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Habitat quality and fish populations: impacts of nutrient enrichment on the value of European perch off the east coast of Sweden

Abstract

Degradation of marine ecosystems through, e.g., eutrophication and climate change is a concern for sustainable fishery management worldwide, but studies on associated impacts on fish populations are rare. This study examines the effects of eutrophying nutrient loads on the economic value of perch populations along the Swedish east coast by estimating the effects of nutrient loads on the population of perch and, then, simulates the harvest value of future perch population under the changes in nutrient loads. A modified Gordon-Schaefer logistic growth model was used for econometric estimation of perch populations based on annual time series data for the period of 1970-2014. Regression analysis using the fully modified ordinary least square (FMOLS) estimator revealed that phosphorus loads had significant effects on the perch population. A 40% decrease in phosphorus loads, as suggested by the international HELCOM agreement, could increase the steady state perch population by 50%. Simple calculations showed that this could increase the total discounted recreational and commercial harvest value of the perch by 30% over a 30 year period.

Keywords: nutrient loads, harvest value, perch populations, fishery management, logistic growth model, estimation, eutrophication, Swedish east coast.

JEL Classification: Q22, Q53, Q57.

Introduction

Fishery is an important activity in the Baltic Sea region in terms of income generation, food supply, tourism, and recreational services. However, changes in marine ecosystems such as rising nutrient loads, overfishing, climate change, and predation are now jeopardizing the sustainable future of marine biodiversity, and of fish species in the Baltic Sea region (Anne et al., 2012; Engström, 2001; Larsson et al., 2015; Moyle and Leidy, 1992; Rice and Garcia, 2011). As an integral part of the Baltic Sea aquatic environment, the east coast of Sweden has experienced ecological changes arising from nutrient loading, overfishing and other socio-economic activities. For instance, a significant amount of nutrient loading occurred between 1970 and 2014 (HELCOM, 2015, Svendsen et al., 2013). This has led to an increase in filamentous algae, disappearance of perennial furoid algae, increased frequency of toxic algal blooms, and reductions in fish populations in the marine system (SwAM, 2013). It is also claimed that an increase in sea temperature as a result of climate warming can cause major changes to the physical and chemical properties of the water, which may impact marine species such as fish, invertebrates, and plants in the aquatic system (Roessig et al., 2004; McGinn,

2002). There has already been a rise in mean annual sea temperature in the Baltic Sea region over the past few decades (EEA, 2015; Böhling et al., 1991; Karas, 1996).

Economic evaluation of the impacts of these changes on fish populations requires quantification of their effect on the dynamics of fish populations, based on which associated economic effects can be estimated. This production function approach to assessing impacts on coastal waters has been developed within the literature on coastal habitat quality and its role for provision of ecosystem services (e.g., Barbier, 2007, 2013). It considers habitat quality as an input to production of provisioning services, such as fish for food and feed, and the estimated effects of factors affecting habitat quality are taken to indicate the associated impacts on ecosystem services. However, despite recognition of the different pressures on fish populations, most studies investigate the effects of only one of these, such as eutrophication (e.g., Vitousek et al., 1997; Schmidt et al., 2012; Bergström et al., 2013). There is a relatively large body of literature on the impacts of climate change on fish populations in freshwater systems (e.g., Sharma et al., 2007; Hobday and Lough, 2011), but corresponding studies on large-scale brackish water bodies, such as the Baltic Sea off the east coast of Sweden, are lacking.

The main aim of this study was, thus, to estimate the effects of nutrient loads to the Baltic Sea on the value of populations of European perch (*Perca fluviatilis*) off the east coast of Sweden, while also considering other factors such as pressures from commercial and recreational fishery, predation on perch by cormorants, and sea temperature. Predation

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by cormorants can be substantial in the area, corresponding in volume to removal by commercial and recreational fishing combined (e.g., Boström et al., 2012). The explanatory power of the different variables was estimated by means of econometric tools applied to time series data. A common approach in fishery economics is application of a logistic growth function (Schaefer, 1954; Prager, 2002; Kataria, 2007). Latent fish population variables are, then, usually estimated using data on harvest and fishing effort (e.g., Kataria, 2007). Similarly to many other fish species, European perch is subject to both commercial and recreational harvesting, but data on fishing effort are only available for commercial harvesting units such as fishing boats and fishermen. We, therefore, needed to construct a model that accounted for these two harvesting pressures, but based on effort data only for the commercial form. The model we constructed is one novel contribution of this study. The other is assessment of the effects of nutrient loads in sea water on the value of European perch populations by means of econometric tools applied to time series data, which to the best of our knowledge has not been performed previously for any region or fish species.

The remainder of this paper is organized as follows. First, we present the fish population model and associated derivation of the econometric regression equation. We, then, describe the data, followed by a presentation of the results. The paper ends with a brief summary and some conclusions.

1. Derivation of regression equations

Much of the early literature on estimation of fish population growth rates assumes that the change in the total stock over a given period depends solely on the natural growth and total harvest (Schaefer, 1954; Kataria, 2007). Later studies also consider habitat quality characteristics, such as weather conditions and landscape elements, as applied, e.g., to mammal populations (e.g., Gren et al., 2016).

A well-known problem when estimating the effects of any exogenous factor on fish populations is the lack of data on population levels. A common approach for circumventing this problem is to use catch per unit effort (CPUE) as a proxy for relative population abundance (e.g., Arreguín-Sánchez, 1996). Such a construct was also used in the present study, where the point of departure for derivation of regression equations was the commonly used logistic growth function (Schaefer, 1954; Kataria, 2007). It takes the form:

$$\frac{dP_t}{dt} = rP_t \left(1 - \frac{P_t}{K} \right) - H_t^C - H_t^R + \sum_j a^j M_t^j \quad (1)$$

$$P_0 = \bar{P},$$

where P_t is population of perch at time t , r is the intrinsic growth rate, K is the maximum carrying capacity, and H_t^R and H_t^C denote recreational and commercial harvest, respectively. The intrinsic growth rate reflects the possible growth rate under ideal conditions, and K the associated carrying capacity. The variables M_t^j denote the habitat quality parameters $j=1, \dots, n$, and \bar{P} is the given population level at $t=0$.

The regression estimates are based on relative changes in the population growth. We, therefore, divided the left-hand and right-hand sides of equation (1) by P_t , giving:

$$\frac{\frac{dP_t}{dt}}{P_t} = r \left(1 - \frac{P_t}{K} \right) - \frac{H_t^C}{P_t} - \frac{H_t^R}{P_t} + \frac{\sum_j a^j M_t^j}{P_t} \quad (2)$$

Measurement of CPUE requires data on harvest and effort, but data on effort are only available for commercial harvest. The associated construct denoted by S_t was written as:

$$S_t \equiv \beta P_t = \frac{H_t^C}{E_t}, \quad (3)$$

where β is the catchability coefficient, and E_t is the effort level. Rearranging (3), $P_t = \frac{S_t}{\beta}$, inserting this into equation (2) gives:

$$\frac{\frac{dS_t}{dt}}{S_t} = r \frac{r}{\beta K} S_t - \beta E_t + \frac{H_t^R}{S_t} + \frac{\sum_j \beta a^j M_t^j}{S_t} \quad (4)$$

Equation (4) provides the basis for the regression equation used for estimating intrinsic growth rate and the impact of ecosystem characteristics as:

$$Y_t = \theta^1 - \theta^2 S_t - \theta^3 \left(E_t + \frac{H_t^R}{S_t} \right) + \sum_{j=1}^n \lambda^j \frac{M_t^j}{S_t} + \varepsilon_t, \quad (5)$$

where ε_t is the error term. The corresponding coefficients in equation (5) in relation to equation (4) are:

$$Y_t = \frac{dS_t}{S_t}, \theta^1 = r, \theta^2 = \frac{r}{\alpha K}, \theta^3 = \beta, \lambda^j = \beta a^j \text{ for } j=1, \dots, n \quad (6)$$

Thus, from equation (6), the intrinsic growth rate, the catchability coefficient, the carrying capacity, $K = \frac{r}{\theta^2 \theta^3}$, and the impacts of habitat quality characteristics can be estimated.

It is assumed in the above that habitat quality characteristics have a linear direct impact on the population growth rate, but they can also affect the intrinsic growth rate r and thereby have an indirect effect on the growth rate. The intrinsic growth rate is the growth rate, which determines the maximum population in ideal conditions in the absence of any limiting pressure such as commercial or recreational harvest, predation or competition for food with other species. Disturbances in habitat conditions are regarded as pressures in equations (1) to (6). On the other hand, habitat quality attributes can be regarded as variables determining the intrinsic growth rate and maximum viable population of fish species, and, hence, enter equation (1) as exogenous variables. Assuming that the intrinsic growth rate shows a linear dependence on habitat characteristics, $r_t = b + \sum_j d^j M_t^j$, equation (1) is modified to:

$$\frac{dP_t}{dt} = \left(b + \sum_{j=1}^n d^j M_t^j \right) P_t \left(1 - \frac{P_t}{K} \right) - H_t^C - H_t^R. \quad (1')$$

Based on the same assumption and steps as in derivation of the direct effect model, the indirect effect model gives the logistic function:

$$\frac{dS}{dt} = b - \frac{1}{\beta K} S_t - \beta \left(E_t + \frac{H_t^R}{S_t} \right) + \sum_{j=1}^n d^j M_t^j \quad (4')$$

and the associated regression equation is:

$$Y_t = \gamma^1 + \gamma^2 S_t + \gamma^3 E_t + \frac{H_t^R}{S_t} + \sum_{j=1}^n v^j M_t^j + \varepsilon_t^{ID}, \quad (5')$$

where the dependent variable, Y_t , is defined in the same way as in the direct effect model specification, ε_t^{ID} is the error term, and the other parameters are related to the logistic model in equation (4') as:

$$\gamma^1 = b, \gamma^2 = \frac{r}{\beta K}, \gamma^3 = \beta, v^j = d^j \text{ for } j=1, \dots, n, \quad (6')$$

where $r_t = \gamma^1 + \sum_{j=1}^n v^j M_t^j$ and the carrying capacity is calculated as $K_t = \frac{\gamma^1 + \sum_{j=1}^n v^j M_t^j}{\gamma^2 \gamma^3}$.

The differences between the direct and indirect effect model specification appear in the estimates of the parameters, intrinsic growth rate, and the calculated carrying capacity. In the direct effect model, both parameters are constant over time, whereas they vary over time with changes in habitat characteristics in the indirect effect model. Since we had no prior information on which of these models best describes perch population dynamics, we tested both specifications.

2. Description of data

In order to determine perch population dynamics using the models, time series data were needed on commercial and recreational harvests, effort for commercial harvest, nutrient loads to seas and other habitat quality variables. Time series data on commercial catches of perch off the east coast of Sweden are available for the period 1970-2014 (in Annual Fishery Statistics for the period 1970-1992 and in Swedish Statistics (2015) and Swedish Agency for Marine and Water Management (2015) for the period 1993-2014). Since there are no official data on recreational harvest, we used data for the period 1970-2009 constructed by Zeller et al. (2011) and extrapolated these data to 2010-2014. Figure 1 shows the compiled data on annual commercial and recreational harvest of European perch off the east coast of Sweden.

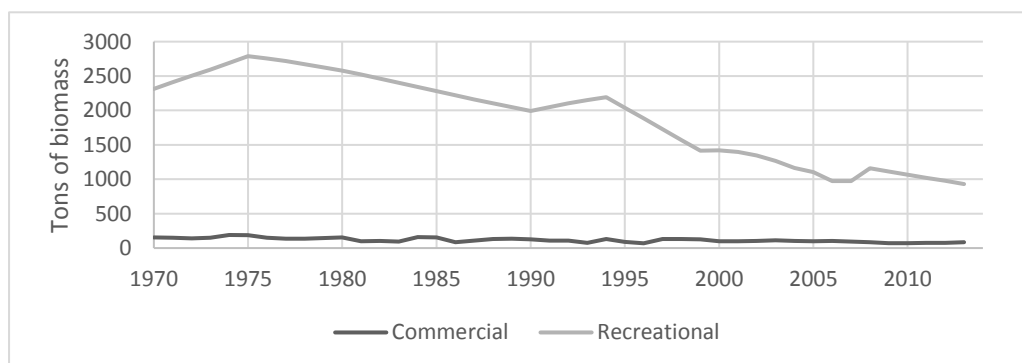


Fig. 1. Commercial and recreational harvest (tons) of perch off the east coast of Sweden, 1970-2014

As shown in Figure 1, commercial harvest of perch was relatively low compared with recreational harvest, but remained relatively constant between 1970 and 2014. In contrast, the constructed data for recreational harvest showed an average annual decline of 2%, or 60% in total, over the period.

The standard way of calculating fishing effort requires data on the numbers and types of fishing vessels or boats and fishing days (Foley et al., 2010). However, such data are not available for recreational fishery and, therefore, we used the total number of private fishing boats registered as a proxy variable for fishing effort (Transportstyrelsen, 2015). The number of recreational fishing vessels registered decreased steadily, from 2100 to 495, over the entire 1970-2014 period. This decrease was larger than that in

commercial harvest vessels and the growth rate in CPUE was positive over the period.

Data on nutrient loads are available for the seven marine basins in the Baltic Sea and for the entire Baltic Sea. However, nutrient loads into any of the seven Baltic basins are dispersed in the entire sea because of streams and other oceanographic conditions (e.g., Savchuk and Wulff, 2009). Therefore, we tested the impact of two alternative nutrient load variables; one on nutrient loads to the Baltic Proper (BP) marine basin, off the Swedish east coast, and the other on nutrient loads to the entire Baltic Sea (Baltic Nest Institute 2015; HELCOM, 2015). The loads of nitrogen and phosphorus to the entire Baltic Sea decreased on average by 1% per year between 1970 and 2014, whereas those to the Baltic Proper decreased by 2% in the same period (Figure 2).

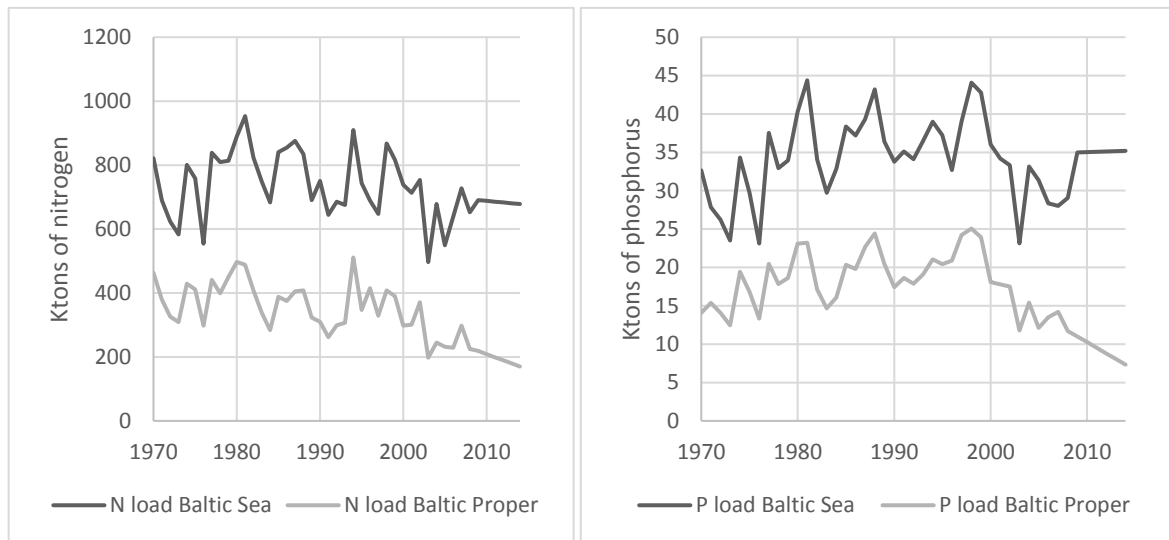


Fig. 2. Loads (kttons) of (left) nitrogen (N) and (right) phosphorus (P) to the Baltic Sea and the Baltic Proper, 1970-2014

In addition to nutrient loads, we included number of cormorants and sea bottom temperature as constructs of habitat quality characteristics. As mentioned earlier, cormorants feed extensively on fish and the sea bottom temperature affects fish population growth. Data on mean annual sea

bottom temperature ($^{\circ}\text{C}$) off the east coast of Sweden were obtained from Havsmiljöinstitutet (2015) and data on cormorant populations were compiled from Swedish Environmental Protection Agency (2013). Descriptive statistics of all variables included in the models are presented in Table 1.

Table 1. Descriptive statistics used in models, observations=45

Variables	Description	Mean	Std. Dev.	Min	Max
H^C	Perch, commercial landing per year on east coast of Sweden (ton/year)	112	25.16	69	197
H^R	Perch, recreational harvest per year on east coast of Sweden (ton/year)	1886.5	634.4	975	2789
E	Total number of commercial fishing boats per year on east coast of Sweden (x100)	11.11	6.31	4.41	21.25
N_{bs}	Nitrogen load per year to Baltic Sea (10^3 ton/year)	739.61	10.29	496.6	953.2
P_{bs}	Phosphorus load per year to Baltic Sea (10^3 ton/year)	34.42	5.31	23.11	44.43
N_{bp}	Nitrogen load per year to Baltic Proper (10^3 ton/year)	353.15	76.52	198.4	511.3
P_{bp}	Phosphorus load per year to Baltic Proper (10^3 ton/year)	18.23	3.61	11.73	25.13
$Temp_{bottom}$	Mean annual sea bottom temperature on east coast of Sweden ($^{\circ}\text{C}$)	5.87	0.96	4.8	7.8
$Cormorant$	Total number of cormorants on east coast of Sweden (10^3)	1.43	1.56	0.02	4.38

3. Econometric method and results

3.1. Method. It may take a certain time before nutrient loads to seas result in effects on perch populations and, therefore, we included a lagged form for each of the nutrient load variables presented in Table 1. Regarding the estimation procedure, Stock and Watson (2012) suggest that an ordinary least square (OLS) estimator can be best, linear, unbiased, and efficient (BLUE) if the series fulfils the stationarity requirement. However, as most economic time series datasets are non-stationary with varying statistical properties over time, it is vital to check whether the variables used in the model have unit root or not. Otherwise, the estimator provides spurious regression results and violates the asymptotic properties of the OLS regression, even if it provides unbiased and consistent results (Wooldridge, 2012). Moreover, the potential presence of serial correlation and heteroscedasticity in the error term makes the OLS estimator inefficient, but still unbiased and consistent (Giles, 2007; Phillips, 1986). Therefore, it is important to begin the estimation process by checking the stationarity of the regressors from equations (5) and (5') using the augmented Dickey-Fuller test³.

In the present case, the test statistics failed to reject the null hypothesis for most variables, showing the presence of unit root (Table A1), which implies that the variables are non-stationary and that the OLS estimator cannot give efficient estimates. This requires the OLS estimator to be diagnosed for serial correlation and heteroscedasticity in the error term, as it will govern the final decision on whether to accept or reject the OLS estimator as a BLUE estimate. In the present case, the Breusch-Godfrey test for serial correlation rejected the null hypothesis for equations (5) and (5'), indicating absence of serial correlation in the error term (Table A1).

Despite absence of serial correlation, it is vital to check whether the variance in the standard error is constant over time, which was done here using the Breusch-Pagan test for heteroscedasticity. The test statistics rejected the null hypothesis for both the direct and indirect effect models, which indicates the presence of heteroscedasticity (Table A2). Therefore, the OLS estimates produced could not be BLUE, as they violated the asymptotic requirement on the OLS estimator. In order to address the issue of unit root in OLS regressors and the related problem of serial correlation and heteroscedasticity

in the stochastic error term, an alternative robust estimator, fully modified ordinary least square (FMOLS), was implemented. This estimator uses the OLS estimate, but corrects the standard error for arbitrary forms of serial correlation and heteroscedasticity (Davidson and MacKinnon, 1993). In addition, FMOLS accounts for endogeneity in the regression model (Inder, 1993; Phillips, 1995; Vogelsang and Wagner, 2014).

3.2. Results. The regression results for the direct and indirect effect models, as specified in equation (5) and (5'), respectively, are presented in Table 2.

The coefficients S and $E+H^R/S$ had negative values, as expected, but the latter was significant only in the direct effect model. Both models provided significant estimates of the constants, although the value was negative for the indirect effect model. This shows consistency of the intrinsic growth rate value produced by the direct effect model, which amounted to 0.33. This seems to be adequate, considering that the perch population can double within 1.5-4.5 years (Rowiński et al., 2015). The intrinsic growth rate in the indirect effect model depended on the level of the explanatory variables included in equations (4) and (4'). When evaluated at the mean of these variables it amounted to 0.30, which is quite close to the intrinsic growth rate value in the direct effect model (Table 2). However, since the direct effect model gave a better fit, as measured by R^2 and F-statistics, we only discuss the results from that model in the following.

With respect to nutrient loads, only phosphorus loads gave significant estimates. This is in line with previous results showing that phosphorus is the limiting nutrient for biological production in the Baltic Proper (e.g., Savchuk and Wulff, 2009). A reduction in phosphorus load to the Baltic Proper of 10000 tons, which represented a decrease of 55% compared with the average total level, gave an increase in perch population growth of 0.091 at the average level of S (which was 12.92), while holding other factors constant. There was also a positive effect on the population from *Temp_bottom*, which is supported by the evidence that a rise in the temperature along the Baltic Sea has a beneficial effect on growth rates of fish species of freshwater origin, such as perch and pike perch (Mackenzie et al., 2007; Ložys, 2004; Lappalainen et al., 2000). It is also well known that the pressure exerted by cormorants on fish stocks is substantial, with the volume extracted corresponding to that landed in harvest and recreational fishery combined (e.g., Boström et al., 2012). The estimated effect on perch growth rate of marginal increases in temperature and predation by cormorants was 0.098 and -0.133, respectively.

³The null hypothesis is that the variable contains a unit root, and the alternative is that the variable was generated by a stationary process.

Table 2. Fully modified ordinary least square (FMOLS) estimates of growth function for perch populations off the east coast of Sweden. For abbreviations, see Table 1

Variables	Model 1: Direct effect model		Model 2: Indirect effect model	
	Coefficient	Std. Error	Coefficient	Std. Error
Constant	0.330*	(0.016)	-1.598***	(0.000)
S	-0.006	(0.230)	-0.007	(0.102)
E+H ^R /S	-0.002***	(0.000)	-6.E-05	(0.798)
N_bp/S	0.0119	(0.575)		
N_bp			0.003	(0.164)
P_bp/S	-1.174**	(0.008)		
P_bp			-0.104*	(0.015)
lagN_bp/S	-0.003	(0.108)		
lagN_bp			-0.004	(0.057)
lagP_bp/S	-0.038	(0.348)		
lagP_bp			-0.072	(0.096)
Temp_bottom/S	1.259***	(0.000)		
Temp_bottom			0.421***	(0.000)
Cormorant/S	-1.714***	(0.000)		
Cormorant			-0.264***	(0.000)
Observations	42		42	
R-squared	0.27		0.11	
Long run SE	0.043		0.045	
F-statistics	86.13***		84.23***	
Bandwidth(neweywest)	13.323		13.165	

***p<0.01, **p<0.05, *p<0.1

4. Predicted perch population and value under different phosphorus load scenarios

In order to predict populations based on equation (1), we needed to calculate initial population level and the carrying capacity, as shown by equation (6), and the net pressure on the population. The population size in 2014 at the levels of H^C and E in this year (99 and 4.95, respectively) amounted to 10000. Similarly, we calculated the carrying capacity, K , as 27 500. Unfortunately, it is difficult to compare our results with those from other studies, since estimates are lacking for European perch populations off the east coast of Sweden. However, calculations of populations of cod, sprat, and herring in the entire Baltic Sea

indicate a factor relating commercial harvest and population biomass of between approximately 4 and 15 (Sparholt, 1994). Our results showed a factor of 10 for the year 2014, which is within this range.

The net pressure on the population is given by the sum of marginal effects of $Temp_bottom$, $Cormorant$, P loads, and $E+H^R/S$. When evaluated using the 2014 figures, this gave a net pressure of -0.12 ($Temp_bottom$ 0.56, $Cormorant$ -0.20, P load -0.18, $E+H^R/S$ -0.31). This allowed us to compare future development of the population at an unchanged P load level and following a development path, where P load is reduced by 40%, as suggested by the latest intergovernmental agreement on nutrient loads to the Baltic Sea (HELCOM, 2013).

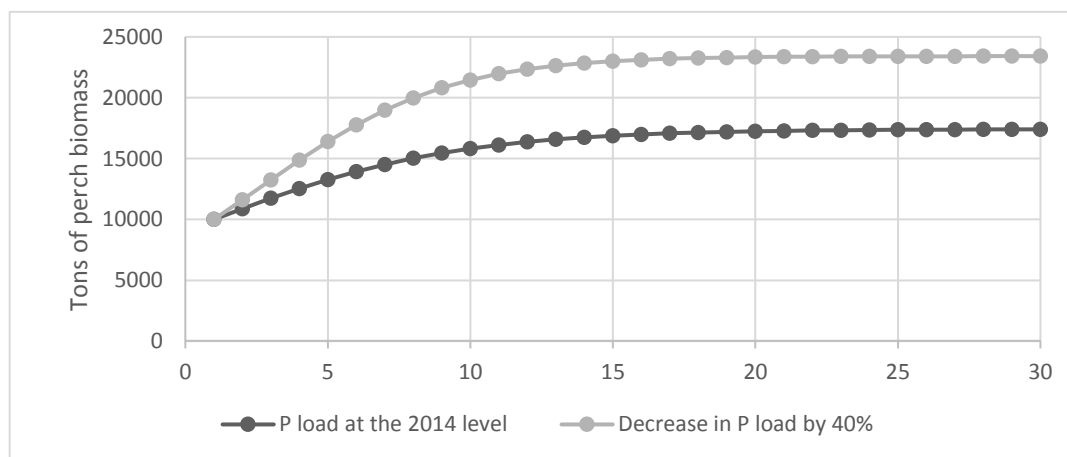


Fig. 3. Predicted development in perch population (ton biomass) off the east coast of Sweden in different phosphorus (P) load scenarios

As can be seen in Figure 3, an unchanged load of approximately 21000 ton phosphorus to the Baltic Proper would result in steady state perch population level of 17500 ton. A reduction in *P* load of 40% would increase the steady state level to 24000 tons of European perch. In both cases, the steady state level would be reached within 15 years.

The economic value of this decrease in *P* load depends on the net unit value of perch, adjustments in fishery harvests to match the changes in the perch population, and the discount rate. The net unit value of commercial and recreational harvest is likely to differ. Unfortunately, there are no data available on the net income from perch for recreational fishing. However, one previous study has estimated the value of recreational fishery of perch in the Stockholm archipelago at the east coast of Sweden (Söderqvist et al., 2005). Those authors applied the travel cost method and estimated willingness to pay (WTP) for perch, pike, pike perch, sea trout, and herring. The estimated marginal WTP for perch amounted to SEK 88/kg (in 2014 prices when 1 Euro = 8.83 SEK). From the descriptive statistics in Table 1, it can be seen that harvest in recreational fishery accounts for 94% of total harvest, and, therefore, we assigned a value of 88 SEK/kg to all harvests.

Changes in population are most likely to result in changes in harvesting practices, which can be calculated by means of a numerical dynamic optimization model. Furthermore, the optimal level of harvest will depend on the discount rate. In order to get some information on the order of magnitude

with respect to impacts of different phosphorus loads in monetary terms, we made the simplifying assumption that the average harvest pressure of 0.2 of the population would remain unchanged. We, then, calculated the associated value of the population increases over a 30-year period under two different discount rates, 0.015 and 0.03, and two phosphorous scenarios, unchanged load and reduction by 40% in 2014. Admittedly, such a drastic load reduction in one year is unrealistic in practice, but it gives some information on the maximum value of the perch population if it had occurred.

Table 3. Predicted total discounted values of perch populations for a period of 30 years from 2014 at two different discount rates, *r*, and phosphorus load scenarios, million SEK

	Unchanged phosphorus loads at 2014 level	Decrease in phosphorus load in 2014 by 40%
<i>r</i> =0.015	6593	8674
<i>r</i> =0.030	5296	6931

For both discount rates, the total value over a 30 year period when there is a decrease in phosphorus loads is approximately 31% larger than without the decrease. The total economic value of the phosphorus decrease, then, amounted to 2081 and 1635 million SEK when the discount rate is 0.015 and 0.03, respectively.

The developments of the economic value of the phosphorus reduction over time arising from an increase in catch owing to increased perch populations are shown in Figure 4.

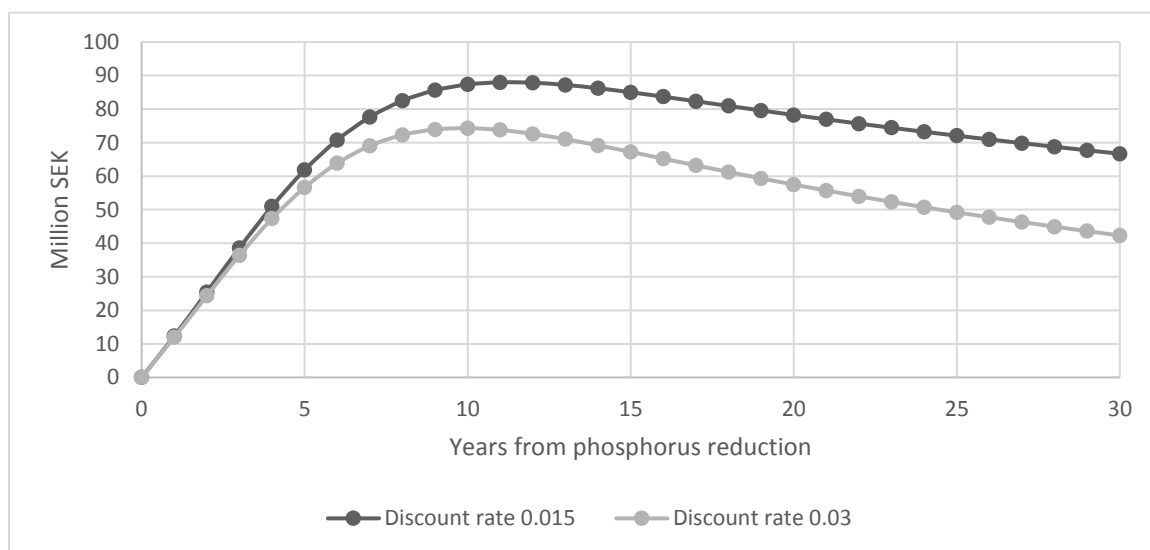


Fig. 4. Predicted annual value (million SEK) of the increase in the perch population off the east coast of Sweden over time following a 40% reduction in phosphorus loads to the Baltic Proper, calculated using two different discount rates (0.015 and 0.03)

Under both discount rates, the value increased until the steady state level of the population was reached. The harvest was unchanged, but the

difference between harvests with and without the phosphorus reduction decreased because of the discount rate. However, it is likely that the harvest

increases as a response to the increased population when phosphorus load decreases, which would increase the values presented in Figure 4.

Discussion and conclusions

This study examined the effects of nutrient loads on the growth rate in European perch populations off the east coast of Sweden. Other pressures in terms of commercial and recreational harvest, predations by cormorants, and temperature were also accounted for. A relatively simple logistic population growth function was assumed, by means of which two alternative regression functions were derived depending on assumption of the impacts of habitat characteristics. One assumption was that there are direct impacts on population growth (direct effect model), and the other was that the characteristics affect the intrinsic growth rate (indirect effect model). Since the estimation procedure relied on time series data ranging from 1970 to 2014, we considered the stationarity of the variables and found that all the explanatory variables had a unit root. Therefore, we used an FMOLS estimator, as it gives more robust parameter estimates than the usual OLS estimator.

We found the direct effect model to be more robust in explaining the dynamics of perch populations, as it satisfied most of the statistical requirements. Among the estimates produced using this model, those for fishing effort, phosphorus load, bottom sea level temperature, and number of cormorants were statistically significant in determining the growth rate of the perch population. The estimated intrinsic growth rate was 0.33, which represents the growth in the perch population under ideal conditions. The results also indicated that phosphorus loads reduce the growth of the perch population by an amount corresponding to that of predation by cormorants in 2014. On the other hand, a rise in the sea bottom sea temperature proved to have a positive effect on the growth rate of the perch population.

We used the estimated perch population model to simulate future populations under two alternative

phosphorus load scenarios: unchanged at the 2014 level and a 40% reduction, as suggested by the HELCOM agreement in 2013. The results showed that the steady state population would have increased by approximately 40% if the HELCOM agreement had been implemented in 2014. Under simplified assumptions on harvesting behavior among fishers and unit value of perch, this increase in population raised the discounted harvest value by approximately 30%, or 2080 million SEK, over a 30 year period at a discount rate of 0.015. This increase in value corresponds to 0.05% of GDP in 2014. However, the assumption of implementing the phosphorus decrease in 2014 is not realistic, and the estimated value will, then, be lower. Another factor affecting the value is the pressure (recreational and commercial harvest, predation by cormorants, and effects of temperature) on the population, which was assumed to stay unchanged at the 2014 level. The value is reduced if these pressures are increased, and the future population can, then, be below the level in 2014.

Admittedly, our estimates rely on the assumption of a logistic growth function, which has been criticized because of the neglect of composition of population cohorts, proportional relation between population growth and pressure intensity, and disregard of stochastic shocks to the population (e.g., Clark, 1990). Choices of other functions, such as age-structured models, might give other predictions of population developments. Lack of long term time series data on biological parameters such as reproduction and survival rates for different cohorts makes it difficult to estimate such functions. Nevertheless, our estimates of the intrinsic growth rate of European perch population are in the same order of magnitude as estimates from other models.

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Appendix

**Table A1. Results of the augmented Dickey-Fuller unit root test for the regression variables.
CV = confidence level**

Variable	Obs. (N)	Test statistic	1% CV	5% CV	10% CV	p-value
Y _t	37	-2.416	-3.668	-2.966	-2.616	0.137
E+HR ² /S	44	-1.306	-3.621	-2.947	-2.607	0.627
H ^c	44	-2.810	-3.621	-2.947	-2.607	0.057
HR	44	0.675	-3.621	-2.947	-2.607	0.989
BoatC	44	-1.306	-3.621	-2.947	-2.607	0.627
N _{bp}	44	-0.890	-2.630	-1.950	-1.608	0.379
P _{bp}	44	-0.205	-2.630	-1.950	-1.608	0.838
Temp _{bottom}	44	5.331	-3.621	-2.947	-2.607	1.000
Cormorant	44	1.241	-3.621	-2.947	-2.607	0.996

Table A2. Results of the Breusch-Godfrey test for serial correlation

Model	lags(p)	Chi-Square Stat(ch2)	Degrees of freedom	Prob > Chi2
Direct	10	25.037	10	0.0053
Indirect	10	25.562	10	0.0044