

An ecosystem model of food web and fisheries interactions in the Baltic Sea

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Harvey, C. J., Cox, S. P., Essington, T. E., Hansson, S., and Kitchell, J. F. 2003. An ecosystem model of food web and fisheries interactions in the Baltic Sea. – ICES Journal of Marine Science, 60: 939–950.

Because fisheries operate within a complex array of species interactions, scientists increasingly recommend multispecies approaches to fisheries management. We created a food web model for the Baltic Sea proper, using the Ecopath with Ecosim software, to evaluate interactions between fisheries and the food web from 1974 to 2000. The model was based largely on values generated by multispecies virtual population analysis (MSVPA). Ecosim outputs closely reproduced MSVPA biomass estimates and catch data for sprat (*Sprattus sprattus*), herring (*Clupea harengus*), and cod (*Gadus morhua*), but only after making adjustments to cod recruitment, to vulnerability to predation of specific species, and to foraging times. Among the necessary adjustments were divergent trophic relationships between cod and clupeids: cod exhibited top-down control on sprat biomass, but had little influence on herring. Fishing, the chief source of mortality for cod and herring, and cod reproduction, as driven by oceanographic conditions as well as unexplained variability, were also key structuring forces. The model generated many hypotheses about relationships between key biota in the Baltic Sea food web and may ultimately provide a basis for estimating community responses to management actions.

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Keywords: Baltic Sea, cod, Ecopath with Ecosim, fisheries, food web, herring, multispecies virtual population analysis, predator–prey interactions, sprat, top-down control.

Received 27 May 2002; accepted 12 March 2003.

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Introduction

Fisheries in the Baltic Sea have taken 0.5–1 million tonnes of fish annually since 1962 (Thurow, 1997). Intensive fisheries target two clupeid planktivores (herring, *Clupea harengus*; sprat, *Sprattus sprattus*) and a piscivore (cod, *Gadus morhua*). Catches of the large eastern cod stock have regularly exceeded recommended levels (FAO, 1997), and cod recruitment has been highly variable and generally declining in recent decades (Jonzén *et al.*, 2001). Consequently, cod biomass declined severely in the 1980s and remains low (Horbowy, 1996; Jonzén *et al.*, 2001). Herring biomass has declined since the 1970s (ICES, 1999, 2001a), while biomass of sprat, a fish of low commercial value,

increased sharply in the 1990s (Horbowy, 1996; ICES, 1999). Rehabilitating cod and herring stocks is a high priority for Baltic Sea fisheries managers (ICES, 2001b).

Fisheries scientists and managers increasingly feel that proper management involves understanding the ecosystems in which fisheries operate (EPAB, 1999). This concept is recognized in Baltic Sea fisheries, particularly with respect to food web interactions (e.g. Section 1.3 of ICES, 2001a). For example, cod prey on both sprat and herring, which in turn may feed on cod eggs and larvae (Köster and Möllmann, 2000). Intensive fishing thus occurs amid an array of complex species interactions. Understanding the effects of a fishery in the context of such interactions is key to responsible management of aquatic ecosystems.

Much of our understanding of how fisheries and food webs interact in the Baltic Sea comes from multispecies virtual population analysis (MSVPA) (Gislason, 1999; ICES, 1999, 2001a; Collie and Gislason, 2001; Köster *et al.*, 2001a, b). MSVPA is an age-structured model that estimates historic population sizes, fishing mortalities, and predation mortalities of several exploited, interacting fish stocks (Sparre, 1991). MSVPA links species to one another via predation, and thus explicitly accounts for variation in predation mortality, which single-species VPA assumes to be constant. Species that are in the food web but not targeted by fisheries are not explicitly incorporated into the analysis, but rather are pooled as “other food” if they are prey or as “other natural mortality” if they are predators. Thus, MSVPA focuses on how fishing affects targeted species, in the context of those species’ direct predator–prey interactions.

A different approach that simulates a wider range of species and ecosystem processes is Ecopath with Ecosim (EwE; Christensen *et al.*, 2000; Walters *et al.*, 2000). Ecopath models represent a mass-balanced budget of production, consumption, and fishing in a food web, and may include all functional groups, including primary producers and consumers not targeted by fisheries. Ecopath estimates are used to initialize Ecosim, a model that simulates the dynamics of each biomass pool based on specified predator–prey relationships, recruitment processes, fishing, and physical forcing. Using Ecosim, one can examine how a food web might respond to a perturbation, such as a change in fishing pressure or changes in the aquatic environment. Because EwE integrates predator–prey interactions, fisheries, and habitat effects across a broader range of functional groups, it can address questions that MSVPA cannot, including the importance of dynamic feedbacks between lower and upper trophic levels, the importance of bottom-up controls, and specific impacts of fishing on non-target species such as marine mammals.

We used EwE (version 4.1) to analyze the food web of the Baltic Sea between 1974 and 2000. Our central goals were, first, to develop an Ecopath model that approximated the food web in 1974, using MSVPA biomass estimates for sprat, herring, and cod for the same year (ICES, 2001a), and the best available information for the rest of the food web; and then to use Ecosim to reproduce MSVPA biomass estimates of cod, herring, and sprat between 1974 and 2000. Our purpose was to determine what food web interactions and ecological processes would be necessary to produce the biomasses estimated by the MSVPA. In this way, we hope to better understand how Baltic Sea food web structure might influence community-level responses to changes in fishing pressure and oceanographic conditions.

Methods

An Ecopath mass-balance food web model (Walters *et al.*, 1997; Christensen *et al.*, 2000) is based on estimates of

biomass (B), mass-specific rates of production (P/B) and consumption (Q/B), biomass accumulation rates (BA), yield (Y), diets of each consumer, and ecotrophic efficiency (EE), which is the fraction of a pool’s production taken up by model components (predators, fisheries). EE must be between 0 and 1; the remainder ($1-EE$) is the proportion of total mortality unaccounted for by the model system. Thus, each pool has an “other” mortality rate M_0 that includes losses due to unknown rates of predation, senescence, disease, etc. Of the four main parameters (B , P/B , Q/B , and EE), the user must provide three. To meet the mass-balance constraint, Ecopath estimates the fourth unknown parameter by simultaneously solving all equations for each member of the food web:

$$B_i \times (P/B)_i \times EE_i - \sum_{j=1}^n B_j \times (Q/B)_j \times DC_{ji} - Y_i - E_i - BA_i = 0$$

where DC_{ji} is the fraction of i in the diet of predator j and E_i is the net migration (assumed to be zero in all our simulations). Ecosim parameters are initialized from the Ecopath solution and then used to simulate biomass dynamics over time. Biomass dynamics of each pool are simulated using a differential equation

$$dB_i/dt = g_i \sum_j Q_{ji} - \sum_j Q_{ij} + I_i - (M_{0i} + F_i + e_i) \times B_i$$

for the growth rate (dB_i/dt), based on the net growth efficiency (g_i or P/Q), changes in predator and prey biomass, and fishing mortality rate F (immigration I_i and emigration e_i were assumed zero). The BA_i term can be thought of as the solution to dB_i/dt at time zero. Q_{ji} represents consumption by pool i on each prey j , and Q_{ij} represents predation on pool i by each predator j . Consumption in Ecosim is a function of predator and prey biomasses (Walters *et al.*, 2000), such that a change in the biomass of prey i will change the diet composition of predator j depending on a “vulnerability” parameter v_{ij} (described later) and the rate of effective search for prey i by predator j , a_{ij} , which is determined by v_{ij} and the baseline values of consumption and biomass given in Ecopath.

Our model describes Baltic Sea food web dynamics between 1974 and 2000, the same period covered in a recent Baltic MSVPA (ICES, 1999, 2001a). We explicitly attempted to reproduce MSVPA biomass estimates for sprat, herring, and cod in the Baltic Proper and Gulf of Finland (i.e. ICES Sub-divisions 25-29 + 32 for cod and herring, Sub-divisions 25-32 for sprat, including the Gulf of Riga in all cases, as in ICES, 2001a). We include taxa from primary producers to top predators (Table 1). Spring and summer/autumn phytoplankton are edible algal species. All meio- and macrofauna are invertebrates. Sprat, herring, and cod are split into juvenile and adult pools to reflect ontogenetic shifts in diet and size-selective fishing. Seals (primarily ringed seal, *Phoca hispida*, and grey seal, *Halichoerus grypus*), though not a major biomass component at this

Table 1. Basic Ecopath parameters for food web components in the Baltic Sea in 1974 (B, biomass; P/B, production to biomass ratio; Q/B, consumption to biomass ratio; EE, ecotrophic efficiency; and BA, biomass accumulation rate). Codes for each taxonomic pool are used in subsequent tables and figures.

Pool	Code	B (tkm^{-2})	P/B (yr^{-1})	Q/B (yr^{-1})	EE	BA ($\text{tkm}^{-2}\text{yr}^{-1}$)	U/C
Spring phytoplankton	Sp.Phy	20.00	70.00	—	0.20	0	—
Su/Au phytoplankton	SA.Phy	20.00	105.00	—	0.48	0	—
Bacteria	Bact	4.20	142.86	247.62	1.00	0	0.20
Microzooplankton	Mi.Z	1.40	214.29	542.86	1.00	0	0.50
Mesozooplankton	Me.Z	4.00	82.50	300.00	0.76	0	0.25
Pelagic macrofauna	P.Ma	2.70	7.50	25.00	0.50	0	0.19
Benthic meiofauna	B.Me	4.80	6.17	31.17	0.92	0	0.30
Benthic macrofauna	B.Ma	53.80	0.32	13.00	0.37	0	0.53
Juvenile sprat	J.spr	2.86	0.61	21.29	0.16	-0.6	0.16
Juvenile herring	J.her	4.72	0.45	14.71	0.60	-0.3	0.16
Juvenile cod	J.cod	1.40	0.45	2.71	0.63	0.05	0.17
Adult sprat	A.spr	4.86	0.64	10.13	0.51	-0.5	0.16
Adult herring	A.her	6.63	0.39	7.96	0.25	-0.8	0.16
Adult cod	A.cod	0.73	1.06	2.00	0.94	0.11	0.17
Seals	Seal	0.00045	0.10	12.77	0.89	0.00004	0.15

time, are included because they are of concern to conservation groups and are highly piscivorous, and thus may compete with fisheries.

Basic Ecopath parameter estimates for 1974 are given in Table 1. Values for phytoplankton, bacteria, and invertebrates were based on previous work in the Baltic Sea (Elmgren, 1984; Sandberg *et al.*, 2000). Mesozooplankton P/B was increased 10% to facilitate mass balancing. For pelagic macrofauna (“invertebrate carnivores” in Sandberg *et al.*, 2000), mass balance was not possible with literature values. Thus, we assumed $Q/B = 25 \text{ yr}^{-1}$, the same value as for mysids in Lake Superior (Kitchell *et al.*, 2000); $P/B = 7.5 \text{ yr}^{-1}$, yielding a growth efficiency of 30% (Elmgren, 1984); and $EE = 0.5$. The B parameter estimated by Ecopath is consistent with values reported by Hansson *et al.* (1990) for a coastal zone of the northern Baltic Proper. Values of B, Q/B, and total mortality ($=P/B$) for sprat, herring, and cod were averaged from quarterly MSVPA estimates for 1974 (ICES, 2001a). Seal B and Q/B were based on Elmgren (1989) because ~50% of the diet consists of other fish species that are not included in the model (Thurow, 1999), the original estimate of B was divided by 2. These other species (flatfish, salmonids, percids, osmerids, lampreys, and anguillids) were excluded either because we lacked sufficient data for parameterization, or because they are prevalent in near-shore habitats rather than the open water region that we sought to characterize. Seal P/B was arbitrarily set at 0.1 yr^{-1} , a value similar to those used for pinnipeds in other systems (Okey and Pauly, 1999; Bundy, 2001). Non-zero BA values derive from biomass changes in the 1970s. For fish, BA represents the average change in MSVPA average yearly biomass estimates (ICES, 2001a) between 1974 and 1977 (herring and sprat) or between 1974 and 1980 (cod). Seal BA adjustment was based on the population growth observed since these populations began recovering from sterilization

caused by contaminants (Harding and Härkönen, 1999). Fish yields for 1974 were based on quarterly numbers caught and weight-at-age data (ICES, 2001a).

Invertebrate diets (Table 2) are from Sandberg *et al.* (2000), except for pelagic macrofauna (Hansson *et al.*, 1997). Sprat diets are from Elmgren (1984), but we added a small amount of piscivory to reflect predation on eggs and larvae of sprat and cod (Köster and Möllmann, 2000). Herring diets are from Arrhenius and Hansson (1993). Cod diets are based on food composition data for 1977, rescaled to reflect MSVPA abundances of each cod age class in 1974 (ICES, 2001a). Seal diets were made proportional to fish abundances (Thurow, 1997, 1999).

The above inputs were used to generate the balanced Ecopath model. In order to reproduce the MSVPA biomass estimates of cod, herring, and sprat (1974–2000) in Ecosim, the annual averages of quarterly biomass estimates for each age class of each species were pooled into adult and juvenile pools according to our assumptions about age of recruitment (Table 3). To improve model fits, five options in the Ecosim software (Walters *et al.*, 1997, 2000; Christensen *et al.*, 2000; Cox *et al.*, 2002) were used: (1) time-varying forcing functions of fishing mortality for commercially exploited groups; (2) time-varying multipliers of cod egg production; (3) linking juvenile and adult fish pools to simulate reproduction and maturation; (4) adjusting certain prey vulnerabilities; and (5) foraging time adjustments to allow for changes in time spent feeding in response to changes in food availability. More details about options 3–5 are provided below.

For most groups, Ecosim simulates biomass dynamics with a continuous-time logistic model, with competition/predation interactions to account for mortality and production. However, for groups that are split in juveniles and adults, a monthly age-structured model is used based on Deriso–Schnute delay-difference equations and monthly

Table 2. Estimated proportions of prey (rows) in the diets of predators (columns) in the Baltic Sea in 1974.

Prey	Predator												
	Bact	Mi.Z	Me.Z	P.Ma	B.Me	B.Ma	J.spr	J.her	J.cod	A.spr	A.her	A.cod	Seal
Detritus	1				1	0.67							
Sp.Phy		0.08		0.20		0.29							
SA.Phy		0.13	0.75	0.30									
Bact		0.79											
Mi.Z			0.25										
Me.Z				0.50			0.999	0.90		0.999	0.87		
P.Ma								0.07			0.10		
B.Me						0.04							
B.Ma								0.03	0.47		0.03	0.219	
J.spr						0.0009		0.14	0.0009		0.102	0.14	
J.her									0.23			0.296	0.22
J.cod						0.0001			0.0001		0.138	0.07	
A.spr									0.14			0.166	0.23
A.her									0.02			0.079	0.31
A.cod													0.03

calculations of juvenile growth and recruitment to the adult pool (Walters *et al.*, 2000).

Ecosim assumes that prey biomass exists in two states, a vulnerable state (V_{ij}) where prey i is susceptible to consumption by predator j or an invulnerable state ($B_i - V_{ij}$). The flow rate v_{ij} at which prey moves between these states controls the mortality rate that predators may cause. Lowering v_{ij} increases donor (bottom-up) control, whereas increasing v_{ij} leads to standard Lotka–Volterra predator–prey dynamics. These flow rates can be scaled by the user, using the term k_{ij}^* with values between 0 and 1; the form of this equation is:

$$v_{ij} = [(1 + k_{ij}^*) / (1 - k_{ij}^*)] \times M_{0ij}$$

where M_{0ij} is the predation mortality imposed by predator j on prey i in Ecopath. The remaining functional response parameter, the search term a_{ij} , is then solved based on the Ecopath base estimates of Q_{ij} , B_i , B_j , and this value of v_{ij} . These terms are used to solve Q_{ij} in Ecosim (Cox *et al.*, 2002).

Foraging time adjustments enable an organism to respond to changes in prey availability that may affect its Q/B , under the general hypothesis that a scarcity of prey

will result in increased feeding time, and an abundance in prey will result in less time spent foraging (Christensen *et al.*, 2000). Because increased foraging time carries increased risk of predation, a byproduct of the feeding time adjustment is a compensatory relationship between egg production and recruitment for species split into adult and juvenile pools (Cox *et al.*, 2002). For example, if juvenile biomass is low and food is in excess, juveniles achieve a base growth rate by feeding for shorter times. In doing so, they reduce their exposure to predation and improve their chance of recruiting into the adult pool.

Parameterization of all five options is as follows. We forced fishing rates (F) for sprat, herring, and cod (Figure 1) according to catch-at-age data and biomass estimates from the MSVPA. As specified by Ecosim (Christensen *et al.*, 2000), F is defined as yield divided by average total biomass of an age group, where yield was based on empirical data and biomass was equal to MSVPA estimates. These F -values differ slightly from MSVPA rates (ICES, 2001a) because adult and juvenile demographics differed between the two models.

We also used a multiplier of adult cod egg production (RV : reproductive volume), derived from the relative volume of cod reproductive habitat (Figure 2). Recruitment success of eastern Baltic cod is influenced by abiotic factors, particularly salinity, oxygen, and temperature (MacKenzie *et al.*, 2000). Values of RV were relative volumes of water in the Bornholm Basin, the major spawning area, with suitable abiotic conditions for cod reproduction during peak spawning season (Hinrichsen and Weiland, 1996). These volumes were taken from MacKenzie *et al.*, 2000 (Appendix 1, Table A2) for 1974–1996, and updated information was provided by H.-H. Hinrichsen for 1997–2000. Peak reproduction has shifted steadily to later months during the last 25 years. Thus, for 1974–1989, we used RV values for April or May

Table 3. Ecosim parameters used to link juvenile and adult biomass pools (A_r , age at which biomass is transferred from juvenile to adult pool; weight ratio, mass ratio of an average adult to an individual at A_r ; K , shape parameter of von Bertalanffy growth equation).

Species	A_r (yr)	Weight ratio	K
Sprat	2	1.56	0.125
Herring	3	1.51	0.261
Cod	4	3.76	0.040

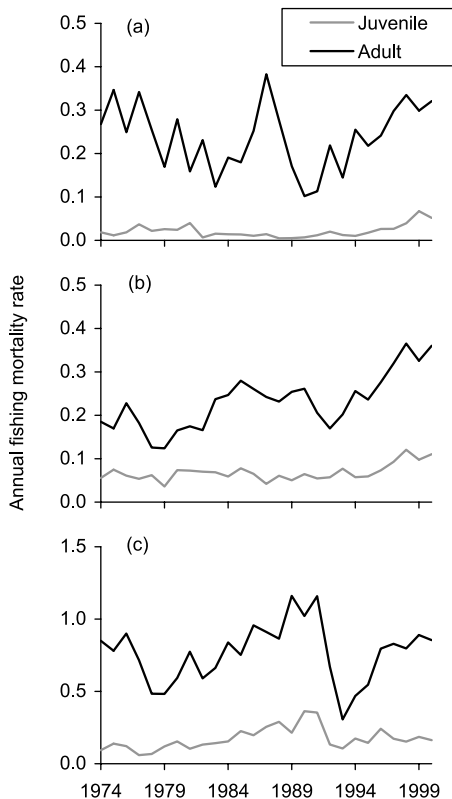


Figure 1. Time-varying estimates of annual fishing mortality rates (yield divided by average annual biomass) for juvenile and adult (a) sprat, (b) herring, and (c) cod used in the Baltic Sea Ecosim model, 1974–2000.

(or the average if both were available), for 1990–1992 for May, and for 1993–2000 for July or August (or the average). Annual RV values were then divided by the long-term average to produce the multiplier profile shown in Figure 2. This multiplier was applied to the number of age-0 juveniles produced as a function of adult biomass, numbers, and consumption (Walters *et al.*, 2000).

Table 3 provides the parameters to link juvenile and adult pools of cod, herring, and sprat. Assumed recruitment ages were compromises between ages of maturation and ages at which species are fully recruited to the fisheries. After incorporating the empirically derived fishing forcing functions, the RV multipliers and adult–juvenile linkages into the model, we iteratively adjusted foraging times and k_{ij}^* (default values = 0.0 and 0.3, respectively) to improve agreement between Ecosim and MSVPA biomass estimates for the fish species. The k_{ij}^* values were only changed (Table 4) from the default if the result clearly improved the agreement. After using a non-linear fitting routine that indicated the k_{ij}^* values to which the model was most sensitive (i.e. those that most strongly affected the fit), those were manually adjusted to minimize differences between Ecosim and MSVPA. This process was repeated until further

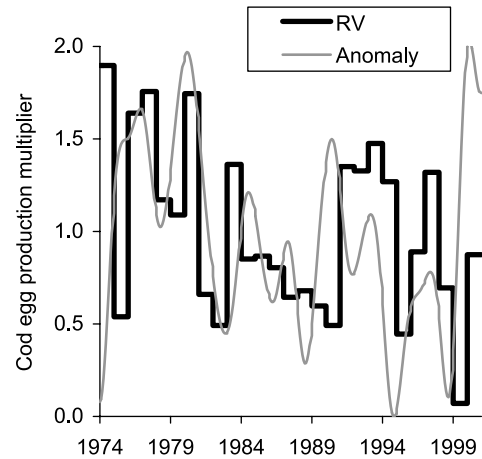


Figure 2. Cod egg production multipliers based on relative reproductive volume in the Bornholm Basin (RV) and on the egg production optimizing function in Ecosim (Anomaly).

changes resulted in little or no improvement in model fit. Foraging time adjustments were done strictly on a trial-and-error basis. Only the parameters for juvenile sprat, juvenile cod, and adult cod were changed (to 0.3 in each case).

Following initial model runs using the parameters described earlier, the RV cod egg production multiplier was replaced with an optimized multiplier, which we will refer to as the Anomaly function (Figure 2). This function uses non-linear regression methods to estimate egg production anomalies in order to minimize deviation of Ecosim predictions from a time series of data (Christensen *et al.*, 2000), in this case MSVPA estimates of juvenile and adult cod biomass. The Anomaly function was estimated only after all empirically derived adjustments (fishing mortalities, juvenile–adult linkages) and iteratively determined parameters from the RV model (k_{ij}^* , feeding times) had been taken into account. The Anomaly multiplier was similar in several respects to the RV multiplier (Figure 2). Both series implied above average, variable recruitment in the 1970s and steadily declining recruitment in the 1980s. The RV model generally predicted higher egg production than the Anomaly model in the 1990s.

From the initial (balanced) Ecopath model for 1974, Ecosim estimated B for all pools between 1974 and 2000, given the adjustments discussed earlier. First, model outputs for simulations using either the RV or the Anomaly multiplier were compared, followed by estimates of biomass, yield, and mortality for cod, herring, and sprat based on Ecosim and MSVPA/catch statistics.

Results

Food web dynamics, 1974–2000

At lower trophic levels, the model projected relatively small changes in relative biomass (B_t/B_{1974}) and because the RV

Table 4. Ecosim vulnerabilities (v) for predator–prey groups deviating from default value (0.3). Higher values indicate an increasing degree of predator control on prey biomass.

Prey	Predator(s)	v
Me.Z	J.spr, A.spr	0.8
Me.Z	A.her	1.0
B.Ma	J.cod, A.cod	1.0
J.spr	J.cod, A.cod	1.0
A.spr	J.cod, A.cod	1.0
J.her	J.cod	0.0
J.cod	A.cod	0.0

and Anomaly models produced nearly identical dynamics, only results from the former are shown (Figure 3). Phytoplankton, bacteria, and microzooplankton biomass changed gradually within $\pm 20\%$ of the starting value (Figure 3a). Such changes are probably within measurement error and would be difficult to confirm with field observations. The change in mesozooplankton maximum biomass

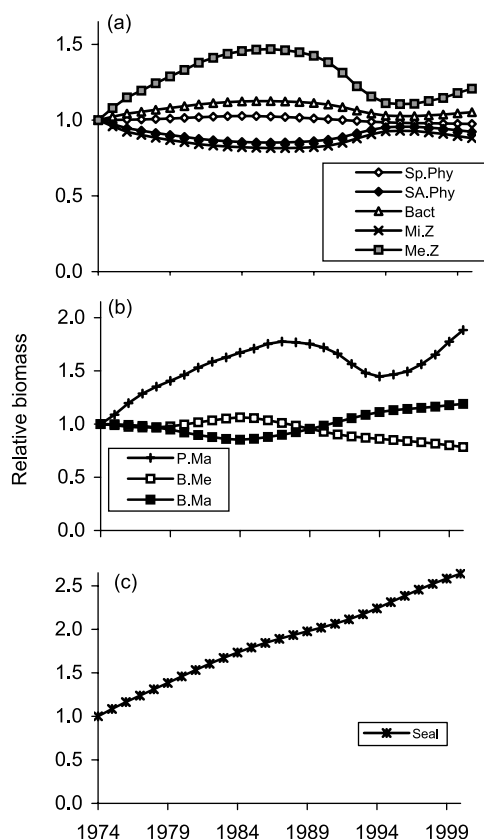


Figure 3. Relative biomasses (B_t/B_{1974}) of all taxonomic groups in the Baltic Sea Ecosim model using the RV model, except fish species: (a) plankton and bacteria, (b) benthic and pelagic invertebrates, and (c) seals.

was larger (45–50%). Benthic meio- and macrofauna responded gradually, with changes of 20–25% by the end of the simulated time period (Figure 3b). Pelagic macrofauna were more variable and almost doubled over the period. The predicted changes in these groups are driven entirely by biomass changes at higher trophic levels caused by variable recruitment and fishing mortality. Bottom-up forcing functions (e.g. changes in nutrient concentrations, hypoxia) directed at lower trophic levels were not simulated, primarily because we were unaware of empirical or theoretical data upon which to base such relationships.

Biomass changed to a greater extent among vertebrates. Seal biomass increased steadily in both models and attained a 165% increase in the RV model (Figure 3c). For the fish species, trends differed by species and age group, and further depended on the cod egg production forcing function applied (Figure 4). Results for these biomass pools are described in more detail in the following section.

Ecosim fits to MSVPA estimates and yields

Ecosim biomass estimates for sprat, herring, and cod fit well to MSVPA estimates (Figure 4). The estimates were positively correlated and had R^2 values >0.70 , except for juvenile sprat (Table 5). Furthermore, model fits had slopes not significantly different from one and intercepts not significantly different from zero (Table 5), according to likelihood ratio tests (Hilborn and Mangel, 1997). These similarities were expected because we explicitly attempted to fit the Ecosim model to MSVPA estimates. Overall, the Anomaly model provided a slightly better fit than the RV model based on the sum of squared deviations (SS) of $\ln(B_{\text{Ecosim}})$ from $\ln(B_{\text{MSVPA}})$ for juvenile and adult sprat, herring, and cod in all years (12.6 and 16.2, respectively). By comparison, SS from a model with a constant egg production multiplier equal to 1 was 21.8. To judge whether the RV and Anomaly models led to significant improvements over the baseline case, we used a likelihood ratio test for nested models to evaluate whether the lower SS of these multipliers was too expensive in terms of additional model parameters (Hilborn and Mangel, 1997). The RV model has no additional parameters compared to the baseline case, because there is only one egg production parameter involved that is variable in one case and constant in the other. Thus, the RV model represents a clear improvement, with no new parameters, over the baseline case. In contrast, the Ecosim fitting routine used for the Anomaly multiplier adds one new parameter for every year of the series (=27 new parameters). To be significant at the 0.05 level with $p = 27$ degrees of freedom (the difference in number of parameters) and $n = 27$ (number of observations or years), the SS ratio should be >4.41 for a full model to offer a significant improvement over the reduced model. This 4-fold difference in SS is far greater than actually observed when comparing the Anomaly model with either the baseline model or the RV model (1.7-fold and 1.3-fold, respectively).

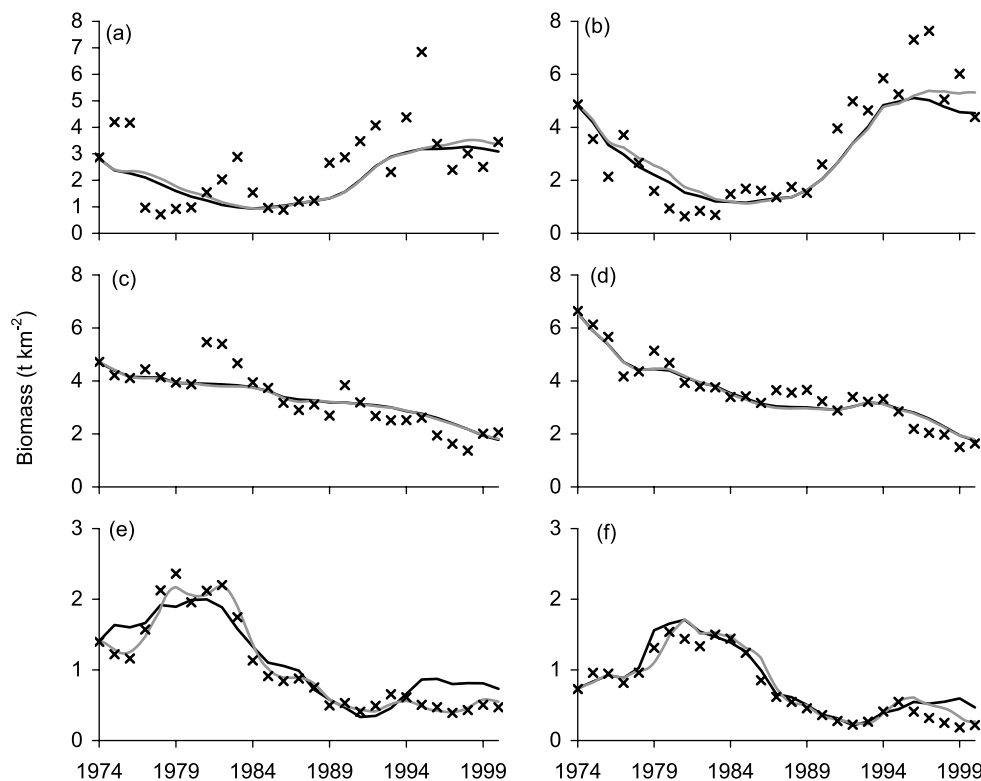


Figure 4. Ecosim (RV, black; Anomaly, grey lines) and MSVPA (crosses) biomass estimates for juveniles (left panels) and adults (right panels) of (a, b) sprat, (c, d) herring, and (e, f) cod in the Baltic Sea.

Ecosim estimates of yields were also consistent with reported values (Figure 5). Yield predictions from the RV and Anomaly models differed most notably for cod and sprat in the late 1990s, with the latter generally performing better. Both multipliers underestimated herring yield in most years and overestimated sprat yields in the first 10

years, but overall trends were similar, as indicated by the positive slopes and large R^2 values (Table 5). Except for herring, all correlations between observed and estimated yields had slopes not significantly different from 1 and intercepts not significantly different from 0 based on likelihood ratio tests (Hilborn and Mangel, 1997).

Table 5. Regression parameters for relationships between Ecosim estimates (based on RV and Anomaly multipliers) and MSVPA biomass estimates and yields. Slope (a), intercept (b), R^2 , and p values describe the relationship between Ecosim estimates and MSVPA or yield, and p^* indicates the probability that a and b differ significantly from 1 and 0, respectively.

Pool	RV model					Anomaly model				
	a	b	R^2	p	p^*	a	b	R^2	p	p^*
Ecosim vs. MSVPA biomass estimates										
J.spr	1.02	0.43	0.37	<0.001	0.32	0.90	0.60	0.32	0.002	0.46
J.her	1.29	-0.96	0.76	<0.001	0.35	1.24	-0.59	0.74	<0.001	0.36
J.cod	1.10	-0.19	0.86	<0.001	0.34	0.97	0.02	0.98	<0.001	0.91
A.spr	1.28	-0.50	0.84	<0.001	0.10	1.15	-0.34	0.81	<0.001	0.44
A.her	1.06	-0.17	0.92	<0.001	0.73	1.00	0.22	0.89	<0.001	0.84
A.cod	0.95	-0.04	0.92	<0.001	0.07	0.94	0.00	0.94	<0.001	0.20
Ecosim vs. observed fisheries yields										
Sprat	1.08	-28.64	0.86	<0.001	0.53	0.97	-20.36	0.87	<0.001	0.20
Herring	1.02	14.43	0.75	<0.001	0.08	0.97	37.87	0.73	<0.001	0.007
Cod	1.04	-11.25	0.88	<0.001	0.85	0.95	12.49	0.93	<0.001	0.69

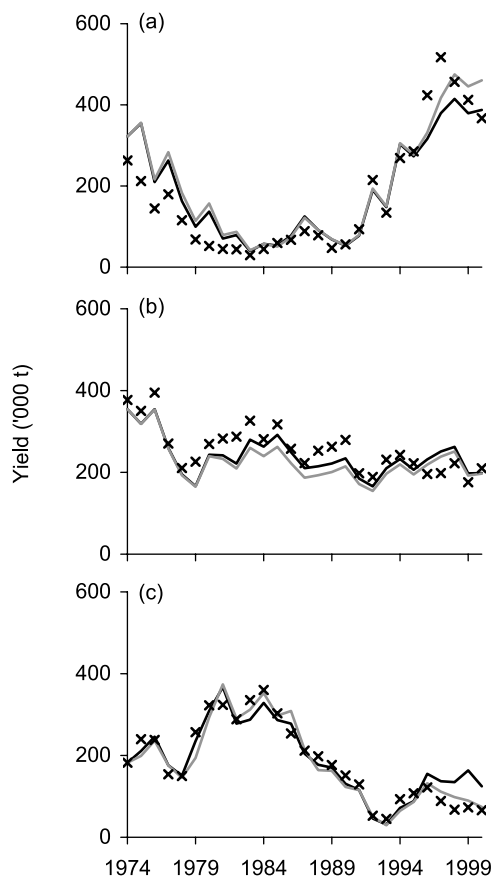


Figure 5. Ecosim estimates (RV, black; Anomaly, grey lines) and reported values (crosses) of yields in the Baltic Sea: (a) sprat, (b) herring, and (c) cod.

Ecosim estimates of predation and “other” (M_0) natural mortality rates for sprat, herring, and cod varied by species and age group and differed slightly depending on which forcing function was used (Figure 6). Predation was a major source of juvenile and adult sprat mortality in the early 1980s, but M_0 was typically higher in most years. Both rates were lower for adults than for juveniles. For juvenile herring, predation mortality was more important than M_0 , while the reverse was true for adult herring. Comparing the predation mortality estimates from the RV and Anomaly model, the greatest differences were for sprat in the early 1980s and late 1990s, and for juvenile herring in the late 1990s. Temporal patterns in predation mortality and M_0 were virtually the same for juvenile cod for which predation mortality was largely caused by cannibalism (>95%). For adult cod, predation mortality (by seals) was negligible, even at the end of the period when seals had steeply increased, and M_0 was also low. Fishing was apparently the chief source of mortality at all times (Figure 1c).

Ecosim estimates of total sprat, herring, and cod biomass lost to mortality (tyr^{-1}) exceeded MSVPA estimates

(ICES, 2001a, Figs. 4.1.1–4.1.3, 4.1.8) for the RV model by 37, 18, and 18%, respectively, and for the Anomaly model by 33, 19, and 18%, respectively. While M_0 differed considerably among species and life history stages (Figure 6), M_0 was fixed at 0.2 for all species and age classes in MSVPA. Ecopath indirectly determines M_0 as the difference between biomass losses (fishing, predation, biomass accumulation) and biomass production (P/B). Fishing and predation mortality terms are derived from fishery data and consumption rates by a species’ predators, whereas BA terms were based on biomass trends in the time series data. These BA terms were critical to fitting Ecosim outputs to MSVPA data; if all $BA_i = 0$, SS for the RV model increased from 16.2 to 48.2, and for the Anomaly model from 12.6 to 44.8. Thus, M_0 values derive from the mass-balance constraints of mortality calculations within Ecopath and are carried forward through time in Ecosim. Variation in M_0 of the three groups with feeding time adjustments (juvenile sprat, juvenile cod, adult cod) stems from the assumption that M_0 is caused by unexplained predation (Christensen *et al.*, 2000).

Discussion

Our simulations of the Baltic Sea for 1974–2000 depict a food web with many strong linkages between predator–prey pairs. Biomass changes at higher trophic levels caused by fishing, trophic interactions, and/or variable recruitment, influenced lower trophic levels, similar to trophic cascades observed in some freshwater-lake food webs (Carpenter *et al.*, 1985). Cascades were initiated by changes in cod biomass and thus were largely caused by fishing. In the pelagic zone, a declining cod stock in the 1980s led to an increase in sprat and a decrease in mesozooplankton, the major prey of sprat. Cascading effects diminished at the base of the pelagic food web, reflecting high production rates of the lower trophic levels. Fluctuating cod biomass also led to inverse responses in benthic macrofauna, in turn causing inverse responses in benthic meiofauna. These trends mirror those observed in the Northwest Atlantic during the 1990s, when removal of cod and other groundfish was concurrent with large increases in the planktivorous capelin (*Mallotus villosus*), decreases in zooplankton, and increases in phytoplankton (Carscadden *et al.*, 2001).

While our analyses imply that top-down control occurs in the Baltic Sea food web, we note that lower trophic levels were not manipulated directly, and therefore we did not examine the potential for bottom-up control from these biota. Specifically, potential effects of deepwater hypoxia on benthic invertebrates could not be investigated in the absence of quantitative information on the relationship between dissolved oxygen and benthic invertebrate biomass upon which to base a forcing function. This oversight might lead to incorrect estimates of parameters (e.g. the k_{ij}^* terms) involving benthic organisms and their predators.

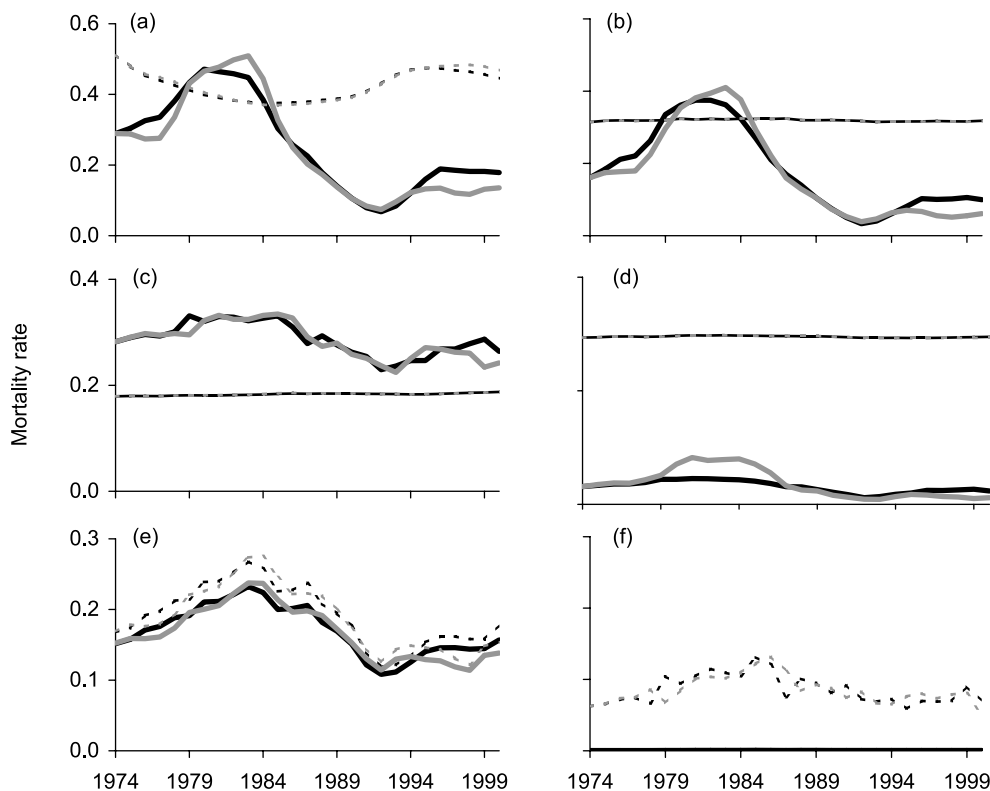


Figure 6. Rates of predation (RV, black; Anomaly, grey lines) and “other” (dashed lines) mortality of juveniles (left panels) and adults (right panels) of (a, b) sprat, (c, d) herring, and (e, f) cod in the Baltic Sea Ecosim model.

The above results, and all interpretations that follow, rely on the assumption that MSVPA estimates provide reasonably accurate depictions of the evolution of the Baltic Sea fish community. However, single- and multispecies assessments may be flawed by poor catch statistics, incomplete sampling of age structure, weight-at-age problems, and consumption estimates. Abundance data from surveys exist for cod, herring, and sprat, but these cannot be used directly to test Ecosim predictions. First, the surveys were conducted at much smaller spatial scales than our models, which cover the Baltic Proper. Second, the survey data were used in the tuning process of the MSVPA (ICES, 2001a) and thus are not independent of the MSVPA results to which we fitted our models. It is therefore important to acknowledge that our results and interpretations are only as reasonable as the MSVPA estimates from which they are derived, and that independent, large-scale monitoring is needed for better validation.

Ecosim may be used to hypothesize what ecological processes and interactions would have to occur to produce a reasonable fit to the MSVPA trends. Five major driving forces appear to govern the top of the Baltic Sea food web in our model. First, fishing was the dominant force structuring the upper trophic levels, particularly adult cod. Fishery-induced changes in adult cod biomass influenced

juvenile cod (through reproduction and cannibalism) and these two predators in turn affected sprat and, to a lesser extent, herring through predation. Thus, fishing affected sprat and herring through direct biomass removal and also indirectly by influencing cod biomass. That fishing affects fish populations may seem self-evident, but the important point is that fishing effects extend beyond target species to their prey and possibly also predators. The indication that Baltic Sea planktivores control zooplankton biomass (e.g. Rudstam *et al.*, 1994) offers further suggestion that fishing is influencing a large part of the food web.

A second key structuring force was cod recruitment, as shaped by the egg production multipliers. Much has been written about salinity, oxygen, and temperature conditions required for successful reproduction in the Baltic (Sparholt, 1996; MacKenzie *et al.*, 2000). The RV multiplier used to represent these abiotic variables improved overall fit to MSVPA biomass estimates. The built-in Anomaly multiplier further improved the fit, but not significantly so according to the likelihood ratio test. Before dismissing the Anomaly model altogether, however, we here point out how the RV and Anomaly multipliers differed, and speculate about whether those differences might be meaningful.

The shapes of the two multipliers (Figure 2) were quite similar in the 1970s and 1980s. However, in the 1990s and

except for 1999–2000, the RV multiplier consistently predicted higher egg production than the Anomaly multiplier and the fit to MSVPA biomass values was particularly improved during this period (Figure 4e). Thus, one could imagine a compromise between the two models in which additional parameters from the Anomaly model were only incorporated in the 1990s and thereby meet the conditions for a significant likelihood ratio test. The implication is that cod recruitment in the 1990s was affected by factors beyond just the abiotic variables quantified in the RV multiplier, for instance biotic effects and biotic–abiotic interactions. For example, predation by clupeids on cod eggs and larvae may be an important source of mortality during this life history phase (Sparholt, 1996; Köster *et al.*, 2001b). The intensity of this predation is related to temperature, for bioenergetic reasons, and to oxygen and salinity, which influence the spatial overlap of clupeids and cod eggs (Köster and Möllmann, 2000). Although predation by sprat on juvenile cod was included in our model, our formulation may not have been suitable to recreate episodes of intense predation. Such episodes could be accounted for in the Anomaly simulation and may explain the differences between the two models in the 1990s. As a preliminary indication of this possibility, the differences between the juvenile cod biomass estimates from the two models were significantly and positively correlated with MSVPA adult sprat biomass (slope = 0.07, $r^2 = 0.41$, $p < 0.001$).

Another factor not represented in the RV model is larval cod dynamics. In our model, juvenile cod do not feed on zooplankton, while larval cod are primarily zooplanktivores. Oceanographic conditions that cause dispersal of larvae to areas without adequate zooplankton production may result in poor recruitment (Hinrichsen *et al.*, 2001). Such events might only be captured indirectly via the Anomaly model. In short, while abiotically defined reproductive volume remains an important determinant of cod recruitment, there are other factors and interactions that are important at different times.

Third, top-down control (high k_{ij}^*) or bottom-up control (low k_{ij}^*) in several predator–prey relationships improved the model fit. Among cod, herring, and sprat, the cod–sprat linkage was strongly top-down controlled while the cod–herring linkage was bottom-up controlled. One possible explanation for this difference is based on the spatial overlap between cod and each of the two prey species. Recent theoretical analyses have indicated that negative spatial covariance between predator and prey distributions can stabilize the effect of predator dynamics on prey mortality (Keeling *et al.*, 2000). Herring spawn in coastal zones of the Baltic Sea and juvenile herring reach high abundances in these areas (Axenrot and Hansson, 2003), whereas cod mostly inhabit the open sea. Conversely, sprat live in open waters and are sensitive to cod predation, consistent with previous suggestions that cod control sprat biomass (Horbowy, 1996). Another key interaction, top-down control by clupeids on mesozooplankton, agrees with

findings that planktivores negatively influence mesozooplankton biomass in the Baltic Sea (Rudstam *et al.*, 1994; Möllmann *et al.*, 2000; Kornilovs *et al.*, 2001). Finally, benthic macrofauna were subject to top-down control by cod. Although there is no empirical support for this feature, the importance of the isopod *Saduria entomon* in cod diets is clear (Uzars, 1994) and this species has been specifically incorporated in other multispecies models (Gislason, 1999). This topic merits further attention because declines in benthic invertebrates during periods of high cod abundance may be exacerbated by deepwater hypoxia that reduces their habitat and may lead to increased predation risk.

Fourth, foraging time adjustments for juvenile sprat and juvenile and adult cod were also important in generating model dynamics. Adjusting feeding time enables consumers to maintain a desired Q/B and/or to balance the costs and benefits associated with extended foraging (Christensen *et al.*, 2000; Cox *et al.*, 2002). In our model, both juvenile and adult cod extended their feeding times during periods of high abundance when prey was limited. In contrast, juvenile sprat feeding time decreased slightly when cod were abundant because high predation mortality rates held their biomass low. Thus, juvenile sprat could maintain a stable Q/B because mesozooplankton was abundant owing to low sprat biomass. Although independent data to verify these compensatory interactions are lacking, they are consistent with the increasing evidence for compensatory increases in juvenile survival during periods of low biomass (Myers and Cadigan, 1993; Myers *et al.*, 1999).

Finally, BA terms for commercially exploited fish pools were adjusted in Ecopath. Without these adjustments, MSVPA biomass trends could not be recreated, even with additional changes in k_{ij}^* and feeding times throughout the food web. The BA terms essentially represent imbalances between combined predation and fishing mortalities and total production rates. These terms therefore indicate how sustainable the initial Ecopath fishing mortality rates are, given the background rates of predation mortality described within the model and other natural mortality (M_0). Because both herring and sprat biomass were declining in the years following 1974, the estimated total mortality was too high to sustain these populations. Mass-balance estimates of M_0 represent equally plausible values for these groups compared to the $M_0 = 0.2$ used in MSVPA.

Gross food conversion efficiency (P/B over Q/B, or P/Q) of adult cod in the model was extremely high (0.53). Wild cod reared in aquaria at optimal temperatures for growth and fed to satiation on a fish and shrimp diet achieved P/Q ratios of roughly 0.45 (Björnsson *et al.*, 2001). Thus, not even under ideal growing conditions could cod achieve the efficiency used in our model. We suspect that the high value is caused by a low Q/B estimate, which we obtained from MSVPA input (ICES, 2001a). Cod consumption rates according to bioenergetics models exceed those used in MSVPA by roughly 2- to 3-fold, and this has been a topic of debate in studies of the Baltic and North Seas (Hansson

et al., 1996; ICES, 1999, 2001a). Thus, cod consumption may well have been underestimated both by MSVPA and Ecopath, and therefore predation mortality on all cod prey, compared to actual rates in the Baltic Sea.

It proves difficult to compare Ecosim biomass estimates against independent historic data for non-target species. The projected increase of seal biomass qualitatively agrees with empirical observations (Jansson and Dahlberg, 1999). Biomass measurements at relevant temporal scales are generally lacking for primary producers and low-level consumers in the Baltic Proper between 1974 and 2000. These organisms have short life histories and respond rapidly to seasonal changes in environmental conditions, making it difficult to monitor trends for comparison with Ecosim predictions. Nevertheless, data exist for some species of mesozooplankton. Kornilovs *et al.* (2001) found negative correlations between sprat biomass and seasonal biomasses of cladocerans and *Pseudocalanus elongatus* in the central Baltic, which broadly supports our findings. In general, our biomass estimates for lower trophic levels should be viewed as hypotheses, which can and should be explored through assessments or experimentation. Such studies would add to our understanding of the importance of large switches in diet, of spatial patchiness, and of responses of lower trophic levels to different abiotic factors such as oxygen concentration, temperature, salinity, and nutrient concentration, none of which are presently handled in the model. We note that incorporating feedbacks from lower trophic levels represents a fundamental difference between Ecosim and MSVPA models, which often consider these “other food” groups to be large, static biomass pools rather than diverse, dynamic pools of interacting organisms.

In conclusion, our model implies that fishing and recruitment variability are major drivers in the Baltic Sea ecosystem, and that fish can influence stocks of invertebrates in both pelagic and benthic communities. The apparent differences in the strengths of the predator–prey linkages of cod to herring and sprat suggest that cod recovery will require careful management of both cod and their prey. Though there was no evidence of a predatory feedback of sprat on juvenile cod, this interaction may be partially represented by the Anomaly forcing function and deserves further study. The strength of our approach is that we have used information from two distinct modeling approaches to gain understanding of the system and to estimate the long-term temporal dynamics of the system up to the present among trophic levels about which MSVPA provides no information. In the future, it is critical that Ecosim estimates be subjected to detailed evaluations, including thorough sensitivity analyses of uncertain parameters, comparisons with independent field estimates for a variety of taxa, and comparisons with outputs of other models, particularly those with different assumptions about functional relationships or with heterogeneous spatial distributions of key taxa. Once those validations have been conducted and the model has been further refined, the next logical step will be to use

Ecosim to hypothesize how the Baltic Sea community might respond to alternative fisheries management strategies and changes in environmental variables.

Acknowledgements

Stefan Neuenfeldt of the Danish Institute for Fisheries Research kindly provided quarterly data that were used in the ICES MSVPA models. We thank the ICES Secretary General for permitting us to cite ICES documents. Niels Daan, Brian MacKenzie, and an anonymous reviewer provided much helpful discussion that greatly improved this paper. This study was funded by the Swedish World Wildlife Fund and the Marine Research on Eutrophication (MARE) program of the Foundation for Strategic Environmental Research (MISTRA).

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