

Relative contributions of evolutionary and ecological dynamics to body size and life-history changes of herring (*Clupea harengus*) in the Bothnian Sea

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ABSTRACT

Question: What ecological and evolutionary processes are associated with the 25% decrease in age-specific body size of herring (*Clupea harengus*) in the Bothnian Sea over the last 30 years?

Data: Four decades of data on length, age, and sexual maturity of individual herrings as well as environmental variables, including abundances of predators, prey and competitors, and estimates of fishing intensity/mortality from the Bothnian Sea.

Search methods: Information-theoretic assessment of the relative influence of ecological and fisheries' effects on temporal changes in body growth. Probabilistic maturation reaction norms to study changes in age-specific size at maturation. Decomposition of trait variation into ecological and evolutionary contributions.

Conclusions: Our evolutionary ecosystem perspective shows that both ecological and evolutionary processes are important contributors to observed phenotypic changes in this commercially exploited species. Around 60% of the decrease in age-specific body length can be attributed to increased density-dependent body growth. Evolutionary changes towards earlier maturation, owing to an indirect effect of size-selective mortality from grey seals and fisheries, account for a further 25% of the decrease in age-specific body size.

Keywords: Baltic Sea, density dependence, fisheries, grey seal, pelagic, zooplankton.

INTRODUCTION

Body size is an important life-history trait that influences fecundity and mortality of individuals (e.g. Roff, 1986; Reznick *et al.*, 1996). For exploited or harvested populations, the body size of individuals is often of economic importance (Edeline *et al.*, 2007; Allendorf *et al.*, 2008). Furthermore, the size distribution of fish populations can affect population recovery rates

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(for reviews, see Hutchings and Reynolds, 2004; Walsh *et al.*, 2006; Conover *et al.*, 2009) as well as community structure (Rochet *et al.*, 2011). The size distribution of fish stocks is a result of multiple processes. Abiotic conditions, food supply, and density dependence can all affect body growth (Flinkman *et al.*, 1998; Carscadden *et al.*, 2001; Zenitani *et al.*, 2009). Exploited fish species may experience high mortality from fishing, which can affect body size distribution through selective mortality (Sinclair *et al.*, 2002). Several studies have shown that size-selective mortality imposed by fisheries can also induce evolutionary responses in body growth and alter size and age at maturation, thus affecting age-specific body sizes (Conover and Munch 2002; Edeline *et al.*, 2007; Jørgensen *et al.*, 2007; Swain *et al.*, 2007; Nusslé *et al.*, 2009; Ab Ghani *et al.*, 2013). In addition to fisheries, natural predators can also impose ecological and evolutionary processes that determine the age and size structure of fish populations (Livingston, 1993; Reznick *et al.*, 1996; Limburg, 2001; Edeline *et al.*, 2007), but this is seldom addressed in studies of size structure and body growth of exploited fish species.

Determining whether size distribution changes have an ecological or evolutionary origin is important. Changes in climate, abiotic factors, competition, and predation can all affect body growth and size distributions within a single generation if it is mainly ecological factors that determine variation in body growth and size distribution, whereas evolutionary changes in life histories and body growth take longer to reverse (Law, 2000; Conover *et al.*, 2009). Finally, the combined selective forces from natural predators and fishing can alter the evolutionary response from single species interactions (Gårdmark *et al.*, 2003; Conover *et al.*, 2009), motivating the study of different evolutionary forces in concert.

Here we take an ecosystem perspective to study how multiple drivers of ecological and evolutionary changes relate to the body size of a commercially exploited fish stock, herring (*Clupea harengus*), in the Bothnian Sea. The Bothnian Sea lies between the Gulf of Bothnia and the northern Baltic Sea (evolutionary-ecology.com/data/2915Appendix.pdf, Fig. S1). Herring is the dominant pelagic fish species here and commercially the most important fish species (ICES, 2013a). From the 1970s to late 1980s, the age-specific body length of Bothnian Sea herring increased, but has since decreased by up to 25% (2915Appendix.pdf, Fig. S2) (ICES, 2013a). Over the same period, population size has increased four-fold (ICES, 2013a), likely mainly due to increased food supplies (Lindegren *et al.*, 2011), and landings have increased five-fold (ICES, 2013a). However, the small body size of herring poses a problem of profitability, especially in coastal fisheries targeting larger spawning herring for human consumption. Since the mid-1980s, the grey seal (*Halichoerus grypus*) population, the main mammal predator in the Bothnian Sea, has increased by approximately 7.5% a year (Harding *et al.*, 2007; Gårdmark *et al.*, 2012). Grey seals consume few herring compared with fisheries but are highly selective for larger herring (Gårdmark *et al.*, 2012). Also, the abundance of the interspecific competitor the sprat (*Sprattus sprattus*), which has been shown to be associated with herring body condition in the Baltic Sea proper (Casini *et al.*, 2010), has more than doubled in the Baltic Sea since the mid-1980s (ICES, 2013a) and shifted its distribution northwards, concentrating in the southern Bothnian Sea (Casini *et al.*, 2014). Thus, there are many potential factors that may have driven both ecological and evolutionary changes in the size at age of Bothnian Sea herring.

Our first aim is to determine which factors are associated with body growth of Bothnian Sea herring cohorts over the last 30 years. Second, we study whether evolutionary changes have occurred in age-specific size at maturation, using individual probabilistic maturation reaction norms [PMRN (Heino *et al.*, 2002)]. Finally, based on these analyses together with estimates of size-specific mortalities (Gårdmark *et al.*, 2012), we estimate the absolute and

relative contributions of environmental factors and genetic changes in life history on the observed changes in body size at age.

MATERIALS AND METHODS

The Bothnian Sea is a shallow (average depth 68 m) part of the northern (60°N to 63°N) Baltic Sea (2915Appendix.pdf, Fig. S1). The water is brackish, relatively oligotrophic with a high organic carbon content (Diekmann and Möllmann, 2010). Herring is the dominant pelagic fish (spawning biomass 200,000–500,000 tonnes), the main fish targeted by fisheries (harvest of 20,000–50,000 tonnes a year), and also the main prey for grey seals [they consume 1800–8300 tonnes a year (Gårdmark *et al.*, 2012)].

Age-specific body size and length-specific body growth

Data on length, age, and maturation status of herrings in the Bothnian Sea were obtained for commercial landings between 1979 and 2009 by the Finnish trawl fleet, which is responsible for >90% of all catches (ICES, 2013a), using mid-water and near-bottom trawls. Average body size of herring in trawl catches deviates <0.3 cm from average body size in fishery-independent surveys (Gårdmark *et al.*, 2012). Herring >18 cm are overrepresented in trawl catches (see figure 1 in Gårdmark *et al.*, 2012), but have little effect on average body size since they are so few in number. The size-structured effects of fishing are furthermore estimated to have only a marginal impact on age-specific size distribution (see Results). We therefore treat trawl catches as a representative sample of the herring population.

Data were compiled and made available by the Finnish Game and Fisheries Research Institute (currently Natural Resources Institute Finland). Random samples of 50–1000 herrings from each trawl type and quarter of the year were aged (in calendar years) from otoliths, and body length and weight measured between 1979 and 1997. Since 1998, length and weight measurements have been taken from a larger random sample (>1000), from which a stratified subsample (of 50–1000) based on length (5 mm strata) was aged. The stratification causes smaller or larger individuals to be overrepresented in an age class relative to a random sample. To correct the age-specific length distributions, we applied a correction term (*CT*) to the number of herring in the stratified sample such that the length distribution in the stratified sample was identical to the length distribution of the random sample, $CT_l = P_{l\text{-random}}/P_{l\text{-stratified}}$, where P_l is the proportion of herring in each length class. From the length-corrected age-specific length distributions ($P_{l\text{-stratified}} * CT_l$), we calculated the mean length for each age class, spanning 1–8 years. We did not include older age classes and young-of-the-year because they were so poorly represented in the samples. Samples had not been collected for all quarters and for both trawl types each year, and we only used samples with ≥ 50 aged individuals. Approximately one-third of all 240 potential sampling periods had missing values. Because of the unbalanced data from quarters and trawl types across years, we calculated the yearly average age-specific body length as least square means to avoid differences in missing values between years affecting the estimated body growth between years.

To study associations between explanatory variables (see below) and body growth of herring, we assumed that the average body length for cohort x at year t ($L_{x,t}$) can be described by the power function: $L_{x,t} = cL_{x,t-1}^b$, where $L_{x,t-1}$ is body length of cohort x in year $t - 1$, c is a length-independent growth constant, and b is a constant describing how

body growth scales with body length. High values of c (>1) and b ($0 < b < 1$) represent high body length increase and a low dependence of body length on body growth, respectively. This function accounts for age-specific differences in body sizes between years, as smaller fish grow faster in absolute terms. To estimate c and b , this function is linearized to:

$$\ln(L_{x,t}) = b\ln(L_{x,t-1}) + c' \quad (1)$$

where $c' = \ln(c)$. We have no information on individual body growth, and stress that all growth refers to average cohort-specific body growth. However, equation (1) approximates the individual growth model for indeterminate growth of von Bertalanffy (1938) as parameterized by Parmanne (1990) for this stock, spanning ages 1–8 years ($r^2 > 0.99$).

To determine whether changes in herring body growth are size-independent (c'), size-dependent (b), or both, we analysed differences in size-specific growth of cohorts (equation 1). We used $\ln(L_{x,t})$ as the dependent variable in a general linear model, together with $\ln(L_{x,t-1})$ and year as covariates, and their interaction. Year was used to test for differences in c' between years and the interaction term for differences in b between years.

In equation (1), environmental variation can be entered as changes in c' , i.e. a similar effect on body growth independent of body size, and in b , describing size-specific changes in body growth. To determine which explanatory variables explained residual variation from equation (1), we used the following model:

$$\ln(L_{x,t}) = (b_1X_{1,t-1} + \dots + b_nX_{n,t-1})\ln(L_{x,t-1}) + c'_1X_{1,t-1} + \dots + c'_nX_{n,t-1} + c'_{1,2}X_{1,t-1}X_{2,t-1} + \dots + c'_{n-1,n}X_{n-1,t-1}X_{n,t-1} \quad (2)$$

where $X_{1,t-1} \dots X_{n,t-1}$ are the environmental states of the n explanatory variables at time $t-1$, and $b_1 \dots b_n$ are the corresponding body-size-dependent coefficients. $c'_1 \dots c'_n$ are body size-independent regression coefficients for the explanatory variables. $c'_{1,2} \dots c'_{n-1,n}$ are coefficients for the two-way interaction terms between explanatory variables.

By fitting environmental data ($X_1 \dots X_n$) to equation (2), we can study the relations between environmental variables for both body-size-dependent and body-size-independent body growth. We did this by entering explanatory variables in a stepwise manner in a linear mixed model using PROC MIXED in SAS v.9.2 (SAS Institute, 2008). Year was considered a random effect to account for the fact that we measured body growth on seven cohorts each year, whose growth rates may be correlated. As each cohort was included in the analyses up to seven times, we used cohort as a repeated factor with an autoregressive one-year time lag covariance structure. Variables were included in the model on the basis of Akaike's Information Criterion (AIC). In each model step and for each explanatory variable, we entered all possible two-way interactions between the new variable and the previously entered variables in the model. Interaction terms were then removed if this improved the fit, starting with the interaction term with the highest P -value. After a new variable was entered into the model, we tested if the model could be improved by removing terms included in earlier steps. We continued to add new explanatory variables until the AIC could no longer be decreased. As the body growth of immature individuals is higher, we separated the growth rates of fish aged 1 and 2 years from older cohorts [most individuals mature between ages 2 and 3 (Vainikka *et al.*, 2009)] using a class variable.

Population sizes and environmental data

We used data on cohort-specific abundances, age-specific fishing mortality, and total stock biomass (TSB) of herring in the Bothnian Sea from standard stock assessments (ICES, 2013a). As an estimate of intraspecific competition, we calculated the cohort-specific abundance plus the abundance of the two adjacent cohorts (termed ‘cohort-specific intraspecific competition’), as adjacent cohorts are likely to have somewhat overlapping diets (Arrhenius and Hansson, 1993). This was calculated for both number of individuals (N-at-Age) and biomass (B-at-Age). The TSB of sprat was not available at the resolution of the Bothnian Sea and we instead used TSB of the Baltic Sea sprat (Subdivisions 22–32), assuming that variation in sprat abundance in the whole of the Baltic Sea reflects changes in the Bothnian Sea. This is justified in that the variation in sprat abundance estimated from the Baltic International Acoustic Survey (ICES, 2013b) performed in the Bothnia Sea in 2007, 2008, and 2010 (2009 removed due to measurement errors) is highly correlated with variation in sprat abundance for the whole of the Baltic Sea ($r^2 > 0.85$).

Grey seal abundance was estimated as a population trajectory from count data, using the data and methods of Gårdmark *et al.* (2012). Because seal abundance is estimated from a population trajectory, there is, artificially, no variation around the trend. The real population size likely deviates from this trajectory between years, but deviation is low because of their long generation time and low annual per capita birth rate. In addition to grey seals, salmon and cod have herring as their main prey, but these species lack stock estimates for the Bothnian Sea and are rare there, so that we consider them unlikely to be important drivers of changes in herring body growth.

Data on summer biomass of planktonic crustaceans in the Bothnian Sea, divided into the copepods *Acartia* spp., *Eurytemora* spp., *Limnocalanus macrurus*, and *Pseudocalanus elongatus*, and the cladocerans *Bosmina* spp. and *Evdadne + Podon* spp., were based on monitoring by the Finnish Environmental Institute, SYKE (Olsonen, 2008). Data on abundance of the benthic crustaceans *Saduria* spp. and *Monoporeia* spp. (in g/m²), deep-water (>30 m) temperatures, and salinity were assembled from the open access SHARK database (<http://www.smhi.se/klimatdata/oceanografi/Havsmiljodata>) at the Swedish Meteorological and Hydrological Institute. The main growth period is during the summer (July–September), so we used summertime temperatures. However, salinity conditions do not vary as much as temperature on a seasonal basis, so we used winter (December–January) salinity, as data were available for all years. We used maximum ice cover (km²) from SYKE as an estimate of growing season length for zooplankton, and hence herring. Data on zooplankton were assembled by ICES (2012).

All fish and zooplankton abundances were lognormal-transformed prior to analyses to better normalize the data. A correlation matrix between explanatory variables is available in the online appendix (2915Appendix.pdf, Table S1). A Variance Inflation Factor (VIF) analysis was applied to all covariates, and subsets thereof, when covariates with high VIF were removed, to indicate the extent of multicollinearity (2915Appendix.pdf, Table S2).

Maturation reaction norms

We address evolutionary changes in life history by studying changes in age-specific size at maturation calculated from individual probabilistic maturation reaction norms [PRNM (Heino *et al.*, 2002)]. To estimate PRNMs, we used data on the body length, age, and maturation

status of individual herring. Because there were too few herring with age and maturity data for each year to obtain robust results, we grouped individuals across nearby cohorts, combining age-specific data from five years into five different periods: 1982–1986, 1987–1991, 1992–1996, 1997–2001, and 2002–2006 (lowest $n = 148$). For each period and age class 2–4, we calculated the body length at 50% probability (μ) of maturation according to Heino *et al.* (2002) using PROC PROBIT in SAS v.9.2 (SAS Institute, 2008). Maturity status was the dependent variable and body length and condition [standardized residuals from $\log(\text{weight}) - \log(\text{length})$ regression] of each herring were the explanatory variables. The 95% confidence intervals of μ were calculated from the variance–covariance matrix using the formula of Collett (1991). Age-specific μ was then correlated with potential environmental (ecological) explanatory factors (averaged over each five-year period) to study their association with herring life-history changes.

Variance decomposition of age-specific body size

We decompose the contributions of the factors identified in the statistical models, as well as disentangle the relative effects of ecological and evolutionary changes on body growth during two periods, 1982–1986 and 2001–2005. We chose these two periods as they are at the beginning and the end of the 30-year study period, and are close to periods when size-selective mortality from fishing and grey seals could be estimated from fishery-independent surveys of Bothnian Sea herring (1981–1983 and 2007–2009). We calculated the expected cohort-specific body growth predicted by each of the following: (i) ecological bottom-up factors; (ii) direct (ecological) effects of size-selective mortality from fishing and predation; (iii) life-history evolution in size at maturation; and (iv) other factors, including evolutionary changes in body growth.

For cohort-specific body growth, we used only the ‘ecological bottom-up factors’ (abiotic condition, food supply, and competition) in equation (2). From this model and the averages of these variables in 1981–1985 and 2000–2004 respectively, we calculated the expected growth due to ecological factors (ΔL_l) for each 5 mm length class (l). A model was run separately for mature and immature herring. First, we set maturation size equal for the two periods at 14 cm (average length at maturation of age 2), so for $l < 14$ cm we used the model for immature herring and for $l \geq 14$ cm the model for mature herring.

We then calculated the length-specific mortality (M_l) from size-specific fishing (F_l) and grey seal mortality (S_l), using data from Gårdmark *et al.* (2012): $M_l = e^{-(F_l + S_l)}$. To estimate expected average body size of a cohort the following year from ecological variables and size-dependent predation (L_{ECO}), we calculated the scalar of the length distribution vector after predation and the vector of expected length the following year for each length class: $L_{ECO} = (P_l * M_l) \times \Delta L_l$, where P_l is the proportion of herring in length class l . By setting F_l or $S_l = 0$, we could estimate the ecological effects of fisheries and grey seals separately.

To estimate the contribution of ecological factors to changes in body growth between periods, we used the observed average length distributions (2001–2005) of each age class 2–7 and predicted the length distribution for each age class at $t + 1$ from the environmental conditions for the respective period. The difference in L_{ECO} between the two periods is the expected difference in body growth due to ecological changes, including fishing and size-structured predation.

To assess the evolutionary contribution to age-specific body size, we altered the age-specific length at maturation, i.e. the size at which herring switched from an immature to a

mature growth model according to the estimated μ at age 2 (when most herring mature) for the respective period. The body size predicted by ecological variables, size-dependent mortalities, and evolutionary changes in maturation size is denoted L_{ECOMAT} .

To assess the presence of systematic process errors in L_{ECOMAT} , we used the residuals of the estimated L_{ECOMAT} and the observed average length for each cohort x and year t . This was done for all years and cohorts in the respective periods, hence $n = 48$. A structural change in residuals between periods is interpreted as a change in process errors between the two periods arising from, for example, evolutionary changes in body growth or any other variable not accounted for (e.g. finfish predation, diseases, cannibalism).

RESULTS

Age-specific length was observed to change between 1979 and 2009, both among immature ($F_{1,1479} = 403$, $P < 0.001$; Fig. 1A) and mature herring ($F_{1,7836} = 784$, $P < 0.001$; Fig. 1B). In the 1980s, an average immature age 2 herring was 13.7 ± 0.75 cm (mean \pm s.d.) and a mature age 4 herring was 18.1 ± 0.84 cm. Twenty years later, the corresponding lengths were 12.6 ± 1.1 cm and 16.1 ± 1.1 cm respectively. Length-specific body growth of cohorts also differed between years, but it was only the intercept (c') that differed between years ($F_{1,193} = 76$, $P < 0.001$; Fig. 1B) and not the slope (b) ($F_{1,193} = 0.2$, $P = 0.7$; Fig. 1B). In the 1980s, a cohort of average length 15 cm increased on average 20 ± 4 mm during one year, whereas in the 2000s a cohort with similar average body length increased on average by 10 ± 3 mm only. Estimated length-specific mortality from fisheries and grey seal predation has been relatively constant for herring < 18 cm but has increased many-fold for larger herring (Fig. 1C).

Environmental covariation with body growth

The first variable entered to explain variation in length-specific body growth of cohorts was a negative association with grey seal abundance (Table 1). Next, in order, were a positive association with the abundance of the zooplankton genus *Eurytemora* spp., a negative association with cohort-specific intraspecific competition, and cohort-specific fishing mortality (Tables 1, 2). There was a negative interaction between *Eurytemora* spp. and intraspecific competition, indicating that the positive association between *Eurytemora* and body growth diminishes at high intraspecific competition. Fishing mortality showed a positive interaction with body length, indicating a greater negative association between fishing mortality and body growth for cohorts of smaller individuals (Table 2).

Cohort-specific intraspecific competition had a similar AIC-value as grey seal abundance in the first selection step, but as grey seal abundance was included in the next step, the order in which these two variables entered the model had no effect on the final model. Fishing effort, which was not included in the final model, showed high covariation with both grey seal abundance and cohort-specific abundances ($r > 0.65$; [2915Appendix.pdf](#), Tables S1, S2).

Life-history changes

There has been a shift in age-specific length at maturation, as estimated by probabilistic maturation reaction norms (Fig. 2). In 1982–1986, a two-year-old herring had a 50%

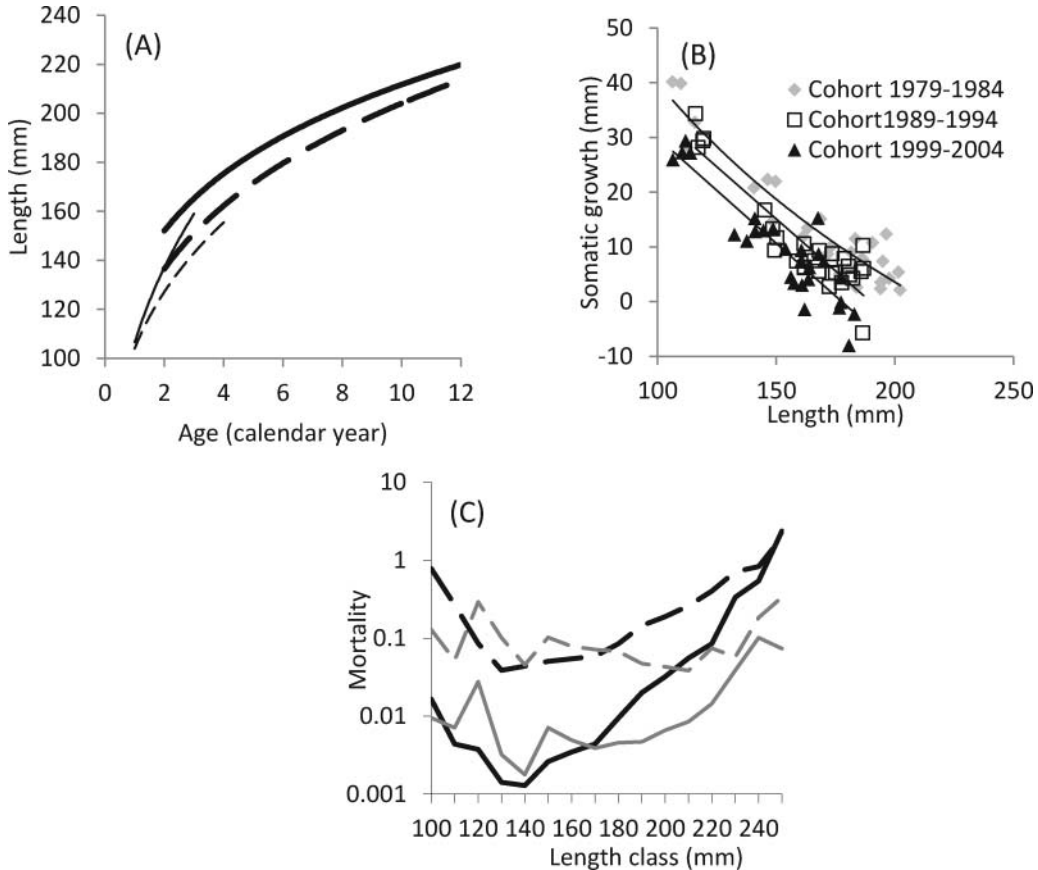


Fig. 1. (A) Best fits of average length at age of immature (thin lines) and mature (thick lines) individuals of 1982–1989 (solid) and 1997–2005 (hatched). (B) Observed average annual body length (L) growth rate ($L_{x+1} - L_x$) of cohorts in relation to body length during 1979–1984, 1989–1994, and 1999–2004 from age 1 to age 8. (C) Estimated instantaneous herring mortality rate owing to grey seal predation (solid lines) and fishing (dashed lines) in two periods: 1981–1983 (before the grey seal expansion, in grey) and 2001–2005 (at end of the grey seal expansion, in black). All length classes >250 mm are lumped into the 250-mm length class. The peak at 100 mm is partly an artefact of surveys being done during the fall when age 0 herring have yet to grow to 100 mm, whereas fisheries and seal consumption are calculated for the whole year.

probability of maturing at $\mu = 16.6$ cm, whereas in 2002–2005, $\mu = 12.8$ cm ($z = 4$, $P < 0.001$). For age class 3, μ increased by a non-significant amount, from 10 cm to 11.5 cm ($z = 0.8$, $P = 0.4$). In the 1980s, <2% of age 4 herring had not matured, but by the 2000s, 5% of age 4 herring had not matured. Thus, the PMRN has become flatter over time. μ for age 2 herring showed negative correlations with both fishing effort and grey seal abundance (Fig. 3). As there was no difference in μ for age 3, and μ could not be computed for age 4 in the 1980s, we did not calculate correlations for these age classes.

Table 1. Model fits, represented by Akaike's Information Criterion (AIC, a lower value indicates a better model fit), on cohort-specific mean body length of Bothnian Sea herring at time t from a mixed linear model

Variable	CV	Model 1 AIC	Model 2 AIC	Model 3 AIC	Model 4 AIC	Model 5 AIC
N-at-age	0.59 ^a	-893	-895	-908		
B-at-age	0.46 ^a	-883	-890	-900	-903	-900
TSB herring	0.45	-884	-886	-895	-903	-904
Seal	0.61	-894				
Fishing effort	0.73	-889	-886	-894	-900	-900
Fishing mortality	0.33	-890	-890	<i>-900</i>	-909	
TSB sprat	0.43	-883	-886	-900	-903	-905
Acartia	0.68	-881	-886	-893	-899	-899
Bosmina	1.71	-873	-890	-892	-899	-900
Eurytemora	0.62	-877	-903			
Limnocalanus	0.81	-877	-886	-892	-899	-901
Pseudocalanus	1.55	-888	-898	-892	-896	-897
Evadne + Podon	0.67	-875	-885	-896	-899	-900
Water temperature	0.17	-881	-887	-895	-899	-900
Salinity	0.05	-882	-886	-898	-901	-902
Ice cover	0.54	-875	-888	-893	-900	-902
Saduria ^b	0.87	-755	-758	-764	-756	-763
		(-768)	(-771)	(-775)	(-772)	(-772)
Monoporeia ^b	0.99	-748	-758	-762	-757	-761
		(-768)	(-771)	(-775)	(-772)	(-772)

Note: All the models include a body length term at time $t - 1$ (L) and a factor indicating if the cohort was mature or not (higher body growth), which had AIC = -884. Model 1 shows the AIC of a single explanatory variable in addition to L and maturation, but may include an interaction term with L (values in *italics*). Models 2 to 4 show AIC of the model when another explanatory variable was added to the previous best model, and may include interaction terms with previously entered explanatory variables. Numbers in **bold** indicate the explanatory variable with the best fit for each number of explanatory variables included, i.e. 'Seal' was included in model step 1, 'Eurytemora' in step 2, and so on. CV = the coefficient of variation for each variable.

^a The value is an average over age classes 2–8.

^b Data were available for biomasses of benthic crustaceans from 1983 onwards and not before. The AIC of models including benthic crustaceans was, however, higher than the AIC of the best model from only including observations 1983 and later (shown in parentheses).

Decomposition of ecological and evolutionary contributions

The estimated average yearly decrease in body growth due to ecological bottom-up factors between the 1980s and 2000s (i.e. the annual difference in body growth due to increased *Eurytemora* and cohort-specific abundances) was 2.5 mm. But the annual difference was larger for smaller herring, 5 mm for cohorts in the 10–15 cm interval and <1 mm for cohorts >17 cm (Fig. 4a). The estimated annual effect of size-selective fishing (M_F) and seal predation (M_S) on cohort-specific growth was averaged over all ages <0.1 mm in both periods. For ages 5–7, M_F and M_S decreased cohort-specific average annual growth 0.36 mm during 2001–2005 compared with <0.1 mm for 1982–1986. The evolutionarily driven decrease in size at maturation, μ , decreased the average annual body growth 5 mm for age 2 herring between the two study periods (Fig. 4a). Average L_{ECOMAT} overestimated average

Table 2. Z-statistics for the best-fit model (see Table 1) to the body length and individual condition of Bothnian Sea herring

Final model	Z	Est.	Δ AIC	Partial r^2
Intercept	14	2.2		
<i>L</i>	35	0.51		
Seal	-5.9	-0.026	14	12
Eurytemora	5.4	0.20	10	9
N at Age	3.3	0.040	14	2
N at Age *Eurytemora	-4.9	-0.014	11	23
Fishing mortality	-4.5	-5.1	6	2
<i>L</i> *Fishing mortality	4.4	0.98	14	4
Covariance parameter Estimate				
Year		0.000087		
Cohort (AR1)		-0.1436		
Residual		0.000369		

Note: Δ AIC shows the difference in AIC between that variable being excluded and the full best model. Partial r^2 is the proportion of additional variation explained by each variable of the residual variation around equation (2).

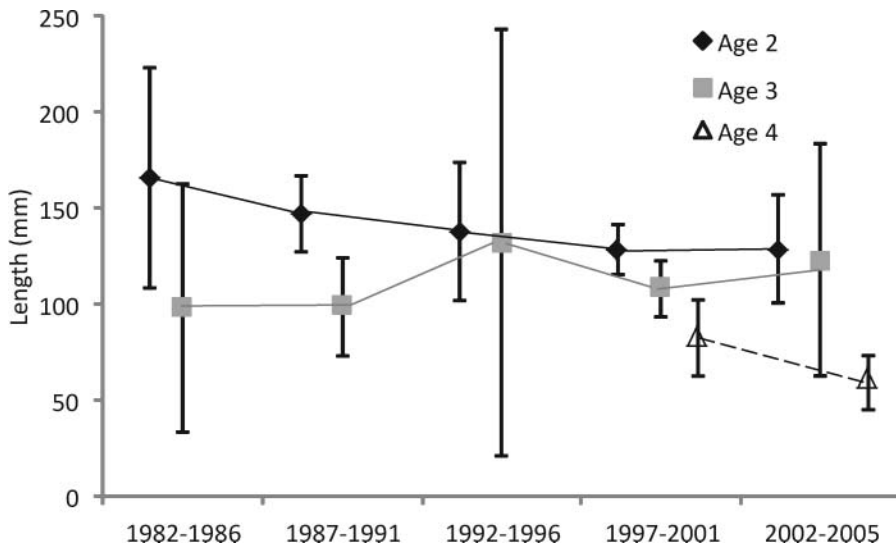


Fig. 2. Estimated age-specific length at 50% probability of maturity, μ , of Bothnian Sea herring during five different periods. Error bars show 95% confidence intervals. It was not possible to calculate age 4 before 1997 because of the low number of immatures. Lines are for illustrative purposes only.

observed length by 0.04 mm in the period 1982–1986 and by 1.0 mm in the period 2001–2005 (Fig. 4b). In particular, cohorts of intermediate body sizes were smaller than expected by L_{ECOMAT} in 2001–2005, deviating by 2–4 mm (Fig. 4b).

The relative contributions of ecological and evolutionary factors differ between ages. The length of age 4 herring has decreased approximately 2 cm during the study period (Fig. 1).

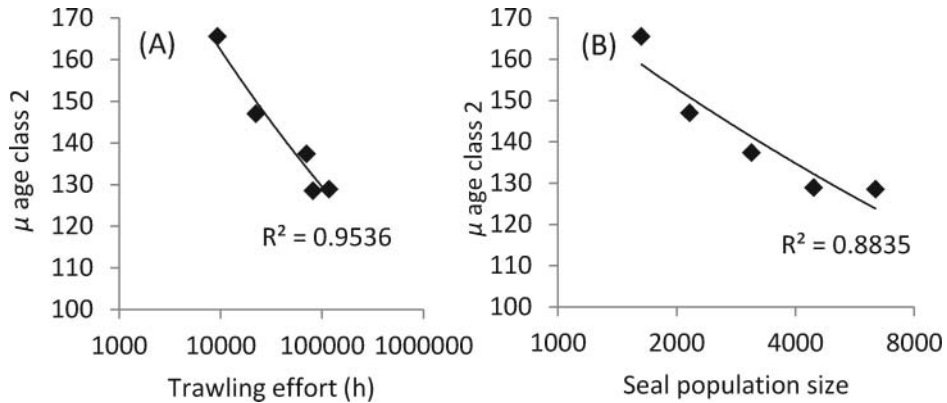


Fig. 3. Associations between μ , the length at 50% probability of maturation, for age class 2 and (A) trawling effort and (B) grey seal abundance.

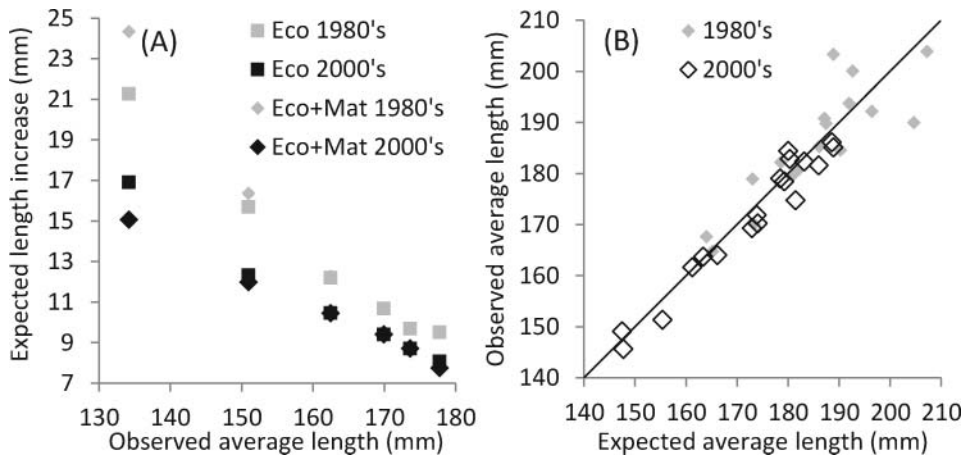


Fig. 4. (A) Expected average cohort length at age $x + 1$ for the different growth models (L_{ECO} , squares; L_{ECOMAT} , diamonds) depending on observed average cohort length in 2001–2005 at age x for ages 2–7. L_{ECO} 1980s and L_{ECOMAT} 1980s are the expected values from the environmental conditions and maturation schedule 1981–1985, whereas L_{ECO} 2000s and L_{ECOMAT} 2000s are the expected values from the environmental conditions and maturation schedule 2001–2005. Differences between squares are due to ecological factors while differences between diamonds are due both to ecological changes and changes in the maturation schedule. (B) Difference between observed and expected average cohort-specific body length from the growth model and estimated size-specific mortality. Each marker is the average among cohorts of a specific age in the respective period. The solid line represents the 1:1 line.

Body length of age 1 herring has been rather constant, indicating no large difference in body growth during the first year (2915Appendix.pdf, Fig. S2). Cohort-specific density dependence (interpreted as an ecological change) explains a decrease of ~ 5 mm between ages 1 and 2 and another ~ 7 mm between ages 2 and 4 (Fig. 4a), or roughly 60% of the total decrease in length between ages 1 and 4. Approximately 5 mm or 25% of the decrease in length at age 4 can be explained by earlier maturation, resulting in slower growth earlier

in life. The residuals between L_{ECOMAT} and observed body length indicate some process errors could account for another 1 mm annual decrease of cohort average body growth, totalling around 3 mm or 15% of the decreased length at age 4. We do not know what this unexplained variance is, but evolutionarily lowered body growth would cause such a deviance. The ecological contribution is estimated to be higher for younger (age <4) herring, and the differences in age-specific body length early and late in the study period remain more or less constant at 2 cm for older and larger herring (Fig. 1).

DISCUSSION

Our results support the general premise that there are multiple ecological and evolutionary mechanisms underlying the decreased size at age of Bothnian Sea herring, highlighting the importance of taking an ecosystem approach to study ecological and evolutionary changes in concert. More specifically, a combination of ecological responses to increased density and evolutionary responses to size-selective mortality were the strongest supported causes for this reduced herring body size. Roughly 60% of the decrease in age-specific body length could be attributed to ecological factors, in particular density dependence. The direct effect of size-selective mortality on size distributions of cohorts is estimated to have only marginal impact on body growth for age classes 2–8 studied here. However, around 25% of the decrease in age-specific body length could be attributed to evolutionary changes in size at maturation resulting in slower somatic growth earlier in life. It is unknown what the remaining 15% can be attributed to, but the systematic increase in deviations from expected body length with time leads us to hypothesize that it may partly be a result of the evolution of reduced length-specific body growth.

The increased density of herring has probably arisen because of an increase in zooplankton abundance, especially zooplankton species that are key resources for smaller, hence younger, herring (Arrhenius, 1996; Lindegren *et al.*, 2011). Although copepods, such as *Eurytemora* on which larger herring feed (Casini *et al.*, 2004), have increased over the study period (ICES, 2012), the higher herring density seems to result in increased intraspecific competition as they grow larger and switch to other prey, decreasing their body growth. This is also supported by the negative interaction between *Eurytemora* and intraspecific density, indicating the positive effect of *Eurytemora* (or other correlated taxa; [2915Appendix.pdf](#), Table S1) has vanished as density increased. Density-dependent body growth is found in many pelagic zooplankton feeding fish species (e.g. Carscadden *et al.*, 2001), but in studies on herring in other parts of the Baltic Sea, where age-specific body size has also decreased, intraspecific density dependence appears to have only weak effects on growth compared with other factors (Flinkman *et al.*, 1998; Rönkkönen *et al.*, 2004; Casini *et al.*, 2010). However, herring population densities in those areas have decreased over time. For the Bothnian Sea herring, density-dependent growth seems to be the main ecological factor lowering body growth.

Fishing and grey seal mortalities were low ($M_t < 0.1$) for herring <18 cm and showed small changes over the study period. But age-specific fishing mortality was negatively associated with body growth of smaller herring (age 1–2), indicating a size structural effect of fishing on younger age classes, i.e. small individuals of younger age classes may escape the trawls or are in areas with lower fishing effort. This is also the only age class in which fishing is negatively related with cohort biomasses in the Bothnian Sea (Lindegren *et al.*, 2011). We only consider body sizes up to age 8, which are on average around 20 cm, and hence face

rather low mortalities from fisheries and grey seals (but face natural and finfish mortalities not considered here). Direct ecological effects of size-structured mortality from fisheries and grey seals may be more evident among older age classes, as they face higher mortality from both but in particular the grey seals' preference for large herring ($M_l > 1$ for length > 23 cm). But as age 9+ comprise $< 10\%$ of the total adult population (ICES, 2013a), there is a lack of concrete data to quantify this size-structured ecological effect. If indeed there were a size-structuring effect on age 9+ individuals, the effect would be small for the herring population as a whole due to their low proportion of the population as a whole.

Size-selective mortality seems instead to have induced evolutionary life-history changes in herring indicated by the changes in the probabilistic reaction norms of age-specific length at maturation (50% PMRN). These changes in maturation probability are presumably independent of changes in individual size or condition at capture (Heino *et al.*, 2002), and are thus generally interpreted as evidence of evolution, but may overestimate evolutionarily induced changes if other relevant parameters are omitted (Kuparinen and Merilä, 2007). Here we accounted for body condition at capture and 50% PMRN was best correlated with fishing effort and seal abundance, which affect individuals mostly after maturation, suggesting this life-history change is indeed evolutionarily induced, but we cannot exclude any other confounding or unaccounted for factors. For example, Kinnison *et al.* (2011) showed a major effect of historic (plastic) growth on 50% PMRN, which might thus be a confounding factor in the present analysis. However, the maturation data used here do at least support evolutionarily induced life-history changes in the Bothnian Sea herring stock.

Here the change in PMRN suggests not a plain decrease in age-specific length at maturation. The reaction norm has become flatter over time. The length at 50% probability of age 2 herring being mature is estimated to have decreased 4 cm, and is negatively associated with fishing effort and grey seal abundance. In contrast, the proportion herring postponing reproduction to age 4 doubled between the 1980s and the 2000s. This is consistent with reports of the proportion of mature herring increasing for age 2, but decreasing for age 4, over the same period (ICES, 2013a). Day and Rowe (2002) suggested for species with a developmental threshold in maturation (individuals need to acquire a certain body size to reproduce) that reaction norms of size at maturation should be flat across ages when body growth is low. No matter how slow individuals grow, they need to reach a threshold size, or acquire energy, to mature. This can explain why length at maturation for age 2 herring has decreased substantially, while the length at maturation for age 3 herring has not changed much and that more herring now mature at age 4. Our results suggest that herrings may need to reach a body length of around 10–12 cm to mature independent of age. Towards the end of the study period, more herring seemed to reach this threshold at a later age due to ecologically induced slower body growth when immature. The decreased size at maturation for age 2 herring results in lower size-specific body growth after maturation as energy is diverted to reproduction. Thus, it is likely that evolutionarily induced changes in maturation size in combination with ecological factors have reduced herring body growth.

Whether size-selective mortality also has caused adaptations in length-specific body growth is uncertain. Life-history theory and laboratory experiments predict that high mortality induced by fishing will lead to evolution of slower growth (Conover and Munch, 2002). Consistent with these predictions, the model of herring growth with only ecological causes and changes in maturation performed well in the 1980s, but overestimated growth in later years. This systematic increase in the model bias could, however, be due to changes in other factors or non-linear relationships not accounted for. In line with the prediction that

size-selective mortality has induced evolutionarily reduced body growth, grey seal abundance was negatively correlated with body growth across the whole 10–20 cm body size spectrum, despite estimated grey seal mortality being low in this size spectrum ($S < 0.01$) over the whole time period. Thus, the increasing mortality imposed by fisheries and grey seal predation on larger herring over the study period may have resulted in selection for slow growing phenotypes decreasing length-specific body growth.

It has been shown that variation in mortality from both a natural predator (Reznick *et al.*, 1996) and fisheries (Edeline *et al.*, 2007; Jørgensen *et al.*, 2007) can induce evolutionary life-history changes and alter body growth in fish (Conover and Munch, 2002; Swain *et al.*, 2007), but indications of predator-induced evolutionary changes in human-exploited populations are few. But whether, or how much, grey seals have contributed relative to fisheries is difficult to tell. Grey seal abundance and fishing effort are independent factors (i.e. fishing effort does not depend on seal abundance, and vice versa), but show a statistical covariation. This makes it difficult to isolate their specific contributions to evolutionary changes in herring. Size-specific fishing mortality is estimated to be 10–60 times higher than grey seal predation mortality up to 18 cm (Gårdmark *et al.*, 2012). For larger herring, grey seal predation mortality has, however, increased up to ten times over the study period compared with around five times for fishing mortality. Thus, the higher overall mortality from fisheries may be a stronger selection pressure against rapid body growth and later maturation than grey seals (Reznick *et al.*, 1996). But during the study period, variation in grey seal mortality was higher and may to a large extent have driven the decrease in body size through evolutionary effects.

Species interactions, as well as human exploitation, have direct and indirect effects on somatic growth of Bothnian Sea herring, via both ecological and micro-evolutionary mechanisms. This highlights the importance of taking a multi-species perspective that addresses ecological and evolutionary processes in concert for understanding phenotypic changes in exploited species. This combined approach is also important for fisheries management. Although fishing may have contributed to the shift in herring body size, other factors (i.e. resource limitation due to intraspecific competition and evolutionary responses to size-selective predation) appear to be important. Our findings suggest that to slow or reverse the decrease in body size of herring, and increase the profitability in particular of the coastal herring fisheries targeting human consumption, harvest efforts would need to reduce the density of smaller herring (10–15 cm) and decrease mortality of herring >20 cm, both of which could reduce density dependence and reverse the evolutionary changes (Edeline *et al.*, 2007; Conover *et al.*, 2009). For these effects to occur, food availability must not be reduced by any compensatory mechanisms, such as increased consumption by interspecific competitors. Similarly, it should be noted that producing such evolutionary responses (larger size at maturation and a higher somatic growth rate) is non-trivial and may even result in the evolution of earlier maturation in some cases (Gårdmark and Dieckmann, 2006). Moreover, the potential selection towards smaller size at maturation and slower growth owing to grey seal predation may override evolutionary responses to fisheries targeting small individuals.

In conclusion, because phenotypic trait variation is related to both ecological and evolutionary processes, it is important to discern their relative importance to effectively manage fisheries within the broad set of factors at play in dynamic ecosystems. The evolutionary component is not the most important factor at play here, but important enough to be considered for management purposes. In fact, this study provides an empirical example of how focusing on harvest and fishing mortalities (e.g. maximum sustainable yield) in

isolation from evolutionary and other ecosystem processes would likely fail to achieve the desirable size structure of harvested stocks and long-term profitability of fisheries.

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