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Review

From individuals to populations: Impacts of environmental pollution on natural eelpout populations

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ABSTRACT

Investigating how individuals are affected by environmental pollution is relatively straightforward, for example through conducting field studies or laboratory toxicity tests. Exploring such effects at a population level is considerably more difficult. Nonetheless, the exploration of population-level effects is important as the outcomes may differ from those seen at the individual level. Eelpout (*Zoarces viviparus* L.) have been used for several years as a bioindicator for hazard substances in both the field and laboratory tests, and individual effects on reproduction have been reported. However, the influence of these effects at the population level remained unexplored. In this study, four Leslie matrix models were parameterized using data from non-polluted eelpout populations (Skagerrak, Baltic Proper, Gulf of Bothnia and Gulf of Finland). The four sites represent an environmental gradient in salinity. Furthermore, life-history data revealed differences between the sites with growth rate, fecundity, age at maturity and longevity being the most significant. The effect of pollution on natural eelpout populations was then simulated by combining the outputs from the Leslie matrices with data from laboratory and field studies exploring reproductive impairment in contaminated environments. Our results show that despite differences in life-history characteristics between sites, survival of early life stages (i.e. larvae and zero-year-old fish) was the most important factor affecting population growth and persistence for all sites. The range of change in survival of larvae necessary to change population dynamics (i.e. growth) and persistence is well within the range documented in recipient and experimental studies of chemicals and industrial waste waters. Overall, larval malformation resulting from environmental pollution can have large effects on natural populations, leading to population losses and possibly even extinction. This study hereby contributes valuable knowledge by extending individual-level effects of environmental contaminants to the population level.

Contents

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1. Introduction

Physiological effects of contamination by toxic substances in aquatic organisms are commonly examined using laboratory tests or by taking field-measurements of individuals. Such studies provide important information about the consequences of environmental pollution and contribute to ecological risk assessments at the individual level. However, the results of such studies cannot simply be extrapolated to the population level. Population growth and persistence are determined by several life-history characteristics (survival rate, fecundity and maturity) (Caswell, 2001). Depending on such crucial life-history characteristics, differing effects of contaminants can be seen in different species. Some species can experience an increased individual mortality rate and/or a reduced reproductive success without resulting changes at the population-level. It is therefore crucial to consider both individual-level effects and population characteristics when exploring the environmental effects of pollutants. Models including such population- and individual-level data present a compelling tool for exploring pollutant effects at the population level (Spromberg and Meador, 2006).

The eelpout (*Zoarces viviparus* L.) is a common species throughout both the Baltic Sea and the North Sea. It has been extensively used in experimental studies exploring effects of contaminant exposure on individual health and as a bioindicator of pollution in the field (Voigt, 2007; see Hedman et al., 2011 for a review). It has also been proposed by both the Regional Conventions Oslo-Paris (OSPAR) and the Helsinki Commission (HELCOM) (OSPAR, 2007; HELCOM, 2008) as one of the preferred sentinel species for monitoring impacts of hazardous substances on marine environmental health (OSPAR, 2007; HELCOM, 2008). This recommendation is based on the numerous reported individual-level effects of exposure to contaminants, such as growth retardation and reduced reproductive performance. For example, it has been shown that pulp mill effluents can induce acute larval mortality (Jacobsson et al., 1986; Vetemaa et al., 1997) and that metal effluents effects juvenile survival (Vetemaa et al., 1997). Differences in the number of malformed larvae between unpolluted Swedish reference stations and polluted Danish and German sites (Gercken et al., 2006; Stuer-Lauridsen et al., 2008) provide further evidence of reproductive impairment. The eelpout is therefore a perfect candidate as a bioindicator for environmental pollution. However, how these individual-level effects are reflected at the population level remains unknown (but see Hanson et al.'s (2005) investigation of effects of sex-ratio change due to endocrine disruption). Changes in population sizes have been reported (Ojaveer, 1966; Voigt, 1997, 2002; Naturvårdsverket, 2010) although the possible causes of these declines have not been investigated.

The eelpout is considered to be a relatively stationary species in coastal waters (Schmidt, 1917; Christiansen et al., 1976; Simonsen and Strand, 2010). Adults range from 20 to 40 cm in size and have a life span of approximately 5–14 years (Ojaveer, 1962; Kristoffersson and Oikari, 1975). Females reach maturity at an age of 1+ or 2+ while males mature at 1+ (Vetemaa, 1999). Reproduction takes place once a year (Kristoffersson and Pekkarinen, 1975). The oocytes are fertilized immediately after ovulation in late summer, followed by 3 weeks of embryological development. After hatching inside the ovary, a 4–5-month development time follows, during which the larvae are dependent on the transfer of maternal nutrients (Vetemaa et al., 2006) and therefore likely to also be affected by contaminants in the environment (Korsgaard and Andersen, 1985). The pregnancy ends during January–February when the larvae are released.

Leslie population matrix models project population abundance over time by using individual age-specific fecundity and survival estimates (Leslie, 1945). They are becoming increasingly popular as a tool in ecotoxicology and risk assessment, linking individual effects to the population level (Caswell, 1996; Klok and de Roos, 1996; Levin et al., 1996; Munns et al., 1997; Miller and Ankley, 2004; Gutjahr-Gobell et al., 2006; Smit et al., 2006; Spromberg and Meador, 2006; Miller et al., 2007; Iwasaki et al., 2010). By using the basic Leslie matrix model, we can get the intrinsic growth rate of the population, its stationary age structure, and the reproductive values for each age class, i.e. which particular life stage will be more influential to the stable population. Furthermore, we are also interested in how a change in fecundity or survival rate will affect the population growth rate λ, namely the sensitivity of the growth rate to different

parameters. This analysis will provide a link between individuals, the life history of the species and population growth. This is crucial for understanding ultimate consequences of environmental pollution.

In order to explore the effects and evolutionary outcomes of environmental pollution, we investigate how natural populations are impacted by reproductive disruption of individuals due to contamination and hazardous substances. The study is based on data collected yearly from three reference sites as part of the environmental monitoring program in Sweden: Skagerrak (SK), Baltic Proper (BP) and Gulf of Bothnia (GoB) (Fig. 1). These reference sites have been recognized by the Swedish national coastal fish monitoring program as locally unpolluted areas (Sandström et al., 2005) and are located far from cities and industrial areas. Since estimation of fecundity (number of larvae) and age determination has been performed yearly as part of the national environmental monitoring program, a discrete age-classed model is appropriate for exploring the effects of reproductive disruption. In addition, as sampling has been done at the same time each year, the time step between age classes is precisely the same (i.e. one year). In order to represent the eastern part of the Baltic Sea, another unpolluted area, in the Gulf of Finland (GoF) (Fig. 1) was sampled. GoF is situated in the middle of the Lahemaa National Park and is isolated from any industrial pollution sources, with only a few small villages in close range. The areas comprise a gradient in salinity ranging from less than 5 PSU to up to 20 PSU (Fig. 1) and can potentially represent different populations throughout the Baltic Sea and the North Sea. We compiled reported individual eelpout responses to pollution (i.e. number of malformed or dead larvae) by conducting a literature review. Pollution effects in natural eelpout populations were then predicted by incorporating these results into a Leslie population matrix. By combining data on individual response with matrix modeling, important conclusions can be drawn regarding the impact of environmental pollution on natural populations and the protection of populations and ecosystems.

2. Material and methods

2.1. Sampling method

Data from the Swedish sites used in the models have been collected annually by Swedish Board of Fisheries using standardized test fishing with small, fine-meshed, fyke nets during November (Thoresson, 1996). Sampling is part of the national environmental monitoring programs funded by SEPA. The brood size

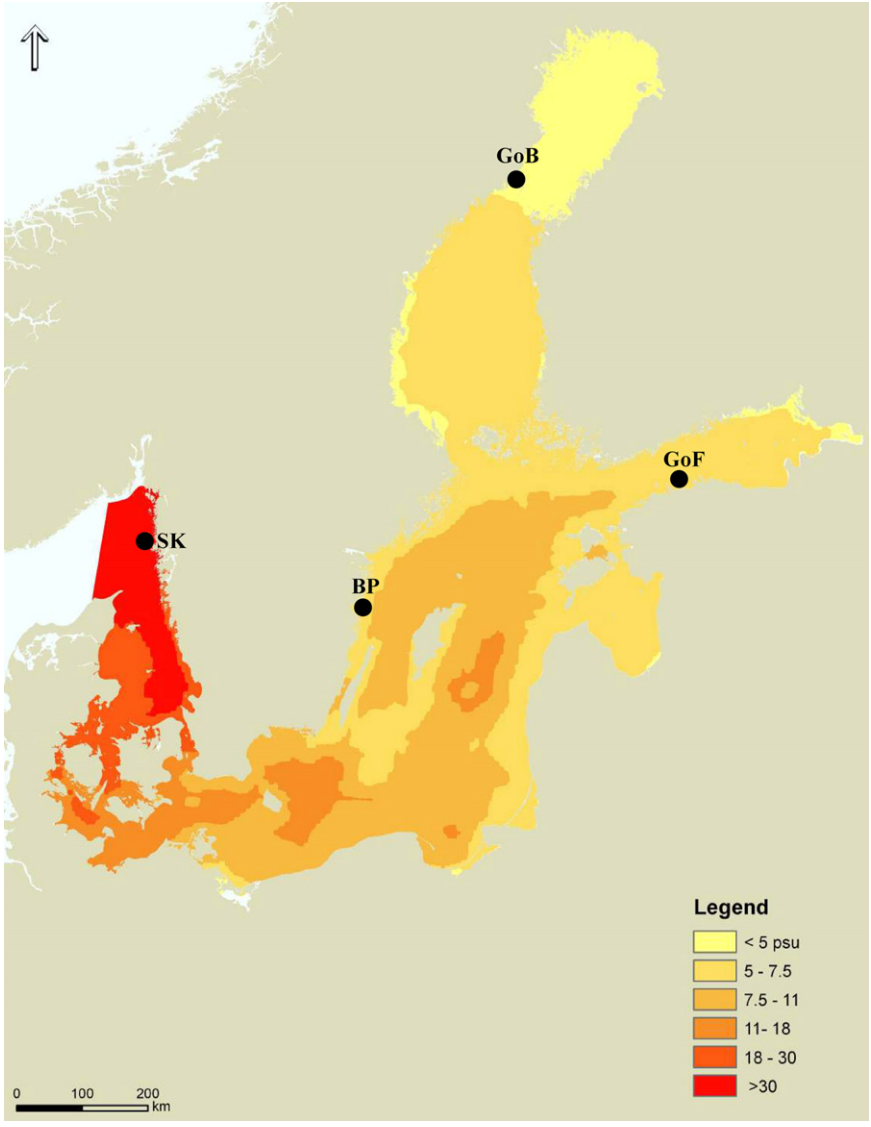

Fig. 1. Map of the sampled sites. Dots refer to the four different populations used to parameterize the population models (Skagerrak (SK); Baltic Proper (BP); Gulf of Bothnia (GoB); and Gulf of Finland (GoF)). The color map indicates salinity levels. Taken from Al-Hamdani and Reker (2007). Towards marine landscapes in the Baltic Sea. BALANCE interim report #10, see http://balance-eu.org/.

from pregnant females is investigated and calculated, and the age of the females determined by the use of otoliths and method by Svedäng et al. (1997). Data from the Gulf of Finland was collected during September 2009 using similar fyke nets. All larvae were counted and the age of females determined by otoliths. All fish were caught under the licenses issued by the responsible national authorities of Sweden and Estonia and killed immediately after capture in accordance with the laws of representative states and international criteria on ethical use of animals in scientific experiments.

2.2. Life history differences

As the four investigated sites represent different abiotic environments, e.g. due to differences in temperature and salinity, life history characteristics that might be coupled to these differences were explored before parameterization of the models.

2.2.1. Growth

Marine fish, such as the eelpout, tend to grow slower and be relatively smaller in size due to metabolic stress caused by low salinity levels. A von Bertalanffy growth function was therefore fitted to size-at-age data for all four study sites to reveal differences in growth patterns among sites.

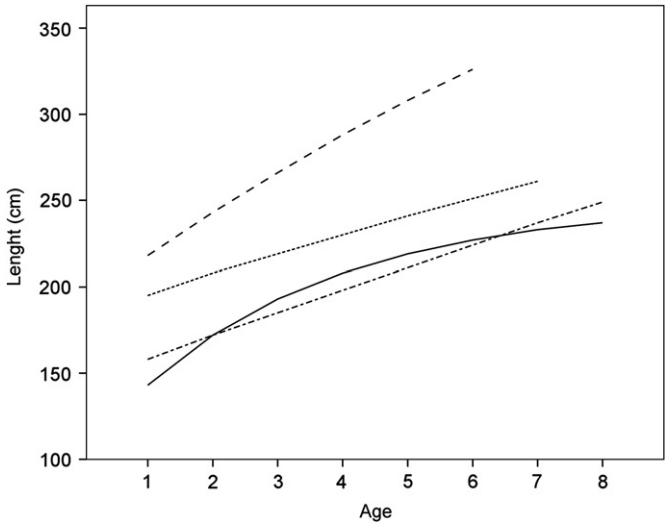

Fig. 2. Predicted growth curves of the four sampled populations. Large-dashed line indicates the Skagerrak (SK) population, small-dashed line to Baltic Proper (BP), solid line to Gulf of Bothnia (GoB), and dashed dotted line to Gulf of Finland (GoF).

Table 1
Fecundity (mean number of larvae per age class) per age and age at maturity in brackets in each age class in each site.

	SK	BP	GoB	GoF
1	34 (100%)	19 (65%)	16 (62%)	12 (59%)
2	46	23 (75%)	17	35
3	52	26	23	31
4	68	31	28	34
5	86	31	38	58
6		38	42	97
7			36	70
8				85

2.2.2. Reproduction

The number of larvae in females is easily assessed. However, the number of eggs, and subsequently the mortality between the egg and larvae stage, is less well understood. In order to collect more detailed fecundity measures, ovaries from different length groups were collected during one week of fishing in the beginning of August 2010 (N=59 pregnant females from SK; 74 from BP and 57 from GoF, note that GoB was not sampled for this analysis) (see Appendix A). The gonads were carefully dissected and fixed in 10% buffered formaldehyde. After 7 days, they were transferred to 70% ethanol and a subsample of the eggs were counted and photographed under a stereo microscope. The photographs were later used to calculate the number of eggs in each female and the size of the eggs were estimated with Adobe Photoshop CS5 Extended version 12.0 (Adobe, 2010). The age of all females was also determined. Differences in egg size between age classes at the sampled sites were tested by a two-way analysis of variance (ANOVA) (SPSS version 15.0.0). The final sample size included in the analysis of egg sizes in relation to female age was 55 females from SK, 66 from BP and 48 from GoF, representing ages from one to seven (see Appendix A). Data from 59 females from SK, 69 from BP and 56 from GoF were included in the analysis of survival from the egg to the larval stage (s_e).

The number of larvae per female, estimated for all years in the environmental monitoring program, was used to provide an estimate of fecundity and calculated as mean number of larvae per female for each age class. This was done by using 10 years of data in BP, GoB and SK and one year of data in the new sample site GoF. Age at sexual maturity was estimated by fitting a logistic function to the fraction of mature fish in each age class (SPSS version 15.0.0).

2.2.3. Survival

Length/age curves were calculated for all fish whose age was determined and used to estimate the age of individuals that had not been age determined. This allowed the calculation of age-specific catch per unit effort (CPUE) values. Age-specific survival rates were then calculated from the total CPUE distribution of age at death as

$$s_i = N_{i+1}(t+1)/N_i(t) \quad (1)$$

where s_i is the survival estimate at age i and N_i is the relative number of females within a given age class. Since the number of zero-year-olds, one-year-olds and to some degree two-year-olds obviously were underestimated due to the fishing equipment used, we estimated number of fish in these age classes using log-linear and maximum likelihood estimates (MLE) based on catch data of older fish. Both methods resulted in similar values, and the log-linear method was therefore used in all further analyses. In SK we only needed to estimate the number of zero-year-olds and one-year-olds as fish here tended to grow faster (see Fig. 2) and 2-year-olds were obviously fully recruited to the fishing equipment. Because some of the youngest fish were underestimated in the catch data, data on their larvae is also missing. Hence, we needed to correct the numbers of larvae in order to obtain the total population size of larvae. The larvae from the missing age classes (L_m) was calculated as

$$L_m = L_{c1}M_1 + L_{c2}M_2 \quad (2)$$

where L_{c1} is the number of larvae that should have been born by one-year-olds and L_{c2} are larvae from two-year-olds (calculated from the few individuals in that age class that were caught) and M_1 and M_2 are female population sizes at ages at maturity (see Table 1). L_m was then added to the older age classes' larval counts as calculated from the sampling data (see Section 2.2.2) in order to obtain the total population size of the larvae class (L).

2.3. Model development

The population was divided into groups of age classes (Fig. 3). The projection interval was set to one year. Larvae were collected in females during November each year. Thus fish in age class 0 are fish that were released from the maternal fish 10 months earlier (i.e. that are 10-months old), fish in age class 1 are one year, 10 months old, etc. Only females were included in all the models and we assume that there are enough males for reproduction. Therefore population size is solely determined by females' reproductive capacity and not influences by but not males'. This assumption is likely to be reasonable as there are indications that the eelpout mates multiply (Hjort, 1971). We also assume that reproductive toxic responses are expressed by the females and not limited to males.

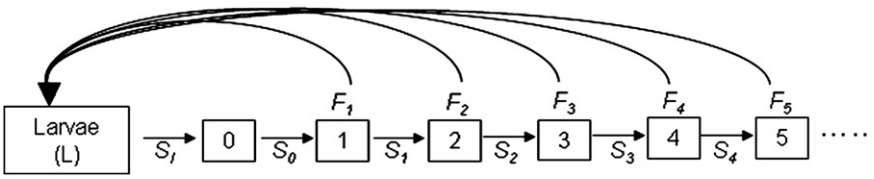

Fig. 3. The life-cycle graph of *Zoarces viviparus*. The different age classes are represented by: L for larvae (L); 0 for zero-year-old fish (i.e. 10 months old), 1 for one-year-old fish (i.e. one year and 10 months old), 2 for 2-year-old fish (i.e. 2 years and 10 months old), etc. F_i and s_i denotes the fertility and survival of age class i, respectively.

2.3.1. The basic Leslie Matrix model

We employed the Leslie model, which was built using birth pulse fertilities and pre-breeding census (Caswell, 2001). The Leslie matrix (M) can be written as

$$M=\begin{pmatrix} 0 & 0 & f_1 & f_2 & \dots & f_i \\ S_l & 0 & 0 & 0 & \dots & 0 \\ 0 & S_o & & & \dots & 0 \\ 0 & 0 & S_l & 0 & \dots & 0 \\ \dots & \dots & \dots & & & \\ 0 & 0 & 0 & \dots & S_i & 0 \end{pmatrix} \quad (3)$$

where f_i is fecundity in each age class and s_i is survival from age i to age $i+1$ at time $t+1$ between all age classes. In the basic Leslie model, the population projection from one time step to the next in the matrix is

$$N(t+1)=MN(t) \quad (4)$$

where $N(t)=(N_1(t),N_2(t),\dots,N_{max\ age}(t))'$ is the vector denoting the population size in each age class at time t, and M is the Leslie matrix stated above. Given the initial population sizes in each age class, the population evolving dynamics will then be

$$N(t)=M^tN(0) \quad (5)$$

In the stable state, the population will have an intrinsic growth rate determined by the leading eigenvalue λ of the Leslie matrix M, and the stable age structure can be obtained by the corresponding right eigenvector of the leading eigenvalue (Leslie, 1945). Meanwhile the left eigenvector of M will provide us the reproductive values of each age class, i.e. how many individuals will be added to the population in the next time step if we introduce one extra individual in a particular age class at the current time.

Survival and fecundity rate was estimated using the methods stated in previous sections, resulting in four separate Leslie matrices for the four studied sites. By calculating the corresponding leading eigenvalues and eigenvectors, population growth rate and stable age-structure and reproductive values for each site can be obtained. Due to differences in the age structures among sites, the models had different maximum ages. For SK the model ran up to age class 5, for GoB to age class 7, for BP to age class 6 and for GoF to age class 8. For SK and BP average cohort data were used (1994–2004 and 1995–2004, respectively). For GoB, CPUE data were not available, so a static method using mean values from total catch data for year 2003–2009 was applied. For GoF, data from one year of sampling was used (one week of fishing in November 2010).

2.3.2. Stochasticity

Survival is assumed to be subject to stochastic variations caused by natural mortality processes. Hence, uncertainty was added to the model by further modifying the Leslie matrix and thereby allowing the calculation of confidence intervals for λ. As cohort data was used, we were unable to take the variance straight from real CPUE. Therefore we included a Gaussian random variable (mean=0, S.D.=0.1) that accounts for annual environmental variation that affects each age class within the vector N_t, as shown by Miller et al. (2002). Monte Carlo simulations was used to iterate Eq. (4) until the population has a stable growth rate, the simulation was run 10,000 times to obtain the 95% confidence interval of λ.

2.3.3. Elasticity analysis

To explore the impacts of fecundity and survival rate on the population growth rate λ, we denote u and v as the right and left eigenvector of the leading eigenvalue of the Leslie matrix M, the sensitivity of λ to fecundity rate f_i and survival rate s_i at age i can be obtained by the derivative of λ respect to f_i and s_i. But to make the results for different parameters more comparable, we rescale the sensitivity to elasticity, namely to calculate $(d\lambda/\lambda)/(df_i/f_i)$ and $(d\lambda/\lambda)/(ds_i/s_i)$ instead. The elasticity are calculated by

$$\left.\frac{d\lambda/\lambda}{df_i/f_i}\right|_{\lambda=\lambda^*,f_i=f_i^*}=\frac{u_iv_1}{v^Tu}\frac{f_i^*}{\lambda^*} \quad (6)$$

$$\left.\frac{d\lambda/\lambda}{ds_i/s_i}\right|_{\lambda=\lambda^*,s_i=s_i^*}=\frac{u_iv_{i+1}}{v^Tu}\frac{s_i^*}{\lambda^*} \quad (7)$$

where λ^*, f_i^* and s_i^* denote the corresponding value of λ, f_i and s_i we got from the data. The elasticity of λ will provide us the percentage change of λ caused by the percentage change of the parameter, i.e. the fecundity or survival rate, therefore we can compare which parameters are more effective to bring changes to the population growth rate.

2.4. Adding changes to the 'basic model'

As described in this section, different modifications to the basic Leslie models were made in order to investigate their relative effects on eelpout population dynamics.

2.4.1. Including an additional egg stage

Degeneration of oocytes (atresia) is to some extent a natural process controlling fecundity. However, atresia during the later stages of oocyte development is largely considered to be the result of environmental stress (Tyler and Sumpter, 1996). Additionally, exposure of adult fish to various chemicals has been seen to result in increased rate of ovarian atresia (Ankely et al., 2005; van der Ven et al., 2007). Atresia therefore has the potential to greatly influence population dynamics. The rate of atresia in natural populations of eelpout is unknown. In order to investigate possible population-level effects in the eelpout, we modified the Leslie models by including an additional egg stage. This stage is shorter than the others (3 weeks) so it could not be incorporated directly in the Leslie matrix. Instead, we investigated the effect of this stage by checking its influence on the survival of larvae indirectly

$$s_l=\frac{N_o}{N_l}=\frac{N_o}{N_es_e} \quad (8)$$

where s_l is survival rate of larvae, N_0 is the number of zero-year-olds and N_l is number of larvae, N_e the number of egg and s_e survival of egg (between the egg stage and larval stage). For s_e, we used the mean of the three latest years of data (2007–2009) (to avoid temporal changes in the number of larvae) to calculate the mortality between the number of eggs (sampled 2010) and number of hatched larvae. If we assume the number of eggs and zero-year-olds are fixed, then the impact of change in survival of egg on the survival of larvae can be explored by taking the derivative of Eq. (8) with respect to s_e.

2.4.2. Changes in individual growth rate and maturity

Growth inhibition may influence the time it takes for individuals to reach sexual maturity, and thereby also population dynamics. The effect of retarded growth on λ was investigated by prolonging the age of maturity in the BP population model, i.e. all one-year-old individuals were set to be immature (instead of 65% being mature, see Section 3.1.2 below) and 100% maturity was reached at an age of 2 years.

2.4.3. Density dependence

The Leslie model describes exponential growth in an environment without resource limitation. This assumption is somewhat unrealistic since resources such as habitat and food are limited and thus constrain population growth. The impact of the environmental carrying capacity on population growth was investigated by applying a simple density-dependent matrix. As described by Jensen (1995), we implemented the logistic factor in the Leslie matrix

$$N_{t+1}=N_t+\mathrm{l}(1-P_t/K)(M-I)N_t \quad (9)$$

where N_t is the number of individuals in each age class at time t, P_t is the total population size at time t, λ is the intrinsic rate of increase of the population, i.e. the leading eigenvalue of the Leslie matrix M, K is the carrying capacity and I is the unit matrix. The Leslie matrix M and the intrinsic population growth rate, λ, were based on the data for the site BP. As no real estimate of K is available, we tested values for K at 0.8, 1.5 and 2 times the total original population size (P_0). Finally, we were able to iterate Eq. (9) to get the dynamics of the total population through time under different carrying capacities by setting the initial population size vector equal to that of the first year (1995) of the BP site.

2.5. Response data

We conducted a literature review in order to identify the effects of various contamination sources on individual eelpouts. The response data were grouped according to different anthropogenic influences, and their effects on the larvae were recorded. Estimated levels of malformed or dead larvae (of total brood) were used as effecting the survival of larvae (s_l), i.e. the survival of larvae was correspondingly reduced in order to reflect the magnitude of the change. These modified larval survival rates were then used in the Leslie models for the different populations. The resulting model projections therefore described how reproductive changes, caused by contaminants, could alter population growth rate in the eelpout. The individually measured impairment effects in the response data was compared to the 'critical level' for the different populations. That is, the amount of change s_l in each population can cope with before λ drops below one. The population is of course affected even before this critical level is reached. However, this critical level was chosen in order to represent a possible effect of pollutants on λ.

3. Results

3.1. Life history characteristics used for parameterization

3.1.1. Growth

The eelpout growth rate differed between the studied sites, most likely as a result of differing environmental conditions. The

SK population, which is the most saline environment, showed a much faster growth rate than the other Baltic Sea populations (see Fig. 2). The slowest growth rates were observed in populations occurring in areas with the lowest salinity levels, GoF and GoB (see Fig. 2).

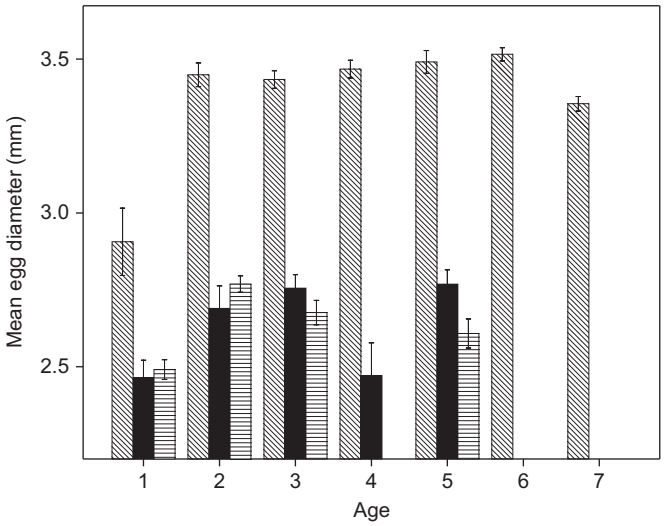

Fig. 4. Egg size (mm) measured as diameter. Colors indicate populations: gray for Baltic Proper (BP): black for Gulf of Finland (GoF): and white for Skagerrak (SK). Error bars represent the 95% CI.

Table 2
Survival rates in each age class for all base model populations.

	SK	BP	GoB	GoF
Larvae	0.026	0.179	0.107	0.031
0	0.599	0.449	0.536	0.506
1	0.681	0.449	0.536	0.886
2	0.416	0.467	0.477	0.670
3	0.566	0.507	0.720	0.790
4	0.631	0.383	0.425	0.875
5		0.697	0.577	0.429
6			0.504	0.667
7				0.050

3.1.2. Reproduction

The SK population showed the highest level of absolute fecundity in all age classes (Table 1). The age at which sexual maturity was reached also differed between populations. For the North Sea (SK) population, all one-year-old fish were mature while only 65% and 59% of BP and GoF females were mature at one year of age (Table 1). This analysis could not be performed on the GoB data as only six one-year-olds were examined. We therefore estimated the proportion of mature one-year-olds in the GoB population to be 62%, by assuming that the age of sexual maturity is dependent upon the size of the female and the abiotic environment and therefore follows the pattern seen in the BP and GoF populations.

All one-year-old fish have smaller eggs than older fish ($p<0.05$). When the fish gets older, the size of the egg is approximate the same in each population (Fig. 4). Unfortunately, we did not collect any 4-year-old fish at the SK site. Females from BP were at a later developmental stage in the maturity process and all eggs observed were already ovulated and fertilized. This resulted in eggs from the BP site being larger than eggs from SK and GoF ($F(8.81)=7$, $p<0.0001$) (Fig. 4). All one-year-old fish had smaller eggs than older fish ($p<0.05$) for all populations. As the fish gets older, the size of the egg is approximate the same within populations (Fig. 4).

3.1.3. Survival

The survival of larvae differed somewhat between populations, with the SK having the lowest larval survival (0.026) and BP the highest (0.179) (Table 2). From zero-year-olds and upwards, the survival increased for all age classes for all populations (Table 2).

The GoF population showed a very high survival (0.875) of the 4-year-old age class. In contrast, the 7-year-old GoF age-class had a survival of only 0.05%. However, since GoF was only sampled one year, the sample size is relatively small and the results may therefore just reflect sampling error.

3.2. Leslie model and population dynamics

The Leslie matrices for the basic model showed intrinsic population growth rates ranging between 0.937 (SK) and 1.129 (BP), however confidence intervals obtained from our Monte Carlo simulation are rather large (Fig. 5). The GoB, GoF and SK population were all close to a stable population size, while the BP population had a clearly

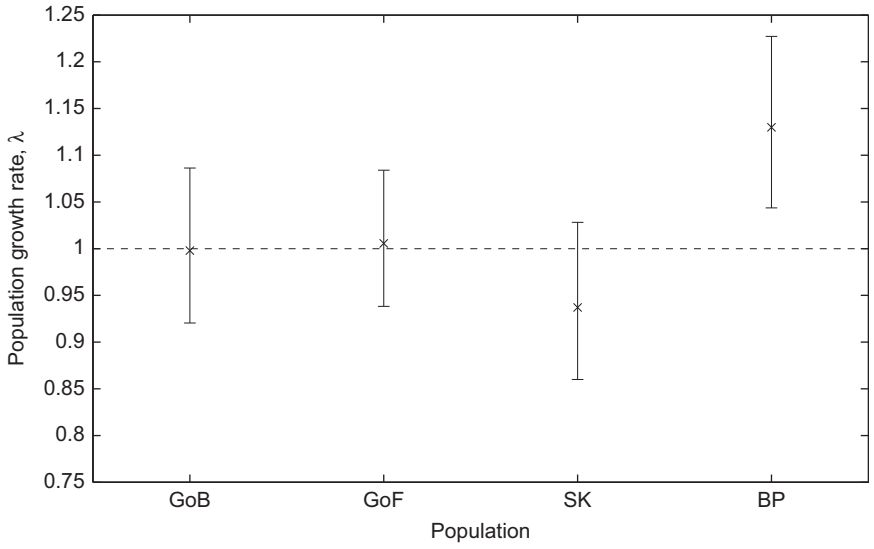

Fig. 5. Intrinsic population growth rates, lambda (λ) for all populations as obtained from the basic Leslie matrix. Error bars represent the 95% CI.

growing tendency. All four sites had similar stable age structures, with the majority of the populations (98%) being comprised of larvae. Meanwhile the reproductive values revealed that individuals in age class 5 in the GoB and BP population and 6 and 3 for the GoF and SK population, respectively, contributed the most to reproduction. Regardless of the different growth rate estimates, elasticity analyses identified survival of the early life stage (larvae and zero-year-olds) as the key vital parameter influencing population growth at all sites (Fig. 6). This means that a change in survival in these age classes impacts λ more than a proportionate change in survival rates of other age classes or fecundity. For example, in the BP site, the elasticity of larvae stage is about 0.26, which means a 10% decrease in survival of larvae will make a 2.6% drop of the population growth rate (1.129 to 1.099). If fecundity of age class one decrease by 10%, this only leads to a 1.3% decrease (1.129 to 1.143).

3.3. Changes to the 'basic model'

3.3.1. Egg stage

As we did not catch any 4-year-old fish in SK, and there was a strong correlation between number of eggs and number of adults in the other age classes ($p < 0.05$), we estimated the number of eggs from 4-year-olds using linear regression. The SK population showed the highest numbers of eggs per age class. Mean egg survival over all ages was 0.656 (SE 0.114) for SK and 0.573 (SE 0.126) for GoF. In the BP populations, the number of eggs from one-year-olds and 2-year-olds was clearly underestimated (as there were more hatched larvae than eggs recorded) and survival was estimated by using the mean from age 3 to 7. This leads to a mean survival rate of 0.865 (SE 0.133). The number of eggs was highly correlated to the number of larvae in BP and GoB ($p < 0.05$) and nearly significant in SK ($p = 0.052$) (Fig. 7). The derivative of s_l with respect to s_e for different sites revealed that the egg stage in the BP site was more influential on the survival of larvae (-0.189) while in SK and GoF the influence was lower (-0.045 and -0.067, respectively).

3.3.2. Individual growth rate and maturity

Growth retardations of young fish (larvae) would lead to maturity being reached at an older age. This would largely influence population dynamics, as exemplified in the BP population. If all one-year-olds are immature (instead of the observed 65% maturity seen for BP) while 100% of the 2-year-olds are mature (instead of the observed 75% being mature) this would lead to a drop in λ from 1.129 to 1.04. If this was to happen in a population with a value of λ closer to a stable population size (that is, $\lambda = 1$), such an effect would obviously have drastic results due to a drop in λ values to slightly below 1.

3.3.3. Density dependence

Adding carrying capacity (K) to the BP population Leslie matrix leads to differences in total population size. The total population size always converges to the carrying capacity (Fig. 8) and hence how large K is has a large influence how the population evolves.

3.4. Including individual-level contamination effects in the Leslie matrix

The decrease in survival of larvae (deducted from the frequency of malformed or dead larvae relative to total brood size) in the reviewed literature ranged from 0.9% (Strand et al., 2004; Table 3) to 71.7% (Gercken et al., 2006; Table 3). Large differences in the rate of increase of reproductive impairment were observed in the literature. Furthermore, no specific trend in the rate of

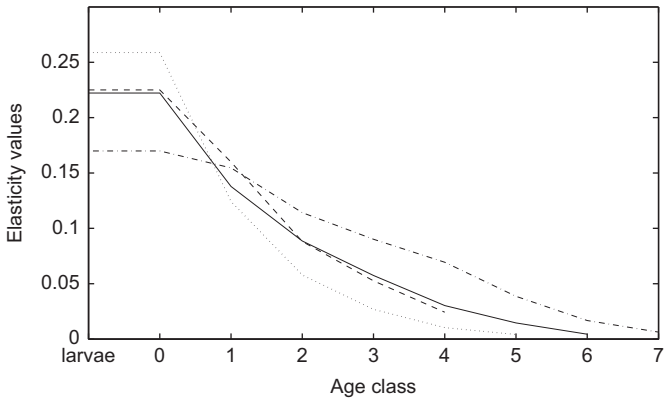

Fig. 6. Elasticity analysis of the Leslie matrix projection showing the relative contribution of the different stages to the population growth rate (λ). Large-dashed line indicates the SK population, small-dashed the BP population, solid-line the GoB population and dashed dot the GoF population.

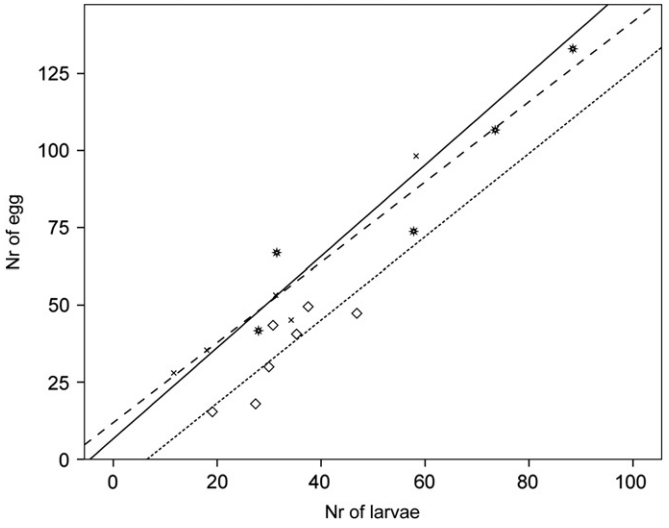

Fig. 7. Mortality between the egg and larvae stage and the associated respective regression lines for each population. Large-dashed line indicated the SK population, small-dashed the BP population and solid-line the GoB population.

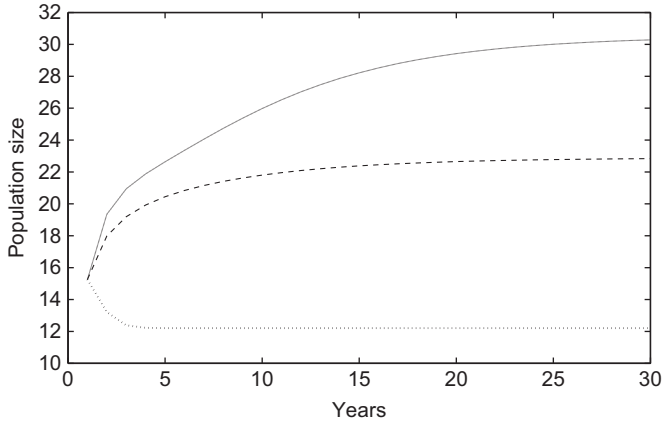

Fig. 8. The effect of carrying capacity (K) on the projection of eelpout population size when exploring the density-dependent Leslie matrix for the BP population. The dotted line refers to $K = 0.8P_0$, the dashed line refers to $K = 1.5P_0$, and the dotted dashed line to $K = 2P_0$. P_0 is the original population size of the BP population. Population size values are scaled for effort.

change in larval survival could be seen in different types of contaminated waters or areas. For the BP eelpout population, which has the highest population growth rate, survival of larvae cannot be reduced more than 39% before λ drops below one. This may appear to be a rather large decrease in larval survival, but such a decrease falls well within the range estimated in the field (Fig. 9 and Table 3). In the GoF population, which has a lower growth rate, only a 3.1% reduction in larval survival is needed to see a drop in λ to below one, a reduction in larval survival which was seen in many of the reviewed studies (Fig. 9 and Table 3). For the GoB and SK populations which already show a decreasing population growth, changing S_l would further increase the rate of extinction rate, with all else being equal.

4. Discussion

4.1. General

This study adds valuable insight into our understanding of the potential ecological effects of hazardous substances in the marine environment, by incorporating data on individual eelpout responses to pollution into a model of natural populations. Survival in early life stages was identified to be the most important factor affecting population growth and persistence in all of the four eelpout populations. By incorporating individual-level pollutant response data, it could therefore be inferred that the documented reproductive impairment due to pollution has serious consequences not only for individuals but also for populations.

4.2. Effects of contaminants on natural eelpout populations

4.2.1. Projected population growth and 'critical values'

That industry effluents and various other contamination sources have a large impact on individuals' health is reasonably well known (Jacobsson et al., 1986, 1992; Jacobsson and Neuman, 1991; Vetemaa et al., 1997; Mattsson et al., 2001; Strand et al., 2004; Fagerholm, 2006; Gercken et al., 2006; Stuer-Lauridsen et al., 2008). Our study shows that contaminations will also affect population growth and persistence. We found that survival of early life stages was most important for eelpout population persistence. The predicted changes in the survival rate of larvae needed for λ dropping below one for our populations fall well

Table 3
Compilation of individual-level responses to pollution (i.e. number of malformed or dead larvae of total brood size) in the reviewed literature used in Fig. 9. Reference, area the study was conducted in, type of study, effect size, type of measurement and description of the area or experiment conducted.

Reference	Area	Study	Effect (%)	Type of measurement	Description area/experiment
Jacobsson et al. (1986)	Kattegatt	Experiment	50	Dead larvae	Pulp mill waste waters at 5% concentrations
Jacobsson et al. (1992)	Kattegatt/	Field	1.4–26	Dead larvae	Near chemical industries, petrochemical and pulp mill effluents Skagerrak
Vetemaa et al. (1997)	Kattegatt	Field	8–9	Dead larvae	Near chemical industries, petrochemical effluents
Strand et al. (2004)	W. Belt	Field	0.9–10.3	Malformed larvae	Near harbors, cities and industries
Gercken et al. (2006)	W. Baltic Sea	Field	50–71.7	Malformed larvae	Inner coastal site, limited exchange of water
Stuer-Lauridsen et al. (2008)	S. Belt	Field	2.1–25.5	Malformed larvae	Several sites with different anthropogenic changes
Gercken. unpublished (2009)	W. Belt	Field	8.6–10.3	Malformed larvae	Inner coastal site and sites near agriculture and outlets with sewage treatment

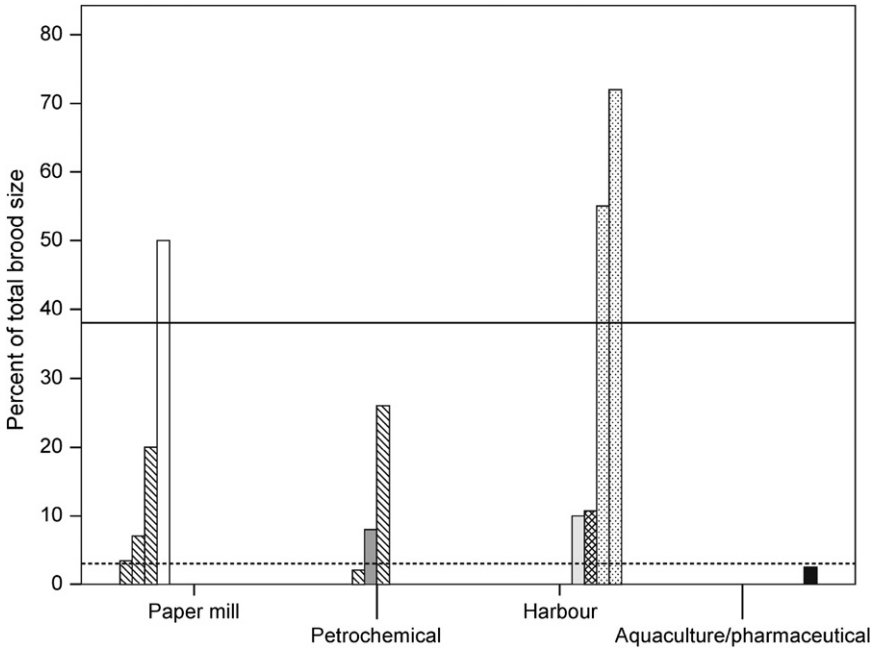

Fig. 9. Summary of studies exploring contaminant effects in individuals. The change in survival of larvae is reported as a percentage of total brood size and is grouped according to anthropogenic change. Colors and patterns of the bars represent the appropriate reference: sidelong crosshatch, Jacobsson et al. (1992) (Kattegat and Skagerrak); white, Jacobsson et al. (1986) (Kattegat); gray, Vetemaa et al.(1997) (Kattegat); light gray, Strand et al. (2004) (Great Belt); checked, Gercken (2009) (unpublished results, W. Baltic Sea); dotted, Gercken et al. (2006) (W. Baltic Sea); black, Stuer-Lauridsen et al. (2008) (Small Belt, Denmark). Lines represent the critical levels leading to a decrease in population size in BP (68% solid) and GoF (3.5% dotted), modeled as reduced survival of larvae.

within the estimated frequencies of malformed or dead larvae reported in waters near petrochemical industries, paper mills, agricultural, cities and aquaculture (Jacobsson et al., 1986, 1992; Sandström et al., 1996; Vetemaa et al., 1997; Strand et al., 2004; Gercken et al., 2006; Stuer-Lauridsen et al., 2008), as well as from laboratory exposure to contaminants (Jacobsson et al., 1986, 1992; Mattsson et al., 2001). The resulting effects on population growth rates depend on the dynamics of the populations. For a population close to stable dynamics ($\lambda \approx 1$), small changes in the larval stage survival may cause severe changes in population growth rate. In populations that are already decreasing in size, such as the SK population, the addition of another negative effect on the survival of larvae from contaminations will further accelerate the extinction rate, assuming other dynamics remains stable. For example, a theoretical population starting at 2000 individuals would show a 50% decrease after 9 years instead of after 11 years. Extinction would thus occur in a much shorter time. Populations will not only decrease due to decreased larval survival above the 'critical level'. Indeed, they will be affected even before lambda drops below one by, for example, resulting changes in the stable age distributions and thus a heightened sensitivity to increased predation. The 'critical levels' are hence just values leading to lambda dropping below one and should not be seen as values that need to be crossed before a negative effect of pollutants on population growth is seen. The stochastic model gave information regarding uncertainty in the population growth estimates. This shows that the 'critical values' are also associated with variance why it should only be seen as a direction of how contaminations may affect populations and not as fixed values for a declining population growth. Further, model simulations show that adding carrying capacity (K) to the Leslie matrix also leads to different patterns, however all depending on what value K was set for. The total population will always converge to the carrying capacity, while the intrinsic growth rate determines how fast the population approaches to the carrying capacity. Since carrying capacity is not known our simulated values of 0.8, 1.5 and 2 times the total original population size of BP only gives an indication how density affects the model and population dynamics. If the purpose of a study is to receive precise estimates of λ values and show a realistic picture of how the population dynamics change with density, true estimate of K is needed.

4.2.2. Individual contaminant response data

The reviewed individual contaminant response data used in this study cover different parts of the Baltic Sea, Skagerrak, Kattegat and Great Belt. The data should therefore accurately reflect the potential effects of pollutants on individuals from the four populations explored in this study. Since much of the response data came from field studies, the effects of pollutants on reproduction could not be directly related to the concentration levels of toxic substances. Petrochemical effluents consist of a range of substances from plant nutrients to persistent organochlorines, with some of the effluents being known to be acutely toxic (Naturvårdsverket, 1992). In the Stenungssund area on the Swedish west coast (the study site explored in Vetemaa et al. (1997)), nonylphenol has been suggested to be one of the risk substances (Jacobsson and Neuman, 1991). There are also other potentially toxic substances in petrochemical effluents, such as different oils, phenols, amines, chlorinated organics and alkylphenol. Pulp mills also release large amounts of complex effluents. However, attempts to introduce more closed systems and the use of non-chlorine bleach have reduced the toxicity of these effluents (Sandström et al., 1997). By relating reproductive impairment due to a variety of sources in the response data, rather than specific concentration levels of some toxic substances, we were better able to simulate how contaminants alter dynamics in natural eelpout populations.

4.2.3. Larval growth inhibition

Larval growth is known to be inhibited at contaminated areas, in addition to acute larval mortality and increased malformation rates (Jacobsson et al., 1986, 1992; Gercken et al., 2006). Many substances, including metals and organic compounds, have also been found to inhibit growth in other fish species (Stein et al., 1995; Hansen et al., 2002). Contamination can therefore indirectly lead to delayed maturation, which in turn serious implications for the asymptotic population growth rate. If this, for example, would happen in the BP population, it would lead to λ dropping from 1.12 to 1.06. Hence, contamination causing growth retardation of larvae will also be reflected by decreased eelpout population growth rates.

4.2.4. Occurrence of atresia

Chemicals have been observed to increase ovarian atresia in other fish species (Ankely et al., 2005; van der Ven et al., 2007). Therefore, although it is not clear whether environmental pollution and toxic substances lead to increased atresia in the eelpout, it was a relevant effect to explore. A decreased survival in the egg stage would ultimately lead to fewer larvae hatching. This will solely affect the number of larvae, and therefore result in a proportional decrease in the number of individuals in the later age classes. Therefore, the effect of atresia only affects the Leslie matrix in terms of a decrease in population size at time t. Survival estimates will therefore remain unchanged (i.e. the slope of change in population size is the same). Importantly, however, the time it takes for a given percentage increase or decrease in population size, would change. This shows that atresia can have potentially large negative consequences and its occurrence in eelpout populations occurring in contaminated waters needs further attention. The egg stage was most influential on population growth rate in the BP population however this comparison assumes the number of eggs and larvae to be constant, which would be unrealistic in the real life.

4.2.5. Possible negative sources

The amount of metals (Hg, Zn, Cd) detected in eelpouts increases with age for individuals occurring in the Baltic Sea. The negative correlation between an eelpout condition measure and the level of metals indicates sub-lethal effects (Voigt, 2007). Cadmium is exchanged between the mother and larvae (Joensen and Korsgaard, 1986). Since metals like cadmium are known to exert toxic effects on fish embryos, e.g. skeletal deformities and reduced hatching and survival rates (Muscatello et al., 2006), sub-lethal effects in the mother would also impact population growth rate. There is evidence that the SK population is in fact affected by contaminants, despite being identified as a clean reference site. Increasing levels of metals (e.g. cadmium and mercury) have been found at the SK site (Naturvårdsverket, 2010). This could explain the negative population growth rate our model predicted. This prediction is supported by catch per unit effort (CPUE) data showing decreasing numbers of fish in this area (Naturvårdsverket, 2010). The decrease in population size was shown to be negatively correlated to increasing water temperatures (Naturvårdsverket, 2010), indicating climatic changes effects eelpout population dynamics. The extent to which unknown contamination sources may also be negatively affecting the populations in this area should also receive more attention.

4.3. Model limitations and reflections

As with most model simulations, there are uncertainties both as a result of the simulation and the model inputs (e.g. fecundity, survival and maturity). However, our model fulfilled the aim of this study. That is to link individual-level responses to population-level consequences. Comparison of the results of the models presented here provides insight into the possible effects of pollution in the natural environment. Density dependence is undoubtedly an important process and in order to evaluate its effect more precisely than a simple logistic function, long term field studies would need to be conducted. Such studies would provide more accurate functions that could describe how individual age classes respond to density dependence. Migration is also not accounted for in this current model and could be predicted to influence simulations and results. However, the eelpout is considered relatively stationary (Schmidt, 1917; Christiansen et al., 1976; Simonsen and Strand, 2010) and it should thus be a realistic assumption. Furthermore, the aim of this model was to evaluate the possible impacts of environmental pollution on eelpout populations, not to provide precise estimates of λ, so low migration rates would be unlikely to greatly affect the conclusions drawn.

When considering the serious consequences of contaminant exposure for fish populations shown in this study, the importance of conducting population model projections becomes even more apparent. Fortunately, interests in the area are increasing, reflected mainly by increasing numbers of laboratory studies exploring exposure and reproductive responses in fish. Recently, Gutjahr-Gobell et al. (2006) found survival have the largest effect on population growth in the cunner (*Tautogolabrus adpersus*) and investigated how estrogen may affect population growth. In addition, Miller and Ankley (2004) conducted a laboratory toxicity test in order to investigate changes in population growth rate of the fathead minnow (*Pimephales promelas*) after exposure to the androgen receptor agonist 17β-trenbolone. They found that large population losses would occur when individuals are continuously exposed to the toxic substance. Other Leslie modeling studies have also been conducted in fish, assessing the impact of toxic substances and pollution on both individuals and populations (Munns et al., 1997; Spromberg and Meador, 2006; Miller et al., 2007; Iwasaki et al., 2010). These studies have revealed how individually measured effects of hazardous substances and contaminants can have substantial negative effects even at the population level.

4.4. Life history characteristics

Our results reveal large variation in eelpout life-history characteristics between the study sites, providing an explanation for the different model projections in the four populations. Absolute fecundity was highest in the SK population, with the highest number of eggs and larvae being found in all age classes. In contrast, mortality between the egg and larval stages did not differ much between sites, suggesting that the external factors influencing egg mortality are similar for all the studied sites. The size of the eggs was not correlated to the age of the females, although eggs from one-year-olds were smaller than eggs from older females in all populations. This is in congruence with the results of Vetemaa (1999), who showed that the smallest females in a Kattegat eelpout population produced the smallest oocytes. The majority of the smallest oocytes were found to be atrethic at the time of ovulation and the few that got fertilized developed into abnormal embryos. Harmful chemicals have been seen to result in increased ovarian atresia in other fish species (Ankley et al., 2005; van der Ven et al., 2007). Therefore, young eelpout females might be more sensitive to contaminants and resulting atresia than older fish due to their smaller eggs. Unfortunately, it was not possible to compare egg sizes among sites, as females from the Baltic Proper were in a later development stage and most of their eggs were therefore already fertilized (and were hence much larger) at the time of sampling.

Individual growth rate was highest in the SK population and all one-year-old females were found to be mature. Furthermore, no individuals older than 6 years have been found since 1994. This corresponds to a typical *r*-selected strategy with early maturation and a lack of older individuals. In contrast, females in the GoB population matured at an older age, had a slower growth rate and were older age classes were also reported. Indeed, the length-at-age in the SK population is the highest reported in any study exploring growth rates in eelpouts. Ojaveer et al. (2004) reported higher eelpout length-at-age in warmer areas of the eastern Baltic than in colder areas. However, length-at-age was still not as high in the areas measured as we found in the SK population. The SK population's length-at-age is also higher than that reported in populations from the Belt Sea and two sites in the southern Baltic Sea (Wiêcaszek, 1998). Our results may suggest that the SK population is exposed to an unstable environment, as it is important to grow fast and reproduce early in such environments. However, further investigations are needed in order to determine whether the observed pattern is due to environmental effects or other factors (e.g. loss of older individuals due to build up of contaminants or bycatch). Addressing the question of environmental instability is especially pertinent in the SK population which is already declining in size.

5. Conclusions

We were able to extrapolate eelpout population growth rates after exposure to contaminants by incorporating data on individual-level reproductive impairment into a mathematical model. Our results show that survival of larvae and juvenile fish was the most influential factor for population growth rate in all populations, despite differences between populations in life-history traits and local dynamics. Therefore, impaired reproductive capacity in individuals due to contaminant exposure has serious consequences even at the population level. The negative evolutionary consequences of contaminants may be even greater when combined with natural climate and stochastic changes, possibly leading to extinction. For example, climate changes in water temperature may hasten the rate of decline of eelpout populations. This is because the eelpout is a cold water species and increased temperatures may affect eelpout reproduction (Vetemaa, 1999). This prediction is further supported by observations of reduced survival of larger eelpout in shallow areas during warm summers (Pörtner, 2001).

ICES/OSPAR's assessment criteria recommend a threshold value of 2% malformation in larvae (ICES, 2007). If we translate such a 2% change in malformation to a reduction in larval survival of 2% in our BP model, we see a 0.5% drop in λ. In a population with a high λ, such as the BP population, a 0.5% reduction in λ would have a minimal effect on population size and growth rate. However, if populations are close to a stable population size ($\lambda \approx 1$), even slight changes in survival at the vulnerable larvae stage may lead to λ dropping below one and thus have a large influence on the population. Thus, even though a threshold value of 2% malformation may seem low, an effect of this size could have serious consequences at the population level. Although setting a fixed threshold might be relevant for environmental monitoring, one has to be aware of differences in outcomes and effect sizes at the population level.

More research into contaminant effects at the population level is sorely needed in order to better protect aquatic populations

from environmental pollution. Due to the complexity of natural environments, we recommend that the response data incorporated into the population model is broad and represents both controlled laboratory experiment and field studies, preferably in different environments. Through adopting this approach, a better understanding of the effects of contaminants on natural populations will be gained.

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Appendix A. Supplementary material

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.ecoenv.2012.01.019.

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