categorized as over-fished or completely depleted (Garcia et al., 2005).

Well known is the collapse of the cod stocks (*Gadus morhua*) in the Northwest Atlantic (NWA, e.g. Hutchings and Myers 1994; Myers et al., 1997; ICES, 2006b) and the Baltic Sea (ICES, 2006a; Osterblom et al., 2006). Both stocks have shown a period of large biomass, where catches were remunerative and the stocks responded with resilience to increasing fishing intensity. In the NWA peak abundances of cod biomass were recorded in the mid 1980s, despite a gradual increase in exploitation since the early 1960s. In the Baltic Sea, cod biomass increased up to the early 1980s. Then, within a relatively short period, the abundances in both stocks fell sharply. In 1992 all stocks in the NWA were at less than 15% of the recorded maximum (Myers et al., 1997; DFO, 2007). In the Baltic Sea, an increase in effort and more efficient fishing techniques (gillnet fishery) led to a decline to an "extremely low level in 1992" (ICES, 2006a). Following these rapid declines the biomass of both stocks has remained extremely low. The stocks are commercially extinct and do not show any sign of a possible increase. In the NWA there has been no recovery already for 15 years (DFO, 2007) despite the establishment of a fishing moratorium in 1993. Cod biomass in the Baltic Sea showed a small increase from 1992 to 1995 but was in 2005 down again to just over 10% of the peak recording in 1982 (ICES, 2006a).

Concomitant with the decline in the cod stocks the ecological communities in the two regions have gone through some significant changes at several trophic levels. These changes include direct effects of cod disappearance, such as increases in prey biomass, as well as indirect effects, such as decreased abundances of zooplankton (Carscadden et al., 2001; Casini et al., 2006) and decreased body condition of prey (Davoren and Montevecchi, 2003; Osterblom et al., 2006). For both ecosystems the collapse of cod has therefore been claimed to induce a regime or catastrophic ecosystem shift (NWA: DFO, 2003; Frank et al., 2005; Baltic Sea: Alheit et al., 2005; Möllmann et al., 2005, 2008) with community-wide effects due to cascading trophic interactions. In the context of any attempt to restore depleted cod stocks it is an important question whether the situation with high cod biomass that preceded stock collapse, and very low cod biomass afterward, represent alternative (stable) equilibrium states of the system. The shift from a high biomass with abundant cod to a low biomass, in which cod is commercially extinct, is almost certainly due to over-fishing. The lack of cod recovery, however, suggests that the shift is irreversible and that mechanisms intrinsic to the community stabilize and maintain the system in its current state with low cod biomass. A number of studies (DFO, 2003; Choi et al.,

2004; Frank et al., 2005) have ascribed the lack of recovery of NWA cod following the fishing moratorium from 1993 to changes in environmental conditions (temperature, salinity). Similarly, climate-induced changes in hydrography leading to changes in temperature and salinity have been argued to keep cod from recovering in the Baltic Sea (Alheit et al., 2005; Möllmann et al., 2005, 2008). These explanations hold bottom-up (environmental) drivers responsible for the sustenance of the new ecosystem state and imply that heavy fishing is merely a reinforcing mechanism: once environmental conditions again change to the better a fishing moratorium will lead to cod recovery. In contrast, if mechanisms intrinsic to the community stabilize the ecosystem in its current state even the combination of improved environmental conditions and reduced fishing may not lead to cod recovery. Several such mechanisms have been proposed to play a role. The high planktivore prey abundance that has resulted from the decline in cod may negatively affect cod population growth, either because of predation by these planktivores of cod eggs (Köster and Möllmann, 2000; Bakun, 2006; Pepin, 2006) or as a consequence of competition for shared resources between the planktivores and juvenile cod (Sparholt, 1994; Walters and Kitchell, 2001; Möllmann et al., 2004). Furthermore, low densities of cod have been claimed to disproportionally reduce the likelihood that cod eggs get fertilized (Rowe et al., 2004). The importance and relevance of these mechanisms have, however, not been investigated in much detail and it even remains unclear whether or not these mechanisms would be strong enough to stabilize the community in the current state with low cod abundance (Pepin, 2006).

In this paper we propose an additional mechanism that may prevent cod stocks to recover from a depleted state due to the occurrence of alternative stable states. This mechanism, referred to as an emergent Allee effect (De Roos and Persson, 2002; see Fig. 1 for a schematic representation), has been shown to occur in predator–prey–resource systems when predators forage exploitatively on selective size ranges of prey only. At low densities the size-selective predators experience a reduced or negative population growth rate because of a low abundance of prey in the size range targeted by the predator (Fig. 1, left panel). This shortage of appropriately sized prey occurs despite a high *total* abundance of prey. With increasing predator abundance the size-selective predation pressure on prey releases competition for resources among prey and thereby speeds up prey growth in body size and reproduction. Due to the increased growth and reproduction the prey size
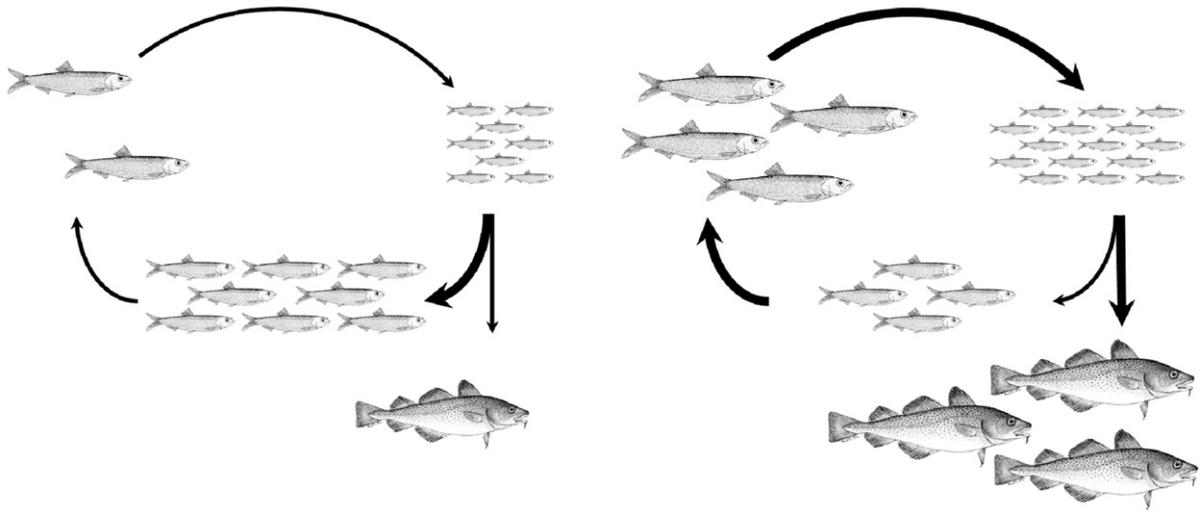
Fig. 1. Sprat population stage distribution in the two alternative community states that give rise to an emergent Allee effect for cod. Left: When cod is absent and predation low, individuals accumulate in the small-adult stage (stunted population); Right: When cod is present and predation high, especially on small sprat, recruitment to large size classes of sprat is high due to reduced intra-specific competition. This results in rapid growth of surviving sprat and high production of offspring (arrows) for (mostly juvenile) cod to forage on. Although cod predation targets all size classes of sprat, only the biomass flow representing predation on juvenile sprat is shown, as it is the crucial interaction that leads to the alternative community states.

distribution changes from dominance by large juvenile and small-adult individuals to dominance by large adults and high numbers of newly produced offspring (Fig. 1, right panel). The high density of prey offspring represents high food availability for the predator, which it however fostered itself by means of its size-dependent predation. The effects of predation on prey size distribution thus lead to positive density dependence in predator population growth rate and growth depensation at low predator abundance, which may prevent it to recover from a depleted state.

Emergent Allee effects have been shown to occur for predators that selectively forage either on small, juvenile prey or on large, adult prey (De Roos and Persson 2005). To investigate whether the emergent Allee effect can provide an explanation for the lack of recovery observed in the depleted cod stocks in the NWA and the Baltic Sea we analyze a population dynamic model that captures in detail the feeding preferences of cod for prey in different size ranges. The model is specifically formulated to account for the two important mechanisms, food-dependent growth in prey body size and size-selective predation, which give rise to emergent Allee effects. For the sake of simplicity we have represented other life history aspects of cod and its main prey in less quantitative detail, which allows us to clearly elucidate how the emergent Allee effect comes about and results

in a lack of recovery. To some extent the model therefore reflects a strategic model of the real ecological community and should not be taken as a detailed, quantitative representation of it. Nonetheless, model analysis leads to testable predictions about changes in the ecological community that are to be expected when cod abundance declines, some of which can uniquely identify the occurrence of an emergent Allee effect. In particular, alternative stable community states occur over considerable ranges of parameters and changes in prey size distribution indeed hamper the recovery of cod after overexploitation. We subsequently review the changes in the food web of the NWA and the Baltic Sea that occurred after the collapse of the local cod stock to assess whether or not these changes support model predictions.

2. Model formulation

We formulate a stage-structured predator–prey–resource model, which we parameterized for the interaction between cod, sprat, and their basic resources in the Baltic Sea. Essentially, the model is a stage-structured extension of the bio-energetics approach introduced by Yodzis and Innes (1992), and De Roos et al. (2007). Dynamics and equilibrium biomass densities of all trophic levels were studied as a function of

resource productivity and fishing mortality imposed on cod. For both sprat and cod we distinguished 3 life history stages: juveniles, small, and large adults. The focus of our analysis is the influence that cod exerts on the prey population. We therefore formulate the model including only interactions of metamorphosed individuals and ignore interactions that take place in the egg or larval stage of the two species, including the possible feeding of sprat on cod eggs (Köster and Möllmann, 2000).

Two functions play an important part in the biomass dynamics of all stages of both cod and sprat: the weight-specific net-biomass production rate, $v(I)$, and the weight-specific maturation rate $\gamma(I)$ that both depend on the weight-specific rate of food ingestion, I. The net-biomass production rate per unit of biomass equals the balance between biomass assimilation and maintenance (Yodzis and Innes, 1992; De Roos et al., 2007):

$$v(I) = \sigma I - T. \tag{1}$$

In this equation σ represents the efficiency with which food is assimilated and T the metabolic requirements per unit biomass. Food ingestion depends on the diet composition, which differs for the different life history stages of cod and sprat, and on the densities of resources that individuals feed upon. Maturation out of a particular life stage is modeled with the following function:

$$\gamma(I) = \frac{\kappa v(I) - d}{1 - z^{1 - d/(\kappa v(I))}}. \tag{2}$$

In this equation κ represents the fraction of net production that individuals in a particular life stage invest into somatic growth. Hence, the product $\kappa v(I)$ equals the weight-specific somatic growth rate. d represents the individual death rate, which is the sum of background and possibly predation and harvesting mortality. The parameter z represents the ratio of the initial and the final body size that a particular life stage encompasses and hence reflects the size range that an individual has to grow through before maturing to the next stage. The maturation function $\gamma(I)$ is food dependent through its dependence on net-biomass production, while it moreover decreases with increasing values of the individual death rate d. This function constitutes the unique feature of the model. De Roos et al. (2008) show that with this particular functional form $\gamma(I)$ describes weight-specific maturation rate at the population level in a way that is consistent with the individual-level assumptions that (1)

individuals in a particular life stage grow in body size at a weight-specific rate $\kappa v(I)$, while (2) experiencing a per capita death rate equal to d throughout the entire life stage.

Net-biomass production and maturation rates of the functional form discussed here occur in all dynamic equations for biomass density in the various life stages of cod and sprat. These rates may differ because of differences in diets and differences in parameter values, which are both species and stage specific. In the following we will hence label variables and parameters with a subscript where needed to indicate the species and life stage the quantity relates to.

2.1. Resource dynamics

The model accounts for biomass densities of three different resources (in gram per unit volume), referred to as R_S, R_J and R_A. Juvenile and adult sprat feed on and compete for the shared resource R_S. Juvenile and adult cod feed on separate resources, R_J and R_A, respectively, and hence do not compete with each other, nor with sprat, for a shared resource. We assume, however, that the productivity of R_J and R_A is too low for cod to persist on. Biomass dynamics for all three resources are described by similar equations:

$$\frac{dR_S}{dt} = P_S - \delta R_S - G_S \tag{3}$$

$$\frac{dR_J}{dt} = P_J - \delta R_J - G_J \tag{4}$$

$$\frac{dR_A}{dt} = P_A - \delta R_A - G_A. \tag{5}$$

These equations reflect that resource dynamics is a balance between a (constant) productivity P, resource turn-over with turn-over rate δ and resource grazing, referred to as G. The productivities of the three resources are considered constant system parameters (see Table 1).

2.2. Sprat dynamics

Biomass densities in the three life stages (in gram per unit volume) are referred to as S_J, S_A and S_B. Juveniles invest all their net-biomass production into somatic growth ($\kappa_{S_J} = 1$), while large adults invest all their net energy into reproduction ($\kappa_{S_B} = 0$). Small adults grow and reproduce. Biomass dynamics are described

Table 1
Model parameters and their default values for cod (*Gadus morhua*), preying on sprat (*Sprattus sprattus*)

Parameter	Value	Unit	Description
Individual energetics			
T_{C_J}	0.015	g g^{-1} day^{-1}	Metabolic rate of juvenile cod
T_{C_A}, T_{C_B}	0.006	g g^{-1} day^{-1}	Metabolic rate of small- and large-adult cod
M_{C_J}	0.08	g g^{-1} day^{-1}	Maximum ingestion rate of juvenile cod
M_{C_A}, M_{C_B}	0.022	g g^{-1} day^{-1}	Maximum ingestion rate of small- and large-adult cod
κ_{C_A}	0.8	–	Fraction of net production channelled to somatic growth
T_{S_J}	0.032	g g^{-1} day^{-1}	Metabolic rate of juvenile sprat
T_{S_A}, T_{S_B}	0.02	g g^{-1} day^{-1}	Metabolic rate of small- and large-adult sprat
M_{S_J}	0.23	g g^{-1} day^{-1}	Maximum ingestion rate of juvenile sprat
M_{S_A}, M_{S_B}	0.078	g g^{-1} day^{-1}	Maximum ingestion rate of small- and large-adult sprat
κ_{S_A}	0.8	–	Fraction of net production channelled to somatic growth
σ	0.3	g g^{-1}	Assimilation efficiency of sprat and juvenile cod
σ_P	0.4	g g^{-1}	Assimilation efficiency of adult cod
Mortality			
M	0.001	d^{-1}	Background mortality
F	Varied	–	Fishing mortality (as multiple of μ)
Body size ratios			
z_{C_J}	0.003	–	Initial–final size ratio of juvenile cod stage
z_{C_A}	0.125	–	Initial–final size ratio of small-adult cod stage
z_{S_J}	0.05	–	Initial–final size ratio of juvenile sprat stage
z_{S_A}	0.7	–	Initial–final size ratio of small-adult sprat stage
Resource dynamics			
δ	0.1	d^{-1}	Resource turn-over rate
P_S	Varied	g V^{-1} day^{-1}	Productivity of shared resource for all sprat stages
P_J	0.075	g V^{-1} day^{-1}	Productivity of shared resource for juvenile cod
P_A	0.1	g V^{-1} day^{-1}	Productivity of shared resource for adult cod

The factors q, indicating the fraction of time that individual cod in a particular life stage spend searching for a particular type of resource, are specified in the food web diagram shown in Fig. 2. The factor V represents the unit of system volume, in which the community is considered to live (see Electronic Appendix).

by the following set of ordinary differential equations (ODEs; see De Roos et al., 2008, for a derivation).

$$\frac{dS_J}{dt} = (1 - \kappa_{S_A})v_{S_A}^+(I_{S_A})S_A + v_{S_B}^+(I_{S_B})S_B$$
$$+ v_{S_J}(I_{S_J})S_J - \gamma_{S_J}^+(I_{S_J})S_J - d_{S_J}S_J \qquad (6)$$

$$\frac{dS_A}{dt} = \gamma_{S_J}^+(I_{S_J})S_J + v_{S_A}(I_{S_A})S_A$$
$$- (1 - \kappa_{S_A})v_{S_A}^+(I_{S_A})S_A - \gamma_{S_A}^+(I_{S_A})S_A$$
$$- d_{S_A}S_A \qquad (7)$$

$$\frac{dS_B}{dt} = \gamma_{S_A}^+(I_{S_A})S_A + v_{S_B}(I_{S_B})S_B - v_{S_B}^+(I_{S_B})S_B$$
$$- d_{S_B}S_B. \qquad (8)$$

Juvenile biomass S_J increases through reproduction by small and large adults, denoted by $(1 - \kappa_{S_A})v_{S_A}^+(I_{S_A})S_A$ and $v_{S_B}^+(I_{S_B})S_B$, respectively, which is in both cases the product of weight-specific net-biomass production and

adult biomass density. In addition, small adults only invest a fraction $1 - \kappa_{S_A}$ into reproduction. Here and below a superscript '+' indicates that a quantity is restricted to non-negative values and equal to 0 when negative values would occur. In the context of reproduction, the superscript indicates that reproduction is assumed to stop when net-biomass production turns negative and individuals starve. Juvenile biomass furthermore increases through somatic growth, $v_{S_J}(I_{S_J})S_J$, and decreases through maturation and death, described by the terms $\gamma_{S_J}^+(I_{S_J})S_J$ and $d_{S_J}S_J$, respectively. Juvenile maturation increases the biomass density of small adults, which moreover increases through net-biomass production by small adults themselves (first and second term in Eq. (7)). Small-adult biomass density decreases through their investment into reproduction, $(1 - \kappa_{S_A})v_{S_A}^+(I_{S_A})S_A$, through maturation, $\gamma_{S_A}^+(I_{S_A})S_A$ and through mortality $d_{S_A}S_A$. Biomass density of large adults increases through maturation of small adults and through net-biomass production by large adults themselves (first and second

term in Eq. (8)). Large-adult biomass density decreases through their investment into reproduction, $v_{S_B}^+(I_{S_B})S_B$ and through mortality $d_{S_B}S_B$. Note that the net-biomass production by large adults and their investment into reproduction cancel, reflecting the assumption that large adults invest all their net production in producing off-spring, except under starvation conditions, when large-adult biomass declines and their reproduction halts (De Roos et al., 2008).

2.3. Cod dynamics

Biomass densities in the three life stages of cod (in gram per unit volume) are referred to as C_J, C_A and C_B. Juvenile cod are assumed to only grow in body size, while large-adult cod do not grow at all. Only small-adult cod both grow in size as well as invest in reproduction. Biomass dynamics in these three life stages are described by a set of 3 ODEs that are analogous to the system of equations for sprat, discussed above:

$$\frac{dC_J}{dt} = (1 - \kappa_{C_A})v_{C_A}^+(I_{C_A})C_A + v_{C_B}^+(I_{C_B})C_B \\ + v_{C_J}(I_{C_J})C_J - \gamma_{C_J}^+(I_{C_J})C_J - d_{C_J}C_J \quad (9)$$

$$\frac{dC_A}{dt} = \gamma_{C_J}^+(I_{C_J})C_J + v_{C_A}(I_{C_A})C_A \\ - (1 - \kappa_{C_A})v_{C_A}^+(I_{C_A})C_A - \gamma_{C_A}^+(I_{C_A})C_A \\ - d_{C_A}C_A \quad (10)$$

$$\frac{dC_B}{dt} = \gamma_{C_A}^+(I_{C_A})C_A + v_{C_B}(I_{C_B})C_B - v_{C_B}^+(I_{C_B})C_B \\ - d_{C_B}C_B. \quad (11)$$

The terms occurring in these 3 equations are entirely analogous to the terms occurring in the ODEs (6)–(8) above and we will hence not discuss their interpretation any further.

2.4. Ingestion and mortality

Feeding relations between resources, sprat and cod are summarized in the schematic representation of the food web shown in Fig. 2. All feeding interactions are assumed to follow type II functional responses with a maximum ingestion rate M and a half-saturation resource density, which is uniformly taken equal to 1 (see the Electronic Appendix for justification of this value). Maximum ingestion rates are species and stage specific and are hence labeled with a subscript, indicating the particular species and stage where appropriate.
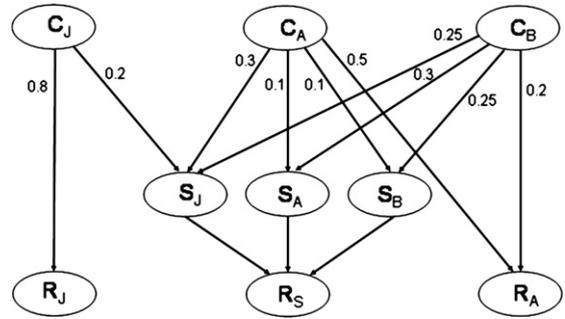

Fig. 2. Schematic representation of the feeding relations between juvenile, small- and large-adult cod (C_J, C_A and C_B) and sprat (S_J, S_A and S_B) and their alternative resources (R_J, R_A and R_S). The values next to all arrows are the factors q that represent the fraction of time spent foraging on the particular food resource.

Juvenile and adult sprat are assumed to feed on their shared resource only (Fig. 2), but with different maximum ingestion rates (see Table 1). Small and large-adult sprat, however, are assumed to have the same weight-specific maximum ingestion rates. Feeding by juvenile, small-adult and large-adult sprat is hence described by:

$$I_{S_J} = M_{S_J}\frac{R_S}{1 + R_S} \quad I_{S_A} = M_{S_A}\frac{R_S}{1 + R_S} \quad I_{S_B} = M_{S_B}\frac{R_S}{1 + R_S}. \quad (12)$$

Grazing by sprat on their shared resource is the sum of the grazing imposed by each of the three sprat stages separately, in which the stage-specific grazing pressure equals the product of the weight-specific ingestion rate and the stage-specific biomass density. Hence:

$$G_S = I_{S_J}S_J + I_{S_A}S_A + I_{S_B}S_B. \quad (13)$$

Juvenile cod are assumed to feed on their own alternative resource R_J, as well as on juvenile sprat. Adult cod are assumed to feed on all stages of sprat in addition to feeding on their alternative resource R_A. To model the relative intensity with which cod individuals forage on different resources, we introduce factors q that indicate the fraction of time that an individual in a particular life stage spends searching for a particular type of resource. For example, for juvenile cod we introduce the parameters $q_{C_J \to R_J}$ and $q_{C_J \to S_J}$ representing the fraction of time that a juvenile cod forages on alternative resource and on juvenile sprat, respectively. The values of these fractions are shown in the food web diagram in Fig. 2 and are derived from literature data on diet composition (see the Electronic Appendix for the derivation of these parameters). For any particular life

stage of cod the various values of q sum to 1, hence $q_{C_J \to R_J} + q_{C_J \to S_J} = 1$. The rate with which cod in different life stages encounter prey biomass now equals a weighted sum over the biomass densities of the different types of prey, in which the factors q are the weighting factors. Hence, for juvenile, small-adult and large-adult cod the prey encounter rate, referred to as E_{C_J}, E_{C_A} and E_{C_B}, respectively, equals:

$$E_{C_J} = q_{C_J \to R_J} R_J + q_{C_J \to S_J} S_J \tag{14}$$

$$E_{C_A} = q_{C_A \to R_A} R_A + q_{C_A \to S_J} S_J + q_{C_A \to S_A} S_A + q_{C_A \to S_B} S_B \tag{15}$$

$$E_{C_B} = q_{C_B \to R_A} R_A + q_{C_B \to S_J} S_J + q_{C_B \to S_A} S_A + q_{C_B \to S_B} S_B. \tag{16}$$

Food intake rates of juvenile, small-adult and large-adult cod depend on these encounter rates following a type II functional response with unit handling time and maximum ingestion rate M:

$$I_{C_J} = M_{C_J} \frac{E_{C_J}}{1 + E_{C_J}} \quad I_{C_A} = M_{C_A} \frac{E_{C_A}}{1 + E_{C_A}} \quad I_{C_B} = M_{C_B} \frac{E_{C_B}}{1 + E_{C_B}}. \tag{17}$$

These expressions for the prey encounter rate and the functional response of cod imply that the grazing rate of juvenile and adult cod on their alternative resources is described by:

$$G_J = M_{C_J} \frac{q_{C_J \to R_J} R_J}{1 + E_{C_J}} C_J \tag{18}$$

$$G_A = M_{C_A} \frac{q_{C_A \to R_A} R_A}{1 + E_{C_A}} C_A + M_{C_B} \frac{q_{C_B \to R_A} R_A}{1 + E_{C_B}} C_B \tag{19}$$

The death rates of juvenile, small-adult and large-adult sprat follow similar expressions, depending on the prey encounter rate of the different cod stages, as well as on their diet composition and the biomass density in a particular cod life stage. These death rates are described by the following equations:

$$d_{S_J} = \mu + M_{C_J} \frac{q_{C_J \to S_J}}{1 + E_{C_J}} C_J + M_{C_A} \frac{q_{C_A \to S_J}}{1 + E_{C_A}} C_A + M_{C_B} \frac{q_{C_B \to S_J}}{1 + E_{C_B}} C_B \tag{20}$$

$$d_{S_A} = \mu + M_{C_A} \frac{q_{C_A \to S_A}}{1 + E_{C_A}} C_A + M_{C_B} \frac{q_{C_B \to S_A}}{1 + E_{C_B}} C_B \tag{21}$$

$$d_{S_B} = \mu + M_{C_A} \frac{q_{C_A \to S_B}}{1 + E_{C_A}} C_A + M_{C_B} \frac{q_{C_B \to S_B}}{1 + E_{C_B}} C_B. \tag{22}$$

Notice that the above expressions specify the per-capita death rates and hence do not include stage-specific biomass density of the target prey stage in the numerator of all functional response terms. Furthermore notice that we have assumed that all individuals experience the same constant background mortality risk, referred to as μ.

For cod we assume that in all life stages cod individuals experience a low background mortality μ, which equals the background mortality of sprat. We furthermore assume that small-adult and large-adult cod are equally vulnerable to fishing mortality, which we express as a multiple of the background mortality rate μ. Hence, adult fishing mortality equals $F\mu$, while we assume juvenile cod to run a reduced risk and experience an additional mortality through fishing equal to $\rho F \mu$. The per-capita death rates of juvenile, small-adult and large-adult cod are therefore described by:

$$d_{C_J} = (1 + \rho F)\mu \quad d_{C_A} = (1 + F)\mu$$
$$d_{C_B} = (1 + F)\mu. \tag{23}$$

In the Electronic Appendix we discuss in detail how we derived default values of the model parameters from published data on individual energetics and diet composition. All parameter values are summarized in Table 1. Analytical expressions for the equilibria of the model cannot be derived. Hence, model analysis was entirely numerical, for which we used CONTENT (Kuznetsov et al., 1996), an interactive software package for numerical bifurcation analysis of dynamic systems (see Kuznetsov, 1995 for an introduction and overview).

3. Model predictions

Fig. 3 illustrates the model predictions regarding the effect of a period of increasing fishing pressure on the cod–sprat community. When the community is unexploited (Fig. 3; first 20 years) and both cod and sprat are present, the cod population is dominated by juvenile individuals, whereas large adults dominate the sprat population. Large- and small-adult cod are present in a ten times lower abundance than juveniles (Fig. 3, lower panel). This population structure reflects that competition among juveniles is strong and that consequently they take a long time to mature. Small- and large-adult cod have ample food, mainly due to the high density of large-adult sprat (Fig. 3), experience low competition for resources and hence have a large reproductive output. This large production of offspring together with
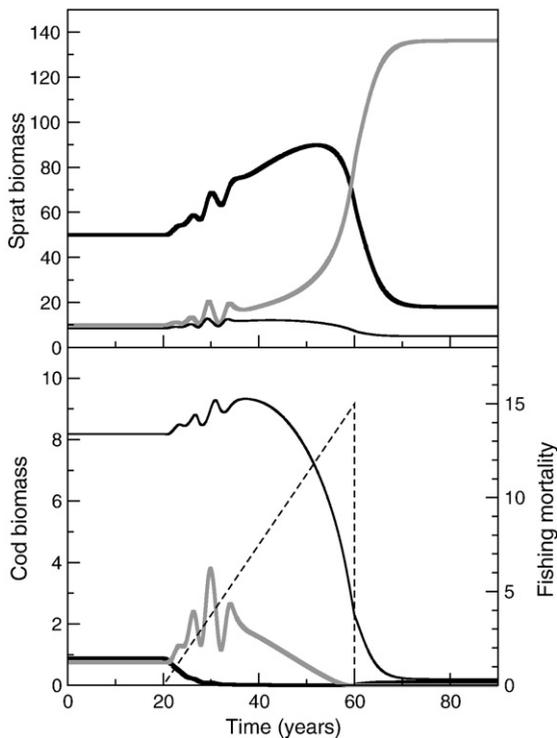
Fig. 3. Response of an unexploited cod–sprat community to a fishing mortality (dashed line; lower panel) that increases linearly over time from $t = 20$ to $t = 60$ and subsequently stops. Top: sprat biomass in the juvenile (thin, black line), small-adult (thick, grey line) and large-adult life stage (thick, black line); Bottom: cod biomass in the juvenile (thin, solid line), small-adult (thick, grey line) and large-adult life stage (thick, black line). Productivity of the sprat resource: $P_S = 12.0$ g V^{-1} day^{-1}; Juvenile cod experience a fishing mortality 20 times lower than adults ($\rho = 0.05$). Note that we have implemented a small invasion of large-adult cod to allow for population recovery if this would at all be possible. Other parameters have default values.

the relatively low availability of juvenile resources causes the accumulation of cod biomass in the juvenile stage. As such, the population is regulated through juvenile maturation (De Roos et al., 2007). In terms of numbers, especially large-adult, but also juvenile sprat are relatively abundant while small-adult sprat are present in low numbers. Because of their larger body size, however, large-adult sprat constitute the main component of the population biomass (Fig. 3, upper panel). Risk of predation by cod is highest for juvenile sprat (result not shown), which keeps their density down and prevents high competition among them. As a consequence, juvenile sprat that survive mature rapidly. Indirectly, cod predation on juveniles also keeps adult sprat density down, as only few juvenile sprat survive till maturation. Adult sprat hence also experience little competition and realize a high reproduction rate. Cod predation is therefore the major factor determining the

U-shaped population structure of sprat and is indirectly responsible for the high growth rate of juvenile and small-adult sprat and the high reproduction rate for small- and large-adult sprat.

Exposing the cod population to an increasing fishing pressure (Fig. 3, lower panel, between year 20 and 60) strongly reduces the biomass of large-adult cod. On the other hand, biomass of juvenile and small-adult cod shows an oscillatory increase. After some twenty years of a gradually increasing fishing pressure cod biomass starts to decline steadily. The decline continues even when harvesting is stopped completely after 40 years. This collapse of the cod population is irreversible as the population fails to recover from low densities (note that we have implemented a small invasion of large cod to allow for population recovery if this would be at all possible). After collapsing adult cod biomass has decreased to zero, while juvenile biomass is some 2% of the biomass before fishing started. The cod biomass that is still present results from the immigration of large-adult cod into the system. These adults produce low numbers of juveniles that themselves fail to mature because the resource densities they encounter are too low. As a consequence, small-adult cod are absent.

The collapse of the cod population leads to a concomitant increase in sprat biomass (Fig. 3, upper panel). Although initially all three stages increase in abundance, only small-adult biomass continues to increase, whereas juvenile and large-adult biomass ultimately decline to biomass densities that are 1.5–2.5 times lower than before the cod collapse. The population shifts from dominance by large adults to being dominated by small adults with low densities of both juveniles and large adults. In the absence of cod predation the sprat population is hence characterized by a unimodal, stunted size distribution as opposed to the U-shaped size distribution before the cod population disappeared. All sprat compete for the same resource, but juveniles have a more positive net-energy production than adults due to their larger ratio of maximum ingestion over maintenance rate (see Table 1). Adult growth and reproduction is much more limited by competition for resources than juvenile growth and maturation. Because of this slow recruitment into and rapid maturation out of the juvenile stage, sprat biomass is concentrated in the small-adult stage. Despite the fact that total sprat biomass is high in the absence of cod predation, the cod population cannot recover after harvesting has stopped completely. Due to the low density of juvenile sprat food availability for juvenile cod is too low for them to grow and mature sufficiently fast. After harvesting has stopped environmental conditions are

identical as before harvesting started (Fig. 3, lower panel, compare before year 20 and after year 60), except for the fact that predation by the cod population shaped the sprat size distribution in such a way that more food was available for juvenile cod. Cod hence exerted a positive feedback on its own food availability through its size-selective feeding on prey fish, which relaxed competition among prey and resulted in asymmetric responses in reproduction and somatic growth rate of the different prey life stages.

Fig. 4 shows the possible equilibria of the cod–sprat community, at different values for the sprat resource productivity, P_S, in the absence of any harvesting of cod. For these results we have assumed that the densities of alternative resources for juvenile and adult cod are so low that an exclusive diet of alternative resources would only satisfy 50% of their daily maintenance requirements. Both juvenile and adult cod hence need to forage on sprat for persistence. At low productivities of the sprat resource ($P_S < 8.7$ g V^{-1} day^{-1}) cod does not encounter sufficient food to persist at all, while at high productiv-

ities of the sprat resource ($P_S > 16.0$ g V^{-1} day^{-1}) cod and sprat coexist. These predictions are in agreement with classic predictions about community structure in a food chain with three trophic levels as a function of system productivity (Hairston et al., 1960; Oksanen et al., 1981). In contrast, however, equilibria with and without cod both represent stable community states in between these two threshold productivities. As discussed before, in a cod–sprat community state the densities of small-adult sprat are considerably lower than when cod is absent in contrast to juvenile and large-adult sprat densities that are higher when cod is present (Fig. 4).

The results shown in Fig. 3 are obtained with a productivity of sprat resource that is within the region with two stable community states. Fig. 1 illustrates schematically how these two states differ in terms of prey size distribution, growth and reproduction. When present cod predation represents a considerable drain of sprat biomass, especially of juveniles, which limits recruitment to larger stages and thereby gives rise to the U-shaped size distribution of sprat. Under these conditions cod cannot recover from low densities after high harvesting mortalities have led to a population collapse, irrespective of whether fisheries is banned completely or not. For the same value of sprat resource productivity Fig. 5 (top panel) shows the total cod population biomass and the yearly harvesting yield as a function of increasing fishing mortality. Given that the community state without cod is stable at zero fishing mortality, it is also a stable equilibrium for any higher level of fishing. Nonetheless, cod and sprat can persist in stable equilibrium for a range of fishing mortality rates, which is significantly smaller if juvenile individuals are exposed to exploitation as well (compare top-left and top-right panel in Fig. 5). The maximum fishing mortality, for which a stable cod–sprat equilibrium can occur, we will refer to as the persistence limit or persistence boundary. The persistence limit occurs at 14 times the background mortality that we assumed in case juveniles are protected from exploitation, but only 7 times the background mortality if juveniles are exposed to a fishing mortality that is just 5% of the mortality imposed on adults. Exposing a population to a higher mortality than this persistence limit will initiate a rapid decline. Indeed, during the period of increasing fishing mortality shown in Fig. 3, cod biomass starts to decline when fishing mortality exceeds the persistence limit (roughly 7 times background mortality).

The same bistability between a stable equilibrium without cod and one with both cod and sprat also occurs at higher values of the productivity of sprat resource (Fig. 5, lower panels). For these higher system
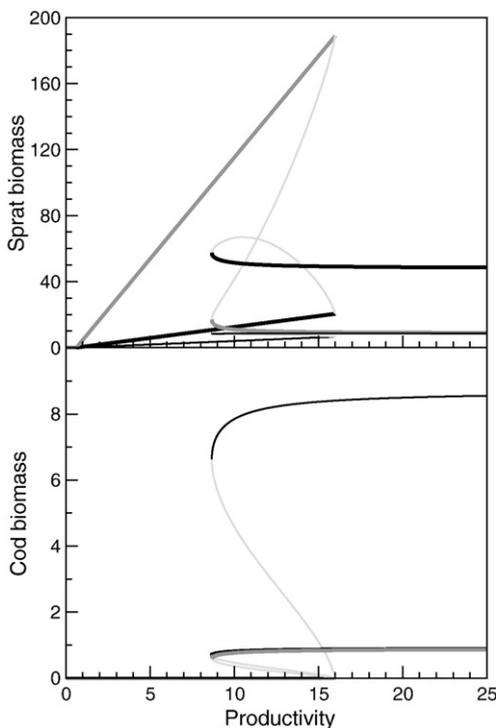

Fig. 4. Possible community equilibria of cod (bottom panel) and sprat (top panel) as a function of the productivity of the resource for sprat, P_S, in the absence of any fishing mortality. Other parameters have default values. Thin, black lines represent biomass in the juvenile stage, while thick grey and black lines represent biomass in the small- and large-adult stage, respectively. Thin grey lines represent unstable equilibria that are only represented for completeness.
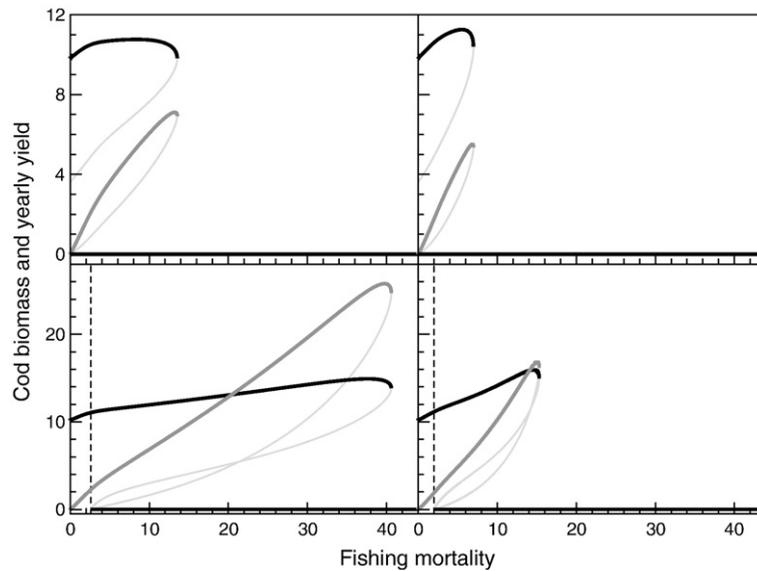
Fig. 5. Total cod population biomass (thick, black lines) and yearly harvesting yield (cod biomass harvested per year; thick, grey lines) as a function of fishing mortality for two different values of the productivity of the resource for sprat, $P_S = 12.0$ g V^{-1} day^{-1} (top) and $P_S = 18.0$ g V^{-1} day^{-1} (bottom). Juvenile cod are either not exposed to any fishing mortality at all (left panels) or experience a fishing mortality 20 times lower than adults ($\rho = 0.05$; right panels). Other parameters have default values. A stable equilibrium with zero density of cod occurs for all values of fishing mortality (top) and all fishing mortalities to the right of the vertical dashed line (bottom), as indicated by the horizontal, thick black lines. Thin grey lines represent unstable equilibria that are only represented for completeness.

productivities the range of fishing mortalities that a cod–sprat community can face without collapsing is substantially larger, especially when juvenile cod is protected against exploitation (Fig. 5, lower-left panel). For higher system productivities a community without cod is no longer a stable equilibrium in the absence of any fishing. Cod can hence recover from low densities if fishing mortality is below a threshold level (vertical dashed line in Fig. 5, lower panels), which we refer to as invasion limit or invasion boundary. After a population collapse, cod may in this case still face difficulties recovering from low densities if fishing mortality cannot be reduced below the invasion limit. This may for example occur when cod is caught as by-catch in fisheries that target other fish species than cod itself.

As a remarkable feature of the results shown in Fig. 5 increased exploitation of the cod population leads to an increase in both total cod biomass as well as total yearly harvest over large ranges of the fishing intensity. This positive response in biomass and yearly yield to an increase in exploitation is especially apparent at higher productivities of the sprat resource and when juveniles are exposed to some exploitation as well (Fig. 6). An increase in exploitation will only lead to a decrease in cod biomass and yield at exploitation levels close to the persistence limit, that is, under conditions when a stock

collapse is imminent. The increase in total biomass is primarily due to an increase in biomass of juvenile cod (Fig. 6). Biomass of small-adult cod shows an initial, weakly positive response over a small range of fishing mortalities, leveling off at higher fishing mortalities (Fig. 6). Biomass of large-adult cod monotonically declines with increasing exploitation. Biomass in all sprat life stages increases with increasing exploitation of cod, especially biomass of large-adult sprat (Fig. 6, top panel). The population stage distribution of sprat is primarily shaped by cod predation, as sprat resource density is consistently high (results not shown). The decrease in large-adult cod biomass especially releases large-adult sprat from predation, which allows them to achieve a high reproductive output. This increased production of newborn sprat implies an increased production rate of food for cod, which results in the increase in biomass of both juvenile and small-adult cod. At the same time, the more abundant cod impose sufficient predation pressure on sprat to prevent any density dependence among them to play a role. In sum, the increase in cod biomass and yearly yield results from a subtle interplay between (1) the stage distribution of cod, (2) the diet preferences of differently sized cod individuals for differently sized sprat, (3) the consequences of the previous two factors for the stage
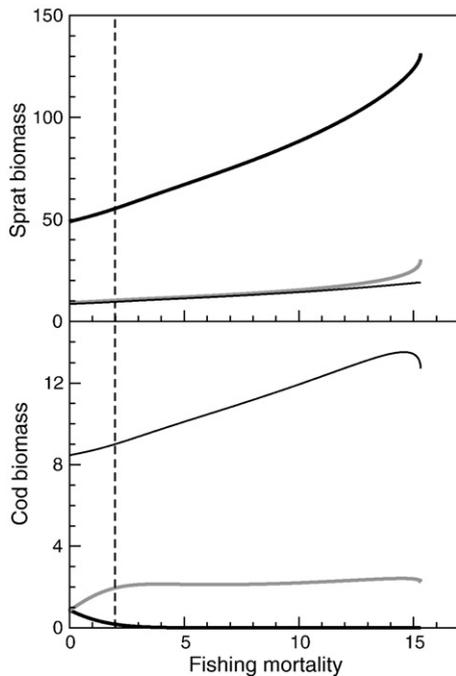
Fig. 6. Changes in equilibrium stage-specific biomass of sprat (top) and cod (bottom) with increasing fishing mortality for a sprat resource productivity of $P_S = 18.0$ g V^{-1} day^{-1}. Juvenile cod experience a fishing mortality 20 times lower than adults ($\rho = 0.05$). Other parameters have default values. Thin, black lines represent biomass in the juvenile stage, while thick grey and black lines represent biomass in the small- and large-adult stage, respectively. Only equilibrium densities for the stable community state in which cod and sprat coexist are shown. A stable equilibrium with zero density of cod occurs for all values of fishing mortality to the right of the vertical dashed line.

distribution of sprat, and (4) the differences in net-energy production capacity of juvenile, small-adult and large-adult sprat.

4. Empirical observations

The food webs in the NWA and in the Baltic Sea are broadly similar. Cod is the top predator in both the NWA (DFO, 2003) as well as in the Baltic Sea (Sparholt, 1994). In the NWA the main prey species of cod is capelin (*Mallotus villosus*), which itself forages mainly on zooplankton. In the Baltic Sea, the main prey species are the clupeids sprat (*Sprattus sprattus*) and herring (*Clupea harengus*) that are both also predominantly zooplanktivorous (Bagge et al., 1994; Rudstam et al., 1994; Sparholt, 1994). Sprat and herring compete with each other for the same resources (Möllmann et al., 2004), which is comparable to the intra-specific competition within both populations. In its simplest form the

food web can thus be described as a three trophic system, consisting of zooplankton, planktivorous prey fish and piscivores.

From the perspective of the community as a "classic" food chain with three trophic levels (Oksanen et al., 1981) a decrease in predator biomass would be expected to (1) decrease predation mortality on its main prey and hence lead to (2) an increase in prey biomass. Indirectly, the increase in prey biomass will lead to (3) a reduction in zooplankton abundance and hence to (4) increased competition among prey for food. This increase in competition may translate into (5) a declining body condition of prey and (6) a slowing down of prey growth in body size. In both the NWA and the Baltic Sea the collapse of the local cod stock has triggered community changes that are in broad agreement with the above predictions. In Table 2 we review and summarize empirical evidence for these changes in different parts of the NWA and in the Baltic Sea. These predictions and observations corroborate the idea that the collapse of cod induces a cascade of community-wide effects (NWA: DFO, 2003; Frank et al., 2005; Baltic Sea: Alheit et al., 2005; Möllmann et al., 2005; Möllmann et al., 2008) and support the perspective of the community as a "classic" food chain with three trophic levels.

The stage-structured predator–prey–resource model that we analyze in this paper generates all of the afore-mentioned predictions as well, but in addition predicts that in low density situations cod suffers from food shortage as a consequence of the changed size distribution of its prey. This latter prediction is in fact at odds with the conceptualization of the community as a classic three-link food chain or a trophic cascade, which would predict that the high prey abundance would result in very favorable growth conditions for cod. Due to the predation on selected size ranges of prey only, however, cod growth is predicted to slow down and hence give rise to an emergent Allee effect. Decreases in body condition and average size at age have indeed been observed for cod in both the NWA and the Baltic Sea, as is summarized in Table 2, which supports the hypothesis that an emergent Allee effect contributes to the lack of cod recovery from its depleted state.

A critical prediction of the stage-structured model is that growth depensation of cod at low densities arises especially because of the lack of juvenile sprat that are appropriately sized prey for juvenile cod. This prediction distinguishes the emergent Allee effect from other mechanisms that might give rise to such growth depensation, in particular the cultivation–depensation mechanism proposed by Walters and Kitchell (2001). We tested this prediction against data from sprat and

Table 2
Community changes in the NWA (codes refer to DFO management regions) and the Baltic Sea after the collapse of the local cod stock

Prediction	Observation	Time period	Area/division	Ref.
A) Northwest Atlantic				
Predation mortality	Capelin predation mortality down by factor 2.5	1980–2000	Gulf of St. Lawrence (4RST)	1
	Increased spawning and recruitment due to reduced cod predation	1990–2000	Eastern Scotian Shelf, Grand Banks	2
	Groundfish biomass declined 2 orders of magnitude	1970–1990	Eastern Scotian Shelf (4VW)	3
Prey biomass	Capelin occurrence up	Since 1990	Gulf of St. Lawrence (4RST)	4
	Pelagic fish biomass up	1980-, highest in mid 1990s	Eastern Scotian Shelf (4VW)	5
	Pelagic biomass increased 2 orders of magnitude	1970–2004	Eastern Scotian Shelf (4VW)	3
	Community shift from groundfish to small pelagic species	1980–2003	Eastern Scotian Shelf (4VW)	6
Indirect effects	Below-average densities of copepods and euphausiid prey of capelin	1990–2000	Gulf of St. Lawrence, Eastern Scotian Shelf, Grand Banks	2
	Capelin body condition declined	1982–1999	Grand Banks (3KL)	7
	Decreased condition of capelin fed to guillemot chicks	1990s	Grand Banks (3KL)	8
	Condition of all pelagic species declined	Since mid 1980s	Eastern Scotian Shelf (4VW)	6
	Reduction in mean size of capelin	Since late 1980s	Gulf of St. Lawrence (4RST)	1
	Capelin body size below pre-1991 average	1991–2005	Gulf of St. Lawrence (4RST)	1, 4
Cod size at age and condition	Size of 5-year old cod declined by 25%	1970–2000	Eastern Scotian Shelf (4VW)	6
	Cod older than 3-years of age show reduced length at age	1970–1998	Gulf of St. Lawrence (4T)	9
	Reduced cod body condition	1970–2000	Eastern Scotian Shelf (4VW)Gulf of St. Lawrence (4RS)	6, 10
B) Baltic Sea				
Predation mortality	Age-specific predation mortality of herring and sprat decreased to below 20%	1980–2005	Baltic Sea	11
	Predation mortality on herring longer than 10 cm decreased 30-fold	1990–1992	Baltic Sea	12
Prey biomass	Total clupeid biomass (sprat, herring) doubled	1988–1995	Baltic Sea	11
	Sprat biomass increased with factor 4	1980–2005	Baltic Sea	11
Indirect effects	Competition for food causes decreased clupeid condition	1980–2005	Baltic Sea	13
	Condition decrease of 22% for sprat and 24% for herring	1990–1995	Baltic Sea	13
	Sprat weight at age (1–8 yrs.) around 70% of weight at age during 1980–1994	1995–2005	Baltic Sea	11
Cod size at age	Decreased mean weight at age of especially older cod	1992–2005	Baltic Sea	11

1: Grégoire et al. (2005). 2: Carscadden et al. (2001). 3: Choi et al. (2004). 4: DFO (2006). 5: Frank et al. (2005). 6: DFO (2003). 7: Carscadden and Frank (2002). 8: Davoren and Montevecchi (2003). 9: Sinclair et al. (2002). 10: Lambert and Dutil (1997). 11: ICES (2006a). 12: Beyer and Lassen (1994). 13: Casini et al. (2006).

herring in the Baltic Sea. Juvenile cod in the Baltic Sea switch to piscivory once they have reached a length of 15–20 cm (Sparholt, 1994), corresponding to a body weight below 100 g (Andersen and Riis-Vestergaard, 2004). Given that predator–prey body weight ratios are in the order of 100 (Ursin, 1973) piscivory by juvenile cod will mainly occur on prey fish well below 4 g in body weight. The latter, however, is the minimum weight at which clupeids first show up in the stock abundance estimates for the Baltic Sea (ICES, 2006a), which can hence not be taken as a reliable estimate of prey fish abundance. We therefore assessed prey fish availability for juvenile cod by estimating from literature data the population fecundity of herring and sprat over the past decades (Fig. 7; see Electronic Appendix for calculation details). Our estimates indicate that total clupeid population fecundity has shown an oscillatory, but consistently declining trend over the period 1974–2004. Over the first half of this period herring produced most of these offspring, whereas sprat dominated the offspring production in the second half, reflecting the trend in total biomass of the two species. Most importantly, over the period 1992–2004, when cod experienced a continued low population biomass, total clupeid population fecundity decreased by a factor of 2.7. Furthermore, temporary increases in cod biomass
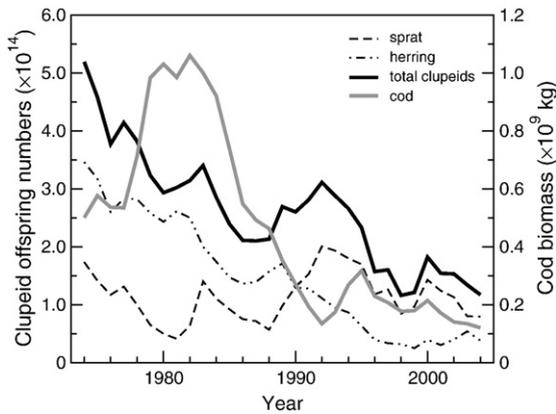
Fig. 7. Estimated total population fecundity (numbers of eggs produced) of herring (dash-dotted line) and sprat (dashed line) and total cod biomass (ICES estimates, thick, grey line) in the Baltic Sea from 1974 until 2004. Total clupeid population fecundity (thick, black line) is the sum of herring and sprat fecundity. See Electronic Appendix for calculation details regarding clupeid fecundity.

seem to mirror brief increases in total clupeid fecundity (for example, in 1992 and 2000). We therefore conclude that these data indeed seem to support the hypothesis that low prey fish availability for juvenile cod plays a role in the lack of recovery of the cod population in recent years and thus identify the emergent Allee effect as a potentially important mechanism.

5. Discussion

The model analysis presented in this paper leads to two main conclusions: (1) the food web interactions between cod and sprat are likely to result in an emergent Allee effect for cod, such that in a depleted stock individual cod encounter too little food to rebuild the population despite high sprat densities; and (2) over a substantial range of conditions increased exploitation of cod may lead to higher biomass densities of both cod and sprat as well as to an increased harvesting yield. Both effects are consequences of the subtle interplay between size-dependent food intake and energetics of both sprat and cod and the size-dependent predation that cod exerts on sprat. This predation releases competition among surviving sprat and thus indirectly increases net-energy production, which subsequently translates into increased somatic growth and maturation to larger size classes as well as to increased reproduction. It is especially the link between food intake on the one hand and individual growth and reproduction on the other that has been ignored in most previous modeling studies of fish population dynamics.

The poor food conditions that individual cod experience in a sprat population that is not exposed to any predation result from the inter-stage differences in net-energy production of sprat. On a weight-specific basis juvenile sprat are more efficient foragers and use less energy for maintenance than adults. As a consequence, a sprat population that is not exposed to predation is dominated by small-adult individuals (with a relatively low reproductive output) and contains only low densities of potential prey especially for juvenile cod (Fig. 1, left panel). Substantial predation on sprat can effectively counter the dominance by small adults and give rise to a U-shaped population stage distribution with higher densities of juvenile sprat that (juvenile) cod can forage on (Fig. 1, right panel). The change in sprat stage distribution comes about because of the indirect, positive effects of cod predation, that is, a release of competition and an accelerated somatic growth of sprat that survive. By feeding size selectively on different sprat stages cod may hence change the structure of its main prey population, exert a positive feedback on its own food availability and thus shape its feeding environment to its own benefit. This positive feedback of cod on its own food environment is possible, as long as predation does not primarily target the small-adult sprat themselves (De Roos et al., 2003). In the Gulf of St. Lawrence cod predation has indeed been shown to be highest for prey individuals of 0.5–2 g (Duplisea, 2005). Therefore, also there cod predation mainly affects prey before they reach the dominant life stage, which is most effective to achieve a release of competition.

The increase in cod biomass and yield with increasing exploitation over substantial ranges of the parameters also results from the effects of cod predation on sprat dynamics, in particular the size selectivity of this predation. The decline in large-adult cod as a result of harvesting releases large-adult sprat from predation, increasing their numbers. These large adults fuel the production of new biomass through their high fecundity, which ultimately translates into an increased production of the sprat population as a whole and hence an increased food availability for cod. The release of large-adult sprat from predation is possible, because small-adult cod forage to a much lesser extent on large-adult sprat than large-adult cod. The differences in prey size preference among differently sized adult cod hence allows for a decreased predation pressure on large-adult sprat despite that total biomass of adult cod increases. Increases in biomass of particular life stages in response to an increase in mortality have been shown to occur in a variety of systems (reviewed in De Roos et al., 2007). The mechanism behind such increases was recently elucidated using a stage-structured biomass model similar to the one analyzed in this paper (De Roos

et al., 2007). In none of these studies, however, total population biomass increased in response to an increased mortality. As explained above, this unique result of the model presented here comes about because of the size selectivity of cod predation and the increase in biomass production by large-adult sprat, which follows from it.

The predictions of the stage-structured cod–sprat model we developed in this paper are qualitatively in agreement with the changes that have occurred in the NWA and Baltic Sea ecosystem after the collapse of the cod population. Most of the observed changes relate to a decrease in top-down effects as a result of the decline of cod as main predator. These changes can hence be explained in terms of a trophic cascade or a classic food chain (Hairston et al., 1960; Oksanen et al., 1981). However, such explanations cannot account for observed declines in cod size at age and cod body condition in the presence of high abundances of prey fish. In contrast, the emergent Allee effect explicitly predicts that cod growth in body size and reproduction is poor in a depleted stock as a consequence of the lack of appropriately sized prey, even though total prey biomass is high. The changes in total clupeid population fecundity in the Baltic Sea in recent decades furthermore support the hypothesis that the emergent Allee effect is at least one of the mechanisms intrinsic to the community that stabilize the current sprat domination in the Baltic Sea and contribute to the lack of cod recovery. Feeding of sprat on cod eggs (Köster and Möllmann, 2000) and competition between sprat and cod larvae for a shared resource (Sparholt, 1994; Möllmann et al., 2004) have also been proposed to play a role in this stabilization, but a more rigorous analysis of these mechanisms is lacking. To compare the importance of all the aforementioned mechanisms for the stability of the current ecosystem state and to study their additive effects on community dynamics are important questions for future research.

On purpose we formulated a strategic model without attempting to be complete, i.e. to capture all known mechanisms affecting cod and prey dynamics, or to construct a detailed, quantitative representation of the system. Rather, we developed a model, which was specifically aimed at identifying the consequences of the basic feeding interactions between cod and sprat for community dynamics, but which could nonetheless generate testable predictions. We therefore did not account for cannibalism in cod (Rudstam et al., 1994; Sparholt, 1994), although we have verified that the inclusion of cannibalism does not qualitatively change the results presented. Furthermore, we used sprat to represent the main prey of cod in the Baltic Sea, even

though cod also feeds on herring. As important qualitative prediction the model reveals that cod collapse is associated with a shift in dominance from large-adult sprat to small-adult sprat, while recovery of the cod population would reverse this shift. For the Baltic Sea we postulate that this shift in dominance from small to large-adult sprat can be interpreted not only intra-specifically but also inter-specifically. Cod recovery would significantly relax competition among prey and make resistance to predation a decisive factor for the outcome of the interaction between different prey species. Because of its larger body size herring can be expected to benefit more from cod recovery than sprat, whereas sprat's smaller body size gives it an edge over herring at low cod abundance when competing for resources, a prediction that corresponds to the observation of continued decline in herring biomass alongside with the increase in sprat biomass in the Baltic Sea. Decline and recovery of Baltic Sea herring can thus be expected to be closely linked to decline and recovery of the cod stock. Preliminary analysis of an extended model that accounts for a second, larger prey species indeed confirms the idea that cod facilitates the persistence of the larger of the two competing prey species and is crucial for its persistence (results not shown).

Österblom et al. (2007) have expressed the expectation that cod stocks in the Baltic Sea would recover if harvesting would be limited. Our model predictions suggest that the likelihood of cod recovery will depend on system productivity. At lower levels of productivity, in the region with two alternative stable states, cod will not be able to recover even if fishing is banned completely. At higher productivities cod recovery is possible, but fishing mortality has to be reduced and be in the same range as background mortality. Measures that would reduce the productivity of the Baltic Sea would hence be counter-productive for rebuilding the cod stock.

The most important aspect of the model developed here is the explicit link between individual food intake, net-energy production, growth in body size and reproduction, in other words, the models' accounting for a complete, individual energy budget. As a consequence of this link size-selective predation exerts an indirect, positive effect on reproduction and somatic growth in prey stages. Clearly identifying the consequences of this positive feedback allows for the development of management actions that at first sight seem counter-intuitive. For example, De Roos and Persson (2002) suggested that, if indeed the change in prey population size distribution after a predator

collapse prohibits recovery of the predator, thinning the prey population might be an effective strategy to foster recovery. Modeling studies suggested that such a counter-intuitive approach might be more successful than release or stocking of predators (van Kooten et al., 2005). The validity of this counter-intuitive approach was recently demonstrated in a whole-lake study, in which substantial thinning of a prey population indeed led to a rapid recovery of the overexploited top predator population (Persson et al., 2007). This study furthermore provided compelling evidence for the occurrence of two alternative community states, one with a depleted predator stock and one in which predators are abundant, as a consequence of an emergent Allee effect for the predator. Given that both the NWA and the Baltic Sea community show signs that cod recovery is impeded by an emergent Allee effect, we suggest that thinning its main prey population should be considered as a serious management strategy, the more so given the other mechanisms, such as egg predation and competition, by which planktivorous prey fish are supposed to negatively affect cod population growth.

Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.seares.2008.02.008.

References

Alheit, J., Möllmann, C., Dutz, J., Kornilovs, G., Loewe, P., Mohrholz, V., Wasmund, N., 2005. Synchronous ecological regime shifts in the central Baltic and the North Sea in the late 1980s. ICES Journal of Marine Science 62, 1205–1215.

Andersen, N.G., Riis-Vestergaard, J., 2004. Alternative model structures for bioenergetics budgets of a cruising predatory gadoid: incorporating estimates of food conversion and costs of locomotion. Canadian Journal of Fisheries and Aquatic Sciences 61, 2413–2424.

Bagge, O., Thurow, F., Steffensen, E., Bay, J., 1994. The Baltic Cod. Dana 10, 1–28.

Bakun, A., 2006. Wasp-waist populations and marine ecosystem dynamics: navigating the "predator pit" topographies. Progress in Oceanography 68, 271–288.

Beyer, J.E., Lassen, P., 1994. The effect of size-selective mortality on the size-at-age of Baltic herring. Dana 10, 203–224.

Carscadden, J.E., Frank, K.T., 2002. Temporal variability in the condition factors of Newfoundland capelin (*Mallotus villosus*) during the past two decades. ICES Journal of Marine Science 59, 950–958.

Carscadden, J.E., Frank, K.T., Leggett, W.C., 2001. Ecosystem changes and the effects on capelin (*Mallotus villosus*), a major forage species. Canadian Journal of Fisheries and Aquatic Sciences 58, 73.

Casini, M., Cardinale, M., Hjelm, J., 2006. Inter-annual variation in herring, *Clupea harengus*, and sprat, *Sprattus sprattus*, condition in the central Baltic Sea: what gives the tune? Oikos 112, 638–650.

Choi, J.S., Frank, K.T., Leggett, W.C., Drinkwater, K., 2004. Transition to an alternate state in a continental shelf ecosystem. Canadian Journal of Fisheries and Aquatic Sciences 61, 505–510.

Davoren, G.K., Montevecchi, W.A., 2003. Signals from seabirds indicate changing biology of capelin stocks. Marine Ecology. Progress Series 258, 253–261.

De Roos, A.M., Persson, L., 2002. Size-dependent life-history traits promote catastrophic collapses of top predators. Proceedings of the National Academy of Sciences of the United States of America 99, 12907–12912.

De Roos, A.M., Persson, L., 2005. The influence of individual growth and development on the structure of ecological communities. In: De Ruiter, P.C., Wolters, V., Moore, J.C. (Eds.), Dynamic food webs: Multispecies assemblages, ecosystem development, and environmental change. Academic Press, San Diego, pp. 89–100.

De Roos, A.M., Persson, L., Thieme, H.R., 2003. Emergent Allee effects in top predators feeding on structured prey populations. Proceedings of the Royal Society of London. Series B, Biological Sciences 270, 611–618.

De Roos, A.M., Schellekens, T., van Kooten, T., van de Wolfshaar, K., Claessen, D., Persson, L., 2007. Food-dependent growth leads to overcompensation in stage-specific Biomass when mortality increases: the influence of maturation versus reproduction regulation. American Naturalist 170, E59–E76.

De Roos, A.M., Schellekens, T., Van Kooten, T., Van De Wolfshaar, K., Claessen, D., Persson, L., 2008. Simplifying a physiologically structured population model to a stage-structured biomass model. Theoretical Population Biology 73, 47–62.

DFO, 2003. State of the Eastern Scotian Shelf Ecosystem. 2003/004. DFO Canadian Science Advisory Secretariat.

DFO, 2006. Assessment of the Estuary and Gulf of St. Lawrence (Divisions 4RST) Capelin Stock in 2005. Science Advisory Report 2006/022. DFO Canadian Science Advisory Secretariat.

DFO, 2007. Stock assessment of Northern (2J3KL) cod in 2007. Science Advisory Report 2007/018. Canadian Science Advisory Secretariat.

Duplisea, D.E., 2005. Running the gauntlet: the predation environment of small fish in the northern Gulf of St Lawrence, Canada. ICES Journal of Marine Science 62, 412–416.

Frank, K.T., Petrie, B., Choi, J.S., Leggett, W.C., 2005. Trophic cascades in a formerly cod-dominated ecosystem. Science 308, 1621–1623.

Garcia, S.M., de Leiva Moreno, I., Grainger, R., 2005. Global trends in the state of marine fisheries resources 1974–2004. Review of the state of world marine fishery resources. FAO.

Grégoire, F., Savenkoff, C., Chabot, D., 2005. Capelin (*Mallotus villosus*) of the Estuary and gulf of St. Lawrence (NAFO Divisions 4RST) in 2004. Research Document 2005/058. Canadian Science Advisory Secretariat.

Hairston, N.G., Smith, F.E., Slobodkin, L.B., 1960. Community structure, population control, and competition. The American Naturalist 94, 421–425.

Hutchings, J.A., Myers, R.A., 1994. What can be learned from the collapse of a renewable resource — Atlantic cod, *Gadus-morhua*, of Newfoundland and Labrador. Canadian Journal of Fisheries and Aquatic Sciences 51, 2126–2146.

Hutchings, J.A., Reynolds, J.D., 2004. Marine fish population collapses: consequences for recovery and extinction risk. Bioscience 54, 297–309.

ICES, 2006a. Report of the Baltic Fisheries Assessment Working Group (WGBFAS). ACFM:24.

ICES, 2006b. Report of the Workshop on the Decline and Recovery of Cod Stocks Throughout the North Atlantic, Including Trophodynamic Effects (WKDRCS). OCC:12.

Jackson, J.B.C., Kirby, M.X., Berger, W.H., Bjorndal, K.A., Botsford, L.W., Bourque, B.J., Bradbury, R.H., Cooke, R., Erlandson, J., Estes, J.A., Hughes, T.P., Kidwell, S., Lange, C.B., Lenihan, H.S., Pandolfi, J.M., Peterson, C.H., Steneck, R.S., Tegner, M.J., Warner, R.R., 2001. Historical overfishing and the recent collapse of coastal ecosystems. Science 293, 629–638.

Köster, F.W., Möllmann, C., 2000. Trophodynamic control by clupeid predators on recruitment success in Baltic cod? ICES Journal of Marine Science 57, 310–323.

Kuznetsov, Y.A., 1995. Elements of Applied Bifurcation Theory. Springer-Verlag, New York.

Kuznetsov, Y.A., Levitin, V.V., Skovoroda, A.R., 1996. Continuation of Stationary Solutions to Evolution Problems in CONTENT. AM-R9611. Centre for Mathematics and Computer Science, Amsterdam.

Lambert, Y., Dutil, J.D., 1997. Condition and energy reserves of Atlantic cod (*Gadus morhua*) during the collapse of the northern Gulf of St. Lawrence stock. Canadian Journal of Fisheries and Aquatic Sciences 54, 2388–2400.

Möllmann, C., Kornilovs, G., Fetter, M., Köster, F.W., 2004. Feeding ecology of central Baltic Sea herring and sprat. Journal of Fish Biology 65, 1563–1581.

Möllmann, C., Kornilovs, G., Fetter, M., Köster, F.W., 2005. Climate, zooplankton, and pelagic fish growth in the central Baltic Sea. ICES Journal of Marine Science 62, 1270–1280.

Möllmann, C., Müller-Karulis, B., Kornilovs, G., St John, M.A., 2008. Effects of climate and overfishing on zooplankton dynamics and ecosystem structure: regime shifts, trophic cascade, and feedback loops in a simple ecosystem. ICES Journal of Marine Sciences fsm197.

Myers, R.A., Worm, B., 2003. Rapid worldwide depletion of predatory fish communities. Nature 423, 280–283.

Myers, R.A., Hutchings, J.A., Barrowman, N.J., 1997. Why do fish stocks collapse? The example of cod in Atlantic Canada. Ecological Applications 7, 91–106.

Oksanen, L., Fretwell, S.D., Arruda, J., Niemela, P., 1981. Exploitation ecosystems in gradients of primary productivity. The American Naturalist 118, 240–261.

Osterblom, H., Casini, M., Olsson, O., Bignert, A., 2006. Fish, seabirds and trophic cascades in the Baltic Sea. Marine Ecology. Progress Series 323, 233–238.

Österblom, H., Hansson, S., Larsson, U., Hjerne, O., Wulff, F., Elmgren, R., Folke, C., 2007. Human-induced trophic cascades and ecological regime shifts in the Baltic Sea. Ecosystems 10.

Pepin, P., 2006. Estimating the encounter rate of Atlantic capelin (*Mallows villosus*) with fish eggs, based on stomach content analysis. Fishery Bulletin 104, 204–214.

Persson, L., Amundsen, P.A., De Roos, A.M., Klemetsen, A., Knudsen, R., Primicerio, R., 2007. Culling prey promotes predator recovery — alternative states in a whole-lake experiment. Science 316, 1743–1746.

Reynolds, J.D., Dulvy, N.K., Goodwin, N.B., Hutchings, J.A., 2005. Biology of extinction risk in marine fishes. Proceedings of the Royal Society of London. B, Biological Sciences 272, 2337–2344.

Rowe, S., Hutchings, J.A., Bekkevold, D., Rakitin, A., 2004. Depensation, probability of fertilization, and the mating system of Atlantic cod (*Gadus morhua* L.). ICES Journal of Marine Science 61, 1144–1150.

Rudstam, L.G., Aneer, G., Hildén, M., 1994. Top-down control in the pelagic Baltic ecosystem. Dana 10, 105–129.

Sinclair, A.F., Swain, D.P., Hanson, J.M., 2002. Disentangling the effects of size-selective mortality, density, and temperature on length-at-age. Canadian Journal of Fisheries and Aquatic Sciences 59, 372–382.

Sparholt, H., 1994. Fish species interactions in the Baltic Sea. Dana 10, 131–162.

Ursin, E., 1973. On the prey size preferences of cod and dab. Meddelelser fra Danmarks Fiskeri- og Havundersogelser (Ny Ser.) 7, 85–98.

van Kooten, T., de Roos, A.M., Persson, L., 2005. Bistability and an Allee effect as emergent consequences of stage-specific predation. Journal of Theoretical Biology 237, 67–74.

Walters, C., Kitchell, J.F., 2001. Cultivation/depensation effects on juvenile survival and recruitment: implications for the theory of fishing. Canadian Journal of Fisheries and Aquatic Sciences 58, 39–50.

Yodzis, P., Innes, S., 1992. Body size and consumer-resource dynamics. American Naturalist 139, 1151–1175.