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Reproductive rate of a top predator, the grey seal, as an indicator of the changes in the Baltic food web

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ABSTRACT

Reproductive rate of grey seal (*Halichoerus grypus*) females has fluctuated during the 2000s, although reproductive disturbances, which occurred earlier, are rare at present. Here we aimed to study especially the food web factors possibly affecting the birth rate of Baltic grey seals and whether birth rate can be used as an indicator of the changes in the Baltic food web. Our results showed that the birth rate of grey seals was significantly related to herring (*Clupea harengus membras*) and sprat (*Sprattus sprattus*) quality (weight) which, in turn were influenced by sprat and cod (*Gadus morhua*) abundance, as well as zooplankton biomass and plankter size. This suggests strong trophic coupling over three trophic levels. We thus conclude that the birth rate of grey seals can be used as an indicator of the status of the Baltic food web. Based on this, we suggest a threshold value for good food web status for a stable, non-growing seal population.

1. Introduction

Reproductive rate of mammals is usually affected by their body condition, as reproduction is energy-demanding and the costs of reproduction are too high for individuals in poor condition (e.g. Clutton-Brock et al., 1982; Boyd et al., 1995; McMahon and Hindell, 2003). Capital breeders, such as the grey seal (*Halichoerus grypus*) mainly rely on their stored energy reserves during reproduction and nursing (Boyd, 2000). In seals, body condition affects the timing of puberty, implantation of embryos and mortality rates of embryos/fetuses and thus the reproductive rate of females (e.g. Boyd, 1984a; Guinet et al., 1998; Bowen et al., 2006; Proffit et al., 2007; Kauhala et al., 2017). Body condition (nutritional status), and thus also reproductive rate, may be affected by environmental conditions, such as the quality, quantity or availability of food resources (Lunn et al., 1994; Crocker et al., 2006; Biuw et al., 2007; Schick et al., 2013). Hence, reproductive rate of Baltic grey seals could be used as an indicator of changes in the Baltic food web, such as the quality or quantity of their main prey (Kershner et al., 2011, HELCOM, 2018a). Their body condition and birth rate has indeed found to be related to changes in the quality of their preferred prey fish, herring (*Clupea harengus*) (Kauhala et al., 2016, 2017).

The grey seal is one of the four marine mammal species in the Baltic Sea and today the most numerous of them. It has been hunted since the Stone Age, at least in the southern Baltic (Härkönen et al., 2007), but the population crashed from about 100 000 in the beginning of the 20th century to only 2000–3000 in the 1970s, mainly due to the high hunting pressure (Jensen et al., 1969; Almkvist, 1978; Kokko et al., 1999; Harding and Härkönen, 1999; Harding et al., 2007). Environmental pollution (PCBs and DDT) in the 1960s and 1970s then hindered population recovery by causing sterility to females (Bergman and Olsson, 1986; Bergman, 1999; Harding and Härkönen, 1999; Nyman et al., 2003). After protection from hunting (1982 in Finland and 1986 in Sweden) and due to the decreased level of environmental pollution, especially PCBs and DDT, in the Baltic Sea during recent decades (Routti, 2009) grey seal numbers have increased since the 1980s, and at present exceed 30 000 in the whole Baltic Sea and 10 000 in the Finnish sea area only (Luke, 2017).

Since the 1980s, reproductive health of grey seals gradually improved, and at present virtually no reproductive disturbances (i.e. sterility of females) are observed (Bäcklin et al., 2011; Kauhala et al., 2014). Reproductive rate of grey seal females has, however, fluctuated also during the 2000s (Kauhala et al., 2014, 2016), and one possible reason behind the fluctuation is the quality of the important prey species, the herring and sprat (*Sprattus sprattus*; MacKenzie and Köster, 2004; Lundström et al., 2007, 2010; Kauhala et al., 2011, Gårdmark et al., 2012). Herring is the most common prey of Baltic grey seals composing about 78% of their identified prey fish, and occurring in 70–85% of their digestive tracks (e.g. Lundström et al., 2010; Scharff-

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Olsen et al., 2018). Sprat composed about 15% of prey fish (Lundström et al., 2007). The fluctuations in the fish prey are caused, e.g. by zooplankton availability (Flinkman et al., 1992; Möllmann et al., 2004). Furthermore, the abundance of cod (*Gadus morhua*), which preys on sprat and herring may have an impact on their numbers (e.g. Rudstam et al., 1994; Casini et al., 2008) and also their quality (weight) due to intra- and interspecific competition for zooplankton between herring and sprat (e.g. Casini et al., 2006). Also the reproductive rate of seals may thus be connected to the abundance of cod. Cod is of minor importance in grey seal diet (Scharff-Olsen et al., 2018; Tverin et al., 2019).

To understand the food web functioning in the Baltic Sea, it is thus crucial to analyze the relationships between invertebrates (especially zooplankton), different fish species and top predators, such as seals (Kuosa et al., 2017). Changes in the seal condition, such as reproductive rate, and ultimately abundance, may reflect changes in the food web of the Baltic Sea (HELCOM, 2018a).

In the present paper, we studied especially which food web factors might affect the birth rate of grey seals and whether birth rate can be used as an indicator of the changes in the food web of the Baltic Sea or not. We also discuss the possible threshold values of the indicator for good environmental status.

The effect of herring quality on the birth rate of grey seals was studied earlier (Kauhala et al., 2016) but since then we have got more data and the effects of the other variables (sprat, zooplankton and cod data) were not tested earlier. With these new parameters and the new focus, we predicted that 1) both herring and sprat quality or quantity have positive impacts on the birth rate of grey seals, and 2) biomass and mean size of zooplankton, as well as cod abundance may have an influence on the quality or quantity of herring and sprat and, thus, on the birth rate of grey seals.

2. Material and methods

2.1. Seal samples

Samples of grey seal females (n = 447) included in this study originated from the Finnish sea area from the Gulf of Finland to the Bothnian Bay (ICES SD 29–32) and most of them (414) were killed in the Gulf of Bothnia (ICES SD 30 and 31; Fig. 1.). Samples used here were collected between 16 April and 30 June (see below the calculation of birth rate) in 2001–2017. Most seals were thus shot during the time when they aggregate on sea ice in the Gulf of Bothnia but they represent actually a larger population which may spread to the southern areas to feed after the molting period in late spring. Therefore the seal reproductive data is also representative to the southern sea area and samples from different areas were pooled. Indeed, birth rate did not

Fig. 1. Map of the study areas: the Gulf of Bothnia (ICES SD 30 and 31) and the southern area (ICES SD 25–29 and 32, except the Gulf of Riga) in the Baltic Sea.

differ between the sea areas (logistic regression: $chi^2 = 0.092$, $p = 0.762$). Samples from hunted grey seals are routinely collected and analyzed at Natural Resources Institute Finland (Luke) for environmental monitoring. Hunting season is from 16 April to 31 December (except in Åland to 31 January). No seals were killed for the purpose of this study but the samples were obtained during regular hunt. No by-caught seals were included in the study.

Samples of each female seal included at least uterus, ovaries and the lower jaw. Seal species was confirmed from the lower jaw. Age determination was done by counting the incremental lines in the cementum from transversal sections of lower canine teeth (e.g. Mansfield, 1991).

Grey seals give birth to one pup in February or March, ovulate during the nursing period two or three weeks later but the embryo does not implant into the uterus until mid-summer (Boyd et al., 1999; Kauhala et al., 2014). During the pre-implantation period all ovulated females have an active *corpus luteum* (CL) and females which gave birth to a pup the present year also have a *corpus albicans* (CA) because CL rapidly atrophies after parturition and changes to CA (Boyd, 1983,1984b). Both the presence of CA and remains of placental scars, which often can be seen in the uterus after parturition, thus indicate that the female gave birth the present year (Kauhala et al., 2014). The birth rate was thus determined as the proportion of females with CA, and it was confirmed from the presence of placental scars. We used only seals killed before the implantation period, i.e. before the 1st of July because thereafter CA and placental scars may disappear (Boyd, 1984b). The birth rate was calculated for females which were 7–25 years old (n = 447) because both younger and older females have lower birth rates (Bowen et al., 2006; Kauhala et al., 2014). Birth rate could not be calculated for each year because sample sizes varied from 3 to 69 per year. Therefore the values for birth rate were smoothed with 3-year moving average. (The first and last values were the means for two years). Sample sizes for each 3-year period varied from 25 to 178, and were 25 and 17 for the first two and the last two years.

Ovaries were removed and cross sections (thickness about 2 mm) were made by knife. They were examined by naked eye for the presence of *corpus luteum* or *corpus albicans* (Kauhala et al., 2014). Both faces of each section were examined for CL (yellowish, soft in texture and occasionally with a hollow center) and CA (whitish in color, scar-like in texture). In cases when CA was not clear, it was confirmed from histological slides. The positions of CL and CA in the left or right ovary were recorded. Seals usually ovulate from alternate ovaries in successive years (Atkinson, 1997; Boyd et al., 1999).

Uterus was cut open and examined for signs of placental scars (Kauhala et al., 2014). We also recorded their place (left or right horn) in the uterus. A fresh scar is like a black belt inside the uterine horn. After some weeks only the rims of the scar can be seen but the horn in question is still thicker at the site of the placental scar than the other horn. Some orange spots may be seen at the site of the placenta (U. Siebert, pers. com.).

2.2. Fish and plankton data

Herring data (weight and catch) were obtained from ICES report from two areas: the Gulf of Bothnia (ICES SD 30 and 31) from 1980 to 2017 and the southern sea areas (SD 25–29 and 32) from 1974 to 2017, hereafter southern area and the Gulf of Bothnia (ICES, 2018; Fig. 1). Fish stocks in the southern sea areas of Finland are considered as part of a wider stock and thus pooled in ICES report (ICES, 2018). Also the sprat data were from the southern area, i.e. from the single stock that lives in the Baltic Sea, from 1974 to 2017 (ICES, 2018). Cod data were from ICES SD 25–32, although cod is very rare in the Gulf of Bothnia (ICES, 2018) from 1974 to 2017. Therefore, cod data are actually from the southern area. Also sprat is sparse in the Gulf of Bothnia, and thus we used only herring data in the analyses from this area.

The mean individual weights (hereafter weight) of fish were used as

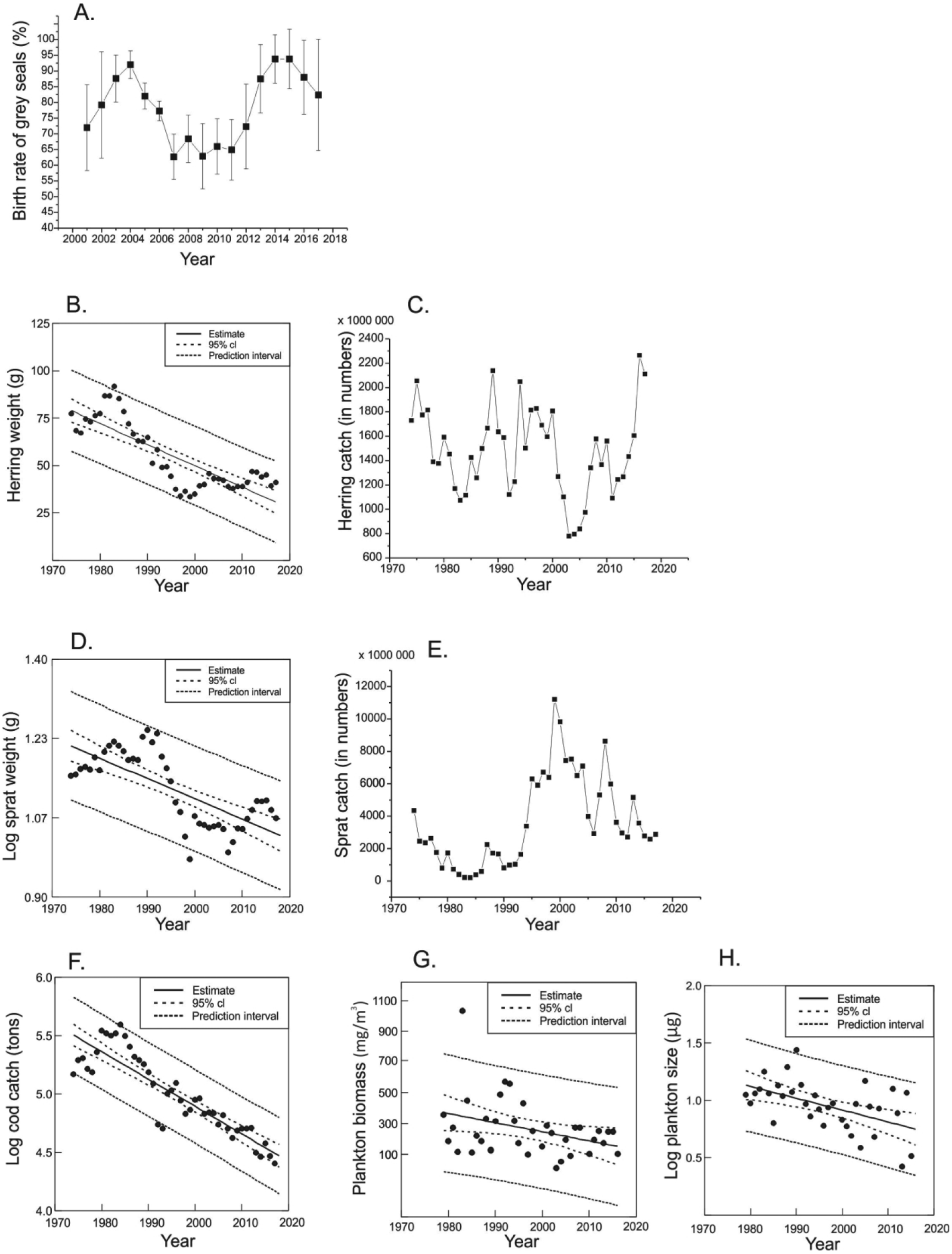

Fig. 2. Birth rate of grey seals ± SE (n = 447) from 2001 to 2017 (A; see also Kauhala et al., 2016), herring weight$_{5+}$ (B) and catch$_{5+}$ in number (C), sprat weight$_{5+}$ (D) and catch$_{5+}$ in number (E), cod catch in tons (F) during the study period 1974–2017, zooplankton biomass (G) and zooplankton size (µg wet weight ind^{-1}; H) from 1979 to 2016. Birth rate was from the whole Finnish sea area (ICES SD 29–32), fish data were from the southern area (ICES SD 25–29 and 32) and plankton data from the Gulf of Finland (ICES SD 32).

indices of fish quality and the catch sizes of commercial fishery for herring and sprat (in number) and for cod (in tons) were used as indices of their abundance (hereafter catch). Catch sizes of fish were used as abundance indices because stock numbers were not available for the whole study period, and it was tested earlier (Kauhala et al., 2017) that catch and stock numbers of herring correlated positively during shorter periods both in the Gulf of Bothnia and Central Baltic Sea. Although used a lot, catch per effort (CPUE) is often problematic in assessing the status of fish stocks, as it may not be proportional to the abundance of a fish population (e.g. Maunder et al., 2006). The catches of the fish populations are more or less following quotas set to the Baltic Sea countries (from total allowable catch), which are based on fish stock assessments. Furthermore, biomass would combine the effects of these two variables but we wanted to test the effects of herring and sprat quality and abundance on the birth rate of seals separately.

We used the age groups five years and older (5+) and 5–6 years of herring because these age groups of herring were found to be the most important for body condition of grey seals, whereas no relation between younger herring and body condition of seals was found (Kauhala et al., 2017). The age distribution of herring in grey seal diet is indeed skewed towards old individuals (mean = 6.3 years, median = 8 years, mean size 18.1 cm) and the mean age is higher than that in the population (3.3 years; Gårdmark et al., 2012). Furthermore, Gårdmark et al. (2012) estimated that herring mortality due to seal predation is greatest in the age group 8+. Weights of herring from the Bothnian Sea correlated positively with those from the Bothnian Bay (age 5+: $r = 0.83$, $p < 0.001$, age 5–6: $r = 0.90$, $p < 0.001$). Therefore we pooled herring data from these two areas, i.e. we used herring data from the Gulf of Bothnia. We also used the age group 5+ for sprat because sprat is much smaller than herring and it is unlikely that seals would prey on sprat younger than five years. All age groups are included in cod data.

Data for zooplankton biomass (average mg wet weight $^{m-3}$) and the mean size of zooplankton individuals (µg wet weight ind^{-1}; hereafter zooplankton size) in the community were obtained from once a year monitoring from 1979 to 2016 of the Finnish Environment Institute (SYKE). For the southern sea areas, we used the data from the Gulf of Finland because in other areas plankton data were too sporadic. We used the plankton data from the Bothnian Sea and Bothnian Bay to represent the Gulf of Bothnia.

2.3. Statistical tests

We examined the possible trends in the birth rate of grey seals, herring and sprat weights, herring, sprat and cod catches, and zooplankton biomass and size from curves and using regression analysis with log transformations when needed to normalize the distributions. We checked the normality of distributions of residuals by using one-sample Kolmogorov-Smirnov test. We compared birth rate from the whole Finnish sea area with fish data from the two areas, the southern area and the Gulf of Bothnia, because fish stocks in these areas differ.

We first calculated correlation matrices between the above mentioned variables. Based on the correlations, we chose the independent variables possibly affecting the birth rate of grey seals and the fish variables, and calculated models with General linear model (GLM, software Systat 13). We tested the possible effects of different independent variables on the birth rate both with and without a time lag of one year. Only one year time lag was tested because it is unlikely that fish quality or quantity would affect birth rate after two or more years, and an earlier study (Kauhala et al., 2017) showed correlation between fish quality and body condition of grey seals without a time lag. One year time lag is reasonable because scarce or poor quality food resources in summer or autumn may cause nutritional stress to females and thus affect implantation and survival rates of embryos and cause low birth rate the next spring. We used stepwise backwards procedure excluding the non-significant independent variables one at a time, the one with the highest p-value first. Only variables which significantly increased the r^2 –values were included in the models. The level of significance was set to 0.05. However, we also took into account the AICc–values (AIC corrected for small sample sizes) in cases when there was a variable with p–value between 0.10 and 0.05, and chose the final model according to the lowest AICc-value. AIC (the Akaike information criterion) provides a means to select the best model, relative to other models, and ranks the regression models from the best to the worst.

3. Results

Birth rate of grey seals in the Finnish sea area (SD 29–32; Fig. 1) increased from 2001 to 2004, then decreased until 2007, remained low until 2011 and increased thereafter (Fig. 2A, Appendix A). The increase in birth rate leveled off during the last two years.

3.1. Southern areas: Long-term trends in fish and plankton

There has been a long-term decline in herring weight from 1974 to late 1990s and thereafter it has remained on the same levels although there were shorter periods of increased growth during the early 2000s and 2010s (Fig. 2B; Appendix A). Herring catch varied during the study period with no clear trend, except for shorter periods: the catch declined from 1975 to 1983, increased from 1983 to 2000 and after a quick decline increased again from 2003 to 2017 (Fig. 2C).

Sprat weight declined from 1974 to 2017 (Fig. 2D, Appendix A), although there were shorter periods of increase or decline during the study period: sprat weight first increased from 1974 to 1983, then declined from 1990 to 1999 and increased from 1999 to 2017. Sprat catch was much larger than that of herring and fluctuated during the study period decreasing from 1974 to 1983, sharply increasing from 1990 to 1999, and declining from 1999 to 2017 (Fig. 2E).

The cod catch declined during the study period (Fig. 2F), although there was a short period of increase from 1974 to 1984. Zooplankton biomass has slightly decreased in the Gulf of Finland with a period of higher values in early 1990s and the lowest biomass in early 2000s (Fig. 2G). Also the zooplankton size has slightly decreased but there have been a few peak years in late 1980s and some years in 2000s (Fig. 2H).

3.2. Southern areas: relations between the trophic levels

We first calculated the correlation matrices for three periods (1974–1983, 1983–1999 and 1999–2017) when herring or sprat weight either increased or decreased but we combined the first two periods to one period from 1974 to 1999 (Appendix B1) because the results for them were almost equal. The results for the last period from 1999 to 2017 differed somewhat from those of the other period and are therefore presented separately (Appendix B2). In the first period (before 1999) cod was abundant and had a stronger effect on herring and sprat populations. The correlation matrices for the whole study period were also calculated (Appendix B3).

The birth rate of grey seals correlated positively with herring and sprat weights (data of birth rate only from the second time period, a time-lag of one year gave the most significant results; Appendix B2). Sprat weight correlated positively with herring weight, whereas sprat catch correlated negatively with both herring and sprat weights during all study periods (Appendix B1, B2 and B3). Also herring catch correlated negatively with herring weight in all study periods, but especially during the whole study period the correlation was weaker than that between sprat catch and herring weight. Cod catch correlated negatively with sprat catch and positively with herring and sprat weights, except in the second period when cod abundance was low. Zooplankton biomass and size correlated positively with herring and sprat weights during the whole study period but no significant correlations were found between plankton data and the birth rate of seals (with or without a time-lag).

Herring and sprat weight together best explained the variation in the birth rate of grey seals with the time-lag of one year (Fig. 3A, B, Table 1, see also Kauhala et al., 2016). Sprat and cod catches together explained well the variation in herring weight during the first and whole study period (Fig. 4A, B), whereas herring catch alone best explained the variation in herring weight from 1999 to 2017 (Fig. 4C). Sprat and cod catches together explained well the variation in sprat weight during the whole study period (Fig. 5A, B). Sprat catch alone best explained the variation in sprat weight during the shorter periods from 1974 to 1999 and from 1999 to 2017, whereas cod catch explained the variation in sprat catch (Fig. 5C), except in the second period.

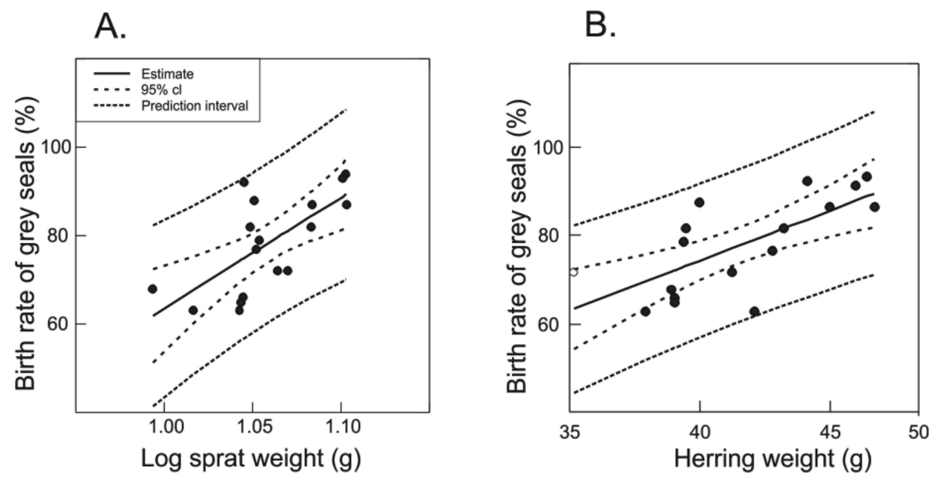

Fig. 3. Relationships between sprat $weight_{5+}$ and birth rate of grey seals (A) and between herring $weight_{5+}$ and birth rate (B). Birth rate was from the whole Finnish sea area from 2001 to 2017 and fish data were from the southern area from 2000 to 2016 (i.e. a time lag of one year was included).

Table 1
Significant models (GLM) of independent variables affecting the birth rate of grey seals, herring and sprat weight and sprat catch in different time periods. No model was obtained for herring catch. A time-lag of one year is included when relationships between birth rate and herring and sprat data were tested. Herring and sprat catches are in numbers, cod catch is in tons. Birth rate was from the whole Finnish sea area and fish data were from the southern area. Age groups of herring and sprat data are also given.

Dependent variable	Period	Independent	Model			
		variables	t	r^2	F	p
Birth rate	2001–2017	Sprat $weight_{5+}$	2.4	0.65	13.2	0.001
		Herring $weight_{5+}$	2.6			
Herring $weight_{5+}$	1974–1999	Cod catch	4.5	0.79	44.2	< 0.001
		Sprat $catch_{5+}$	−3.3			
Herring $weight_{5+}$	1999–2017	Herring $catch_{5–6}$	−3.0	0.35	9.1	0.008
Herring $weight_{5+}$	1974–2017	Cod catch	6.5	0.84	110.6	< 0.001
		Sprat $catch_{5+}$	−6.0			
Sprat $weight_{5+}$	1974–1999	Sprat $catch_{5+}$	−6.1	0.61	37.1	< 0.001
Sprat $weight_{5+}$	1999–2017	Sprat $catch_{5+}$	−2.8	0.31	7.6	0.014
Sprat $weight_{5+}$	1974–2017	Sprat $catch_{5+}$	−5.6	0.70	48.2	< 0.001
		Cod catch	2.5			
Sprat $catch_{5+}$	1974–1999	Cod catch	−4.3	0.44	18.6	< 0.001
Sprat $catch_{5+}$	1974–2017	Cod catch	−5.5	0.42	30.5	0.001

3.3. *The Gulf of Bothnia*

Herring weight declined also in the Gulf of Bothnia ($t = -5.4$, $r^2 = 0.45$, $F = 29.6$, $p < 0.001$; Fig. 6A), whereas herring catch increased in the course of the study ($t = 10.3$, $r^2 = 0.75$, $F = 105.5$, $p < 0.001$; Fig. 6B). Also zooplankton biomass increased during the study ($t = 2.9$, $r^2 = 0.21$, $F = 8.1$, $p = 0.008$; Fig. 6C) in the Bothnian Sea (but not in the Bothnian Bay) whereas there was no significant change in the zooplankton size in the Gulf of Bothnia. Sprat and cod are not significant species in the Gulf of Bothnia and therefore not analyzed.

Birth rate of grey seals and herring weight (without a time-lag) correlated positively ($r = 0.72$, $p = 0.001$), whereas herring weight and catch correlated negatively ($r = -0.73$, $p < 0.001$) in the Gulf of Bothnia from 1980 to 2015. Herring catch correlated positively with zooplankton size ($r = 0.37$, $p = 0.035$) and zooplankton biomass ($r = 0.39$, $p = 0.026$). No significant correlation was found between herring weight and zooplankton data.

Herring weight partly explained the change in the birth rate ($r^2 = 0.52$, $F = 16.3$, $p = 0.001$, Fig. 7A). The change in herring weight was well explained by the change in herring catch ($r^2 = 0.54$, $F = 42.0$, $p < 0.001$; Fig. 7B). Zooplankton biomass from the Bothnian Sea, in turn, explained some of the variation in herring catch ($r^2 = 0.15$, $F = 5.5$, $p = 0.026$; Fig. 7C).

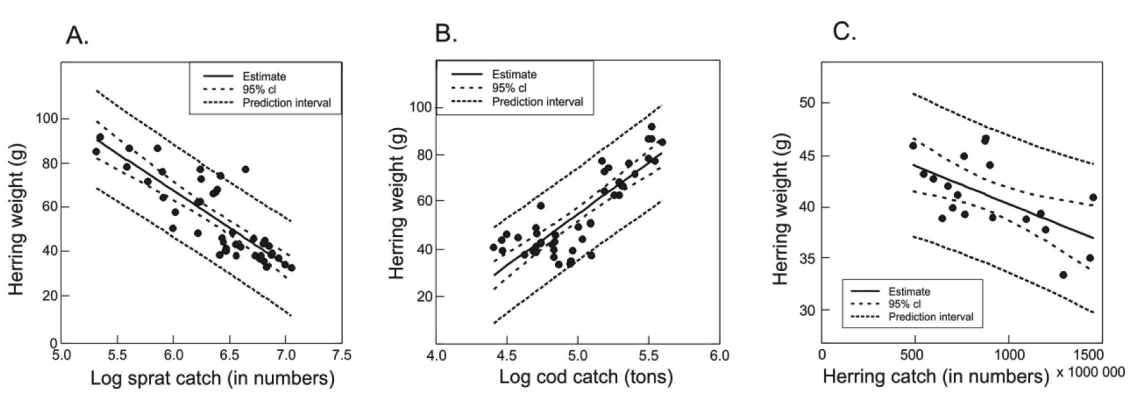

Fig. 4. Relationships between sprat $catch_{5+}$ (in number) and herring $weight_{5+}$ (A) and between cod catch (in tons) and herring $weight_{5+}$ (B) during the whole study period, and between herring $catch_{5\text{-}6}$ (in number) and herring $weight_{5+}$ from 1999 to 2017 (C) from the southern area.

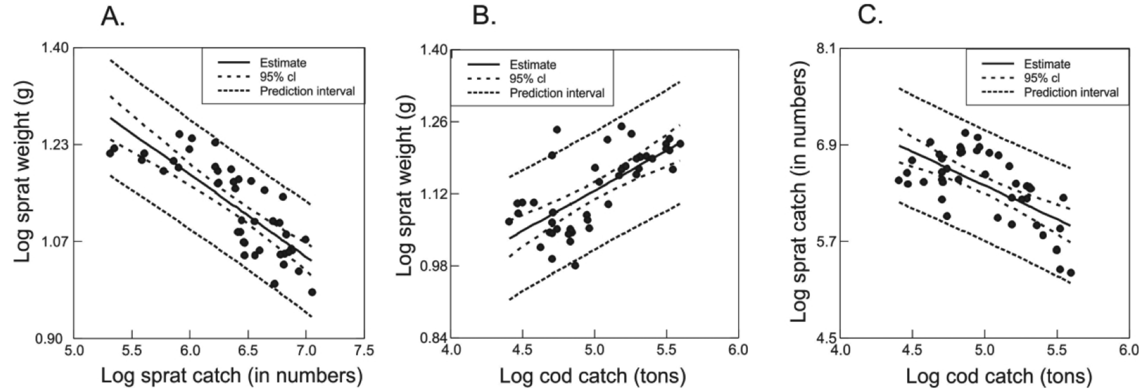

Fig. 5. Relationships between sprat catch$_{5+}$ (in numbers) and weight$_{5+}$ (A), between cod catch (in tons) and sprat weight$_{5+}$ (B), and between cod and sprat catches$_{5+}$ (C) during the whole study period from the southern area.

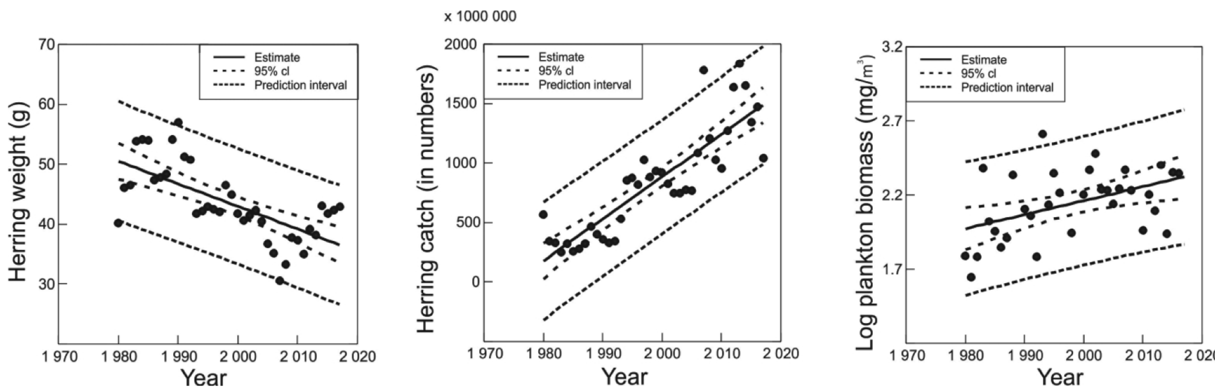

Fig. 6. Trends in herring weight$_{5+}$ (A) and herring catch$_{5+}$ (in number; B) from 1980 to 2017, and zooplankton biomass (C) in the Gulf of Bothnia from 1980 to 2016.

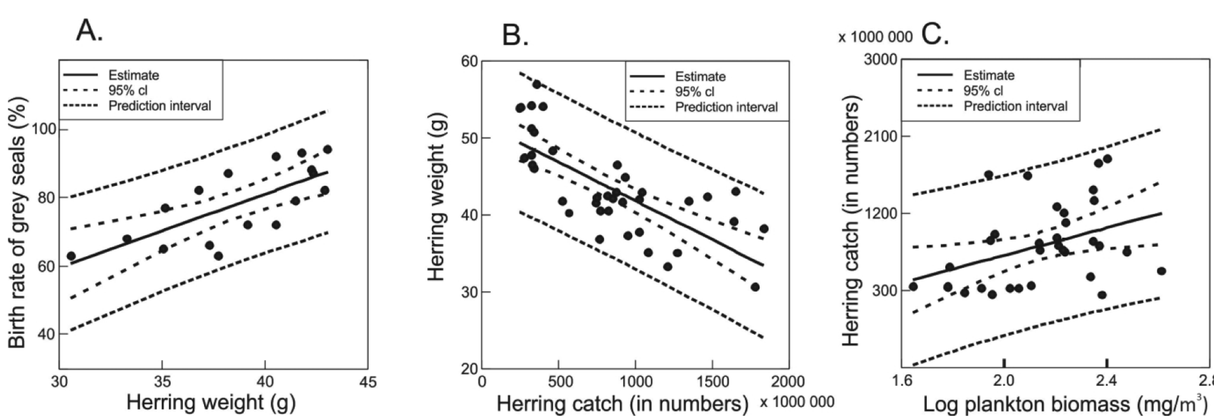

Fig. 7. Relationships between herring weight$_{5+}$ and birth rate of grey seals from 2001 to 2017 (A), herring catch$_{5+}$ (in number) and herring weight$_{5+}$ (B) from 1980 to 2017, and zooplankton biomass and herring catch$_{5+}$ (C) from 1980 to 2016. Herring data were from the Gulf of Bothnia, plankton data from the Bothnian Sea and birth rate from the total Finnish sea area.

4. Discussion

4.1. Relations between the trophic levels

Our first prediction was that herring and sprat quality (weight) or quantity has an effect on the birth rate of grey seals. We indeed found that birth rate of grey seals was positively related with both sprat and herring weight. The weight parameters of fish, on the other hand, depended on the quantity. It was shown earlier (Kauhala et al., 2016, 2017) that herring weight was related to the nutritional status of grey seals and therefore possibly also with their birth rate. Reproductive rate is sensitive to body condition in capital breeders, such as the grey seal (e.g. Guinet et al., 1998; Boyd, 2000). The results thus suggest that changes in the food web which affect sprat and herring quality may be seen on the top of the food web in the reproductive rate of grey seals, both with and without a time lag of one year.

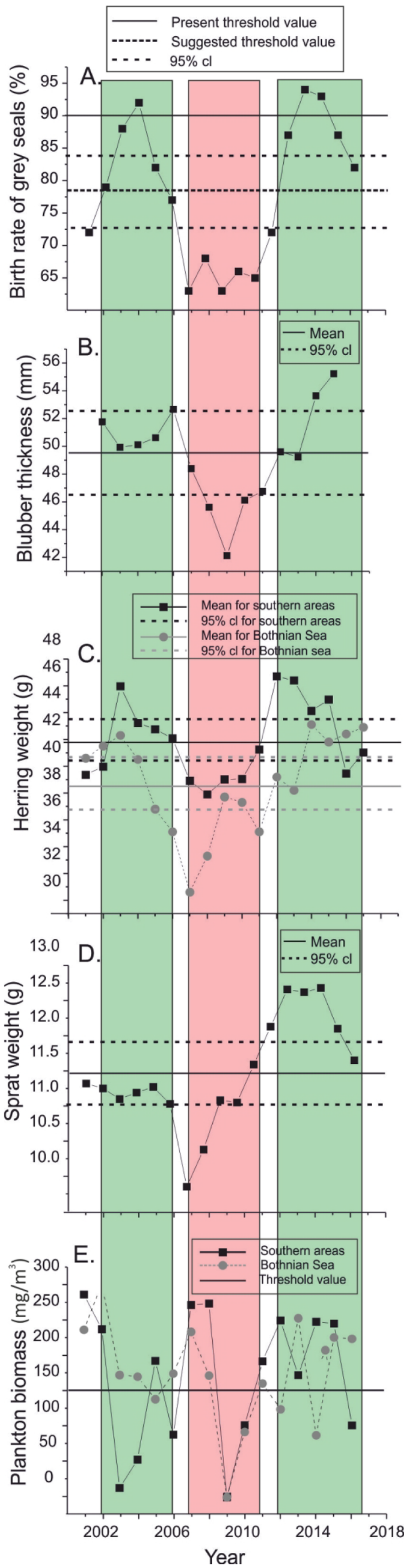

Fig. 8. Birth rate of grey seals in the Finnish sea area with the present threshold value for a growing population and the suggested value for a stable population with 95% confidence limits (A), blubber thickness of adult females (with month as a covariate), modified figure from Kauhala et al. (2017): Fig. 4C (B), herring weight with means and 95% cl in the southern area and in the Gulf of Bothnia for 2001–2017 (C) and sprat weight with mean and 95% cl in the southern area for 2001–2017 (D), and zooplankton biomass in the Gulf of Finland and in the Bothnian Sea for 2001–2016 with a HELCOM threshold value (E). Green areas refer to the time period when birth rate was above the suggested threshold value and the red area refers to the time period when birth rate was below the threshold value.

Our study showed clearly that the abundances (catches in numbers as abundance indices) of both herring and sprat had a negative influence on herring weight, and sprat abundance had a negative impact on sprat weight, suggesting that there is density-dependent competition for zooplankton within and between herring and sprat populations (Möllmann et al., 2004; Casini et al., 2006, 2010; Kuosa et al., 2017). Both species mainly consume copepods and cladocerans but sprat is a more efficient planktivore: at high sprat densities, herring growth is considerably lower than at low sprat levels (Flinkman et al., 1992; Möllmann et al., 2004, Casini et al., 2010). Our models indicate, however, that in the southern areas, herring weight is influenced even more by interspecific competition with sprat than by intraspecific competition within the herring population (Table 1). Furthermore, herring abundance did not have a significant effect on sprat weight, suggesting that mainly intraspecific competition for food resources seems to affect sprat weight. It is thus sprat abundance which has the greatest effect on both herring and sprat weight (see also Möllmann et al., 2004; Casini et al., 2010), probably because sprat is much more abundant than herring (especially in SD 29) and more efficient than herring as a planktivore (Möllmann et al., 2004). Sprat catch increased exponentially from 1990 to 2000 in the southern sea areas, and the largest sprat catches were about 5–6-fold compared to the catch sizes of herring (Fig. 2C and E; ICES, 2018). It is, however, possible that in low sprat densities hydro-climatic conditions, such as salinity, have an effect on the herring population (Casini et al., 2010). In the Gulf of Bothnia, sprat is sparse and herring abundance alone had an impact on herring weight.

Our second prediction was that zooplankton biomass and size, as well as cod abundance have an influence on herring and sprat weights, and, thus, indirectly may affect grey seal reproduction. We found indeed positive correlations between the weights of these fish species and zooplankton biomass and size during the whole study period, supporting our second hypothesis. However, the influence of zooplankton was not strong, and fish population densities seemed to be more important for clupeid (herring and sprat) weight. In the Gulf of Bothnia, zooplankton biomass was, however, a strong predictor of herring catch. Kuosa et al. (2017) also found food limitation of herring in the Bothnian Sea.

As we included cod abundance (catch in tons) into our models, we were able to show that cod had a negative effect on sprat and herring abundances and, therefore, a positive impact on their weights in the southern area especially during the first time period when cod was abundant. The effect of cod abundance on sprat abundance was found also in several other studies (e.g. Rudstam et al., 1994; Casini et al., 2006, 2008; Österblom et al., 2007). Hence, cod abundance probably has an indirect influence on the grey seal reproduction. The whole Baltic food web has, however, changed due to the decline of cod abundance because of a strong pressure by fisheries and the low salinity and oxygen contents of the Baltic Sea (e.g. Casini et al., 2008). In the second time period in the 2000s, the top-down effect of cod on clupeids has thus diminished (Casini et al., 2006, 2008; Kuosa et al., 2017) which resulted in an increase in sprat abundance (Casini et al., 2006, 2008, 2009; Österblom et al., 2007), and consequently, in a decrease in herring and sprat weights, which may be seen in the declining birth rate of grey seals in the 2000s (Kauhala et al., 2014). In recent years, however, sprat abundance declined resulting in an increase in herring and sprat weights and probably also in the birth rate of grey seals. The changes in the birth rate have also influenced the grey seal population growth rate (Kauhala et al., 2016).

Other fish species are also involved in the Baltic food web dynamics. The stickleback (*Gasterosteus aculeatus*) population has increased in recent years, probably because of increased nutrients and suitable zooplankton in the Bothnian Sea and possibly also due to the decline of the populations of predatory fish in more southern areas (Yliportimo, 2017). Competition for food resources between the three planktivorous fish species (Yliportimo, 2017) has probably influenced the loss of weight of individual fish. In the Bothnian Bay, also vendace (*Coregonus albula*) may compete with herring for zooplankton and, thus, have an effect on herring weight (e.g. Bergenius et al., 2013). Unfortunately we did not have data on vendace or three-spined stickleback to be tested here.

4.2. Reproductive status of grey seals as an indicator of changes in the Baltic food web

Reproductive status (birth rate and pregnancy rate) of grey seals, one of the top predators in the Baltic Sea, is used e.g. by HELCOM as an indirect indicator of the environmental status of the Baltic Sea because reproductive rate of seals is related to their body condition, which, in turn, is influenced by food resources (Bowen et al., 2006; Kauhala et al., 2017; HELCOM, 2018a). Pregnancy rate is calculated from the autumn sample of 6–24-year-old females indicating the proportion of females pregnant after the implantation period in mid-summer. Birth rate is calculated from the spring sample of 7–25-year-old females indicating the proportion of females that gave birth the present spring. Indicators should reflect changes in the ecosystem and be warning signals of deleterious changes in the environment. The present study showed likely relations between zooplankton, clupeid quality and birth rate of grey seals, suggesting that the birth rate indeed reflects changes in the food web over three trophic levels. The changes were not only trophic cascades between zooplankton, fish and seals but were also influenced by density-dependent competition for food resources between and among sprat and herring populations, which, in turn, are affected by predation by cod.

According to HELCOM (2018a), a threshold value for good environmental status is reached when the mean pregnancy rate/birth rate of a growing seal population is at least 90% during the past six years. The value in the Finnish grey seal population is 87% (mean for 2012–2017) which is only slightly below this threshold value. It must be remembered, however, that in recent years the growth of the Baltic grey seal population has levelled off in the Finnish sea area (Luke, 2017) and, hence it is possible that the population is approaching the carrying capacity of the environment. In a dense seal population the birth rate often declines and can vary between 50 and 90%, depending on the food resources (e.g. Boyd et al., 1999). In the 2000s, the birth rate of grey seals varied between 63% and 94% in the Finnish sea area (see also Kauhala et al., 2016). We therefore suggest that a lower threshold value for a stable population would still reflect a good state of the environment. In Fig. 8, we have compared threshold values of zooplankton biomass as agreed for the HELCOM zooplankton indicator (HELCOM, 2018b), years of high/low values of sprat and herring weight and birth rate of grey seals, and the indicator thresholds for birth rate. It can be seen from the comparison that, for instance, if the threshold value for birth rate were 78% (mean for the period 2001–2017) for a stable seal population, good state of birth rate would coincide well with the good years of food resources (Fig. 8). Confidence limits (95%) for this threshold value would be 72.6–83.8%. The present threshold value (90%) for a growing population has no confidence limits which makes it fairly arbitrary. One exact value in biological data is not sensible.

Nutritional status (the thickness of subcutaneous blubber layer) of sub-adult grey seals in autumn is another seal health indicator used by HELCOM (2018c). The threshold value for blubber thickness has been set at 40 mm for a growing seal population and at 25 mm for a population at carrying capacity of the environment (HELCOM, 2018c). The mean blubber thickness of sub-adult grey seals has been above 25 mm but below 40 mm during the whole period when we have received seal samples (since 2002; Kauhala et al., 2017), suggesting that the indicator, nutritional status of sub-adult grey seals, is not very sensitive to the changes in the food web.

On the other hand, body condition of pups could be a good indicator because pups are usually the first to react to poor environmental conditions, and their decreasing body condition could thus be the first alarming signal of disturbances in the environment, such as food resources or ice conditions (Kauhala et al., 2017). Body condition of adult females may be the most important for the population because it affects implantation and mortality rates of embryos/fetuses (e.g. Boyd, 1984a; Bowen et al., 2006) and thus the birth rate of females and growth rate of the population. Blubber thickness of adult females varied from 40 mm to 60 mm and was related to herring weight during the study period (Kauhala et al., 2017). In Fig. 8B we compared blubber thickness with the food web variables of this study and show that the variable follows well the changes in the food web and is related to the changes in the birth rate. Thus, we suggest that the mean blubber thickness from 2002 to 2017 (49.5 mm, 95% cl: 46.5–52.5 mm) could well reflect a threshold value for adult female grey seals in a stable population.

5. Conclusions

We conclude that the variability in the birth rate of grey seals is probably related to changes in the Baltic food web, and reproductive rate can thus be used as one indicator of the environmental status of the Baltic Sea. However, as other factors such as environmental contaminants, especially PBCs and DDT, can cause severe reproductive disturbances in seal females (e.g. Bergman and Olsson, 1986; Bergman, 1999; Nyman et al., 2003), the possible roles of other anthropogenic hazardous substances should also be studied. Furthermore, the possible impacts of other fish species, as well as the effect of climate change on the body condition and reproductive rate of grey seals should be investigated. We also suggest that our proposal for a threshold value for the birth rate of a stable seal population would be considered.

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Appendix A

Appendix A
Trends in different variables in different study periods in the southern area, birth rate from the whole Finnish sea area. The models were calculated with General linear model (GLM). Age groups of herring and sprat data are also given.

Variable	Period	Model			
		t	r^2	F	p
Birth rate	2004–2007	−7.8	0.97	61.3	0.016
	2011–2015	5.1	0.90	25.6	0.015
Herring weight$_{5+}$	1975–1983	9.3	0.93	87.1	< 0.001
	1983–1999	−17.6	0.95	308.5	< 0.001
	1999–2017	2.2	0.22	4.7	0.045
	1974–2017	−9.2	0.67	85.4	< 0.001
Herring catch$_{5+}$	1975–1983	−5.5	0.81	29.8	0.001
	1983–2000	2.4	0.26	5.6	0.031
	2003–2017	5.2	0.68	27.3	0.038
Sprat weight$_{5+}$	1974–1983	5.7	0.80	32.3	< 0.001
	1990–1999	−13.4	0.96	178.5	< 0.001
	1999–2017	3.1	0.36	9.6	0.006
	1974–2017	−6.6	0.51	43.9	< 0.001
Sprat catch$_{5+}$	1974–1983	−6.9	0.86	47.3	< 0.001
	1990–1999	9.6	0.92	91.4	< 0.001
	1999–2017	−5.6	0.65	31.8	< 0.001
Cod catch	1974–1984	5.5	0.77	30.5	< 0.001
	1985–2017	−11.8	0.82	138.8	< 0.001
	1974–2017	−12.8	0.80	163.5	< 0.001
Plankton biomass	1974–2017	−2.2	0.12	4.8	0.035
Plankton size	1974–2017	−3.4	0.27	11.8	0.002

Appendix B

Appendix B1
Correlations between the weights of herring and sprat, and the catch sizes of herring, sprat and cod from 1974 to 1999 from the southern area. Hw = herring weight, Hc = herring catch, Sw = sprat weight, Sc = sprat catch, Cc = cod catch. * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$. Age groups of herring and sprat data are also given.

Variable	Hw_{5+}	$Hw_{5–6}$	Hc_{5+}	$Hc_{5–6}$	Sw_{5+}	Sc_{5+}	Cc
P							
Hw_{5+}	1.00						
$Hw_{5–6}$	0.99***	1.00					
Hc_{5+}	−0.41*	−0.40*	1.00				
$Hc_{5–6}$	−0.75***	−0.74***	0.84***	1.00			
Sw_{5+}	0.66***	0.67***	−0.32	−0.47*	1.00		
Sc_{5+}	−0.79***	−0.76***	0.64***	0.71**	−0.78***	1.00	
Cc	0.84***	0.80***	−0.20	−0.48*	0.45*	−0.66***	1.00

Appendix B2
Correlations between the weights of herring and sprat, the catch sizes of herring, sprat and cod from the southern area, and the birth rate of 7–25-year-old grey seal females from Finland. Data for birth rate is from 2001 to 2017, data for fish from 2000 to 2016. Hw = herring weight, Hc = herring catch, Sw = sprat weight, Sc = sprat catch, Cc = cod catch. * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$, $^0 0.05 < p < 0.10$. Age groups of herring and sprat data are also given.

Variable	Hw_{5+}	$Hw_{5–6}$	Hc_{5+}	$Hc_{5–6}$	Sw_{5+}	Sc_{5+}	Cc
Hw_{5+}	1.00						
$Hw_{5–6}$	0.96***	1.00					
Hc_{5+}	−0.44^0	−0.51*	1.00				
$Hc_{5–6}$	−0.59**	−0.64**	0.84***	1.00			
Sw_{5+}	0.64**	0.61**	0.14	−0.16	1.00		
Sc_{5+}	−0.54**	−0.42^0	−0.16	0.13	−0.56*	1.00	
Cc	−0.35	−0.28	−0.50*	−0.26	−0.47*	0.62**	1.00
Birth rate	0.71**	0.65*	−0.13	−0.27	0.69**	−0.10	−0.26

Appendix B3

Correlations between the weights of herring and sprat, the catch sizes of herring, sprat and cod, and plankton biomass and size from 1979 to 2016 (excl. years 1999 and 2009 for plankton biomass and years 1999, 2009, 2010 and 2016 for zooplankton size) from the southern area. Hw = herring weight, Hc = herring catch, Sw = sprat weight, Sc = sprat catch, Cc = cod catch, Plbio = zooplankton biomass, Plsize = zooplankton size. * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$, $^{0}0.05 < p < 0.10$. Age groups of herring and sprat data are also given.

Variable	Hw_{5+}	$Hw_{5–6}$	Hc_{5+}	$Hc_{5–6}$	Sw_{5+}	Sc_{5+}	Cc	Plbio
Hw_{5+}	1.00							
$Hw_{5–6}$	0.99***	1.00						
Hc_{5+}	−0.05	−0.05	1.00					
$Hc_{5–6}$	−0.35*	−0.35*	0.83***	1.00				
w_{5+}	0.80***	0.81***	0.12	−0.09	1.00			
Sc_{5+}	−0.83***	−0.81***	0.13	0.35*	−0.81***	1.00		
Cc	0.84***	0.83***	−0.02	−0.14	0.69***	−0.65***	1.00	
Plbio	0.36*	0.37*	−0.09	−0.15	0.45**	−0.47**	0.24	1.00
Plsize	0.46**	0.48**	−0.11	−0.02	0.52**	−0.51**	0.49**	0.29^{0}

Appendix C. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.ecolind.2019.03.022.

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