esa ECOSPHERE

Size-dependent prey availability affects diet and performance of predatory fish at sea: a case study of Atlantic salmon

Philip Jacobson,[1,†] Anna Gårdmark,[1] Johan Östergren,[2] Michele Casini,[3] and Magnus Huss[1]

[1]Department of Aquatic Resources, Swedish University of Agricultural Sciences, Skolgatan 6, 742 42 Öregrund, Sweden
[2]Department of Aquatic Resources, Swedish University of Agricultural Sciences, Stångholmsvägen 2, 178 93 Drottningholm, Sweden
[3]Department of Aquatic Resources, Swedish University of Agricultural Sciences, Turistgatan 5, 453 30 Lysekil, Sweden

Citation: Jacobson, P., A. Gårdmark, J. Östergren, M. Casini, and M. Huss. 2018. Size-dependent prey availability affects diet and performance of predatory fish at sea: a case study of Atlantic salmon. Ecosphere 9(1):e02081. 10.1002/ecs2.2081

Abstract. Identifying factors determining the performance of individuals is an essential part of resolving what drives population dynamics. For species undergoing ontogenetic shifts in resource and habitat use, this entails assessing individual performance in all habitats used. Whereas survival and growth of anadromous Atlantic salmon, *Salmo salar* L., in its juvenile, river habitat are known to depend on size-dependent foraging and food availability, individual performance of salmon in the growth habitat out at sea is commonly explained only by abiotic factors. Still, individuals undergo this habitat shift to grow large, suggesting performance should be food-dependent also in the growth habitat. Because fish communities are highly size-structured, the link between predators and their prey may depend on their respective body sizes. Here, we study whether the performance of Baltic Sea salmon in its growth habitat is food- and size-dependent, by combining extensive diet and body size data of Baltic salmon with spatially resolved monitoring data on abundance and size distribution of their main prey, herring, *Clupea harengus* L., and sprat, *Sprattus sprattus* L. We found that both the species and size composition of prey in the diet varied with salmon body size. By accounting for this size-dependent predation and the spatially varying size distribution of prey species, we could explain the variation in salmon diet composition among salmon individuals in different Baltic Sea basins and of different length. The proportion of sprat in diet of salmon was better explained by size-specific prey availability (SSP) than total prey biomass, especially for small salmon. Further, salmon body condition increased with SSP, whereas total prey biomass could not explain variation in the condition of salmon. These findings demonstrate that food- and size-dependent processes indeed can influence the performance of anadromous fish also in large marine systems. Thus, we argue that consideration of these processes, stretching across habitats, is important for understanding performance and dynamics of predatory fish in open aquatic systems, as well as for successful management of species such as Atlantic salmon.

Key words: Atlantic salmon; Baltic Sea; body condition; diet composition; ontogenetic niche shifts; predator performance; predator–prey interactions; prey availability; size-dependent interactions.

Received 21 June 2017; revised 21 November 2017; accepted 4 December 2017. Corresponding Editor: Hunter S. Lenihan.

† **E-mail:** philip.jacobson@slu.se

Introduction

Body size is a key trait governing species interactions in ecological communities (Woodward et al. 2005, de Roos and Persson 2013). Especially in aquatic systems, predator–prey interactions have been shown to be highly size-dependent (Mittelbach and Persson 1998, Scharf et al. 2000),

and accounting for size- and food-dependent body growth is important to understand how populations and communities respond to environmental change and human exploitation (Ohlberger et al. 2011, Huss et al. 2012). A consequence of food-dependent body growth and size-dependent trophic interactions is that species shift resource and habitat use over ontogeny (Wilbur 1980, Werner and Gilliam 1984, Huss et al. 2013). Consequently, individuals will affect, and be affected by, different local environments during ontogeny (Miller and Rudolf 2011), which in turn can affect population and community structure (van de Wolfshaar et al. 2011, Reichstein et al. 2015). Thus, accounting for stage- and habitat-specific resource use in species characterized by ontogenetic niche shifts is essential to understand their population dynamics and regulation.

One striking example of ontogenetic niche shifts is anadromy, the movement from freshwater to marine systems and back, which occurs in several fish species including Atlantic salmon, *Salmo salar* L. (Gross et al. 1988, Klemetsen et al. 2003). Anadromous Atlantic salmon develop as juveniles in their birth river and migrate to marine areas where they undergo most of their body growth (hereafter referred to as the growth habitat). After one to several years feeding on fish, squids, and crustaceans in the growth habitat, salmon return, mature, and reproduce in the birth river (Karlsson et al. 1999, Klemetsen et al. 2003, Dixon et al. 2017). This habitat shift in general increases individual fitness, as the reproductive success due to the increased body size associated with the shift to the productive growth habitat is greater than the costs of migration (Gross 1987, Fleming 1996). As individual performance, for example, body growth, condition, and survival, in the growth habitat affects both the number of returning spawners and their reproductive success (Fleming 1996, Vladić and Petersson 2015), identifying factors affecting individual performance in the growth habitat is important for understanding salmon population dynamics and their responses to environmental change.

Size-dependent foraging and food-dependent habitat shifts are known to affect growth and survival of juvenile Atlantic salmon (Wankowski 1979, McCormick et al. 1998, Aas et al. 2011). Individual performance of salmon in the growth habitat is instead commonly explained by abiotic factors (e.g., sea surface temperature [SST] and hydroclimatic indices such as the North Atlantic Oscillation; Friedland et al. 2000, 2005, Todd et al. 2008), ignoring potential biotic effects. Recently, biotic factors have been included in studies about the survival and performance of salmon in marine environments, for example, by correlating variation in phyto- and zooplankton abundance and size at maturation in fish prey with catches and abundance estimates of salmon (Beaugrand and Reid 2012, Mills et al. 2013) and by assessing how changes in prey quality could affect salmon energy intake (Renkawitz et al. 2015). However, because fish feeding is size-dependent, size-dependent predator–prey interactions likely affect salmon performance in the growth habitat. For example, variation in prey size structure (Davoren and Montevecchi 2003, Golet et al. 2015) and size-specific prey availability (SSP; Gårdmark et al. 2015) has been shown to be important for the performance of other predators in open systems, but how it affects individual salmon performance has to the best of our knowledge not yet been addressed.

In this study, we ask whether performance of Baltic Sea salmon in its growth habitat is food- and size-dependent, by combining extensive diet and body size data of Baltic salmon (Karlsson et al. 1999, Hansson et al. 2001) with spatially resolved data on prey fish abundance and size distribution (ICES 2016*a*). Baltic salmon are strictly piscivorous at body sizes >30 cm and feed almost exclusively on three prey species: sprat, *Sprattus sprattus* L.; herring, *Clupea harengus* L.; and three-spined stickleback, *Gasterosteus aculeatus* L. (Karlsson et al. 1999, Salminen et al. 2001, Vuorinen et al. 2014). Here, we ask whether Baltic salmon diet composition at sea depends not only on prey taxonomy but also on prey body size, as common in piscivorous fish, and whether SSP at sea affects salmon condition. We therefore re-examine the diet biomass composition of Baltic salmon and found minimum and maximum consumable sizes of prey (i.e., a predation window) to depend on salmon body size. Using this predation window, we estimate the prey availability for differently sized salmon in each basin of their main feeding grounds in the Baltic Sea. Finally, we show that our spatially resolved estimate of SSP can be used to explain the diet composition and to understand resource limitation of individual body condition of salmon out at sea.

Methods

Salmon diet, performance, and prey availability data

We retrieved individual morphometric measurements and stomach content information from 4801 salmon. These were caught all year around in 1994–1997 in commercial longlines and drift nets in different areas of the Baltic Sea (corresponding to the International Council of the Exploration of the Sea (ICES) subdivisions, hereafter "SDs"; Fig. 1), from an existing data set. Fishing vessels operating in SDs 25, 26, and 28 were equipped with smaller mesh-sized drift nets to also enable sampling of salmon <60 cm (Karlsson et al. 1999, Hansson et al. 2001). Each salmon stomach was examined individually, and all prey items were determined to species level, counted, weighed, and measured. We only used maximum length measurements of intact prey in this study. We refer to Karlsson et al. (1999) for more details on data collection and stomach content analysis. We used annual and SD-specific length–weight estimates from sprat and herring caught in the annual Baltic International Acoustic Survey (BIAS), for the same time period as the diet data (1994–1997), to convert the number of consumed whole prey into consumed prey biomass (ICES 2016*a*). When estimates were lacking for a specific SD, we used estimates from the closest SD. We obtained the annual SD-specific biomass and length distributions of salmon prey, that is, sprat and herring, with a size resolution of 0.5 cm, from the BIAS for the same years as the salmon diet data, as well as for the whole survey period 1984–2015 (ICES 2016*a*). The BIAS is conducted annually in September–October. For three-spined stickleback, we derived the length–weight relationship from Bergström et al. (2015). To visualize the SD-specific prey biomass composition, we calculated the consumed biomass proportions of sprat, herring, and three-spined stickleback for each of four length classes of salmon: 30.0–59.9, 60.0–89.9, 90.0–120.0, and 30.0–120.0 cm (i.e., for the whole size spectrum of sampled salmon).

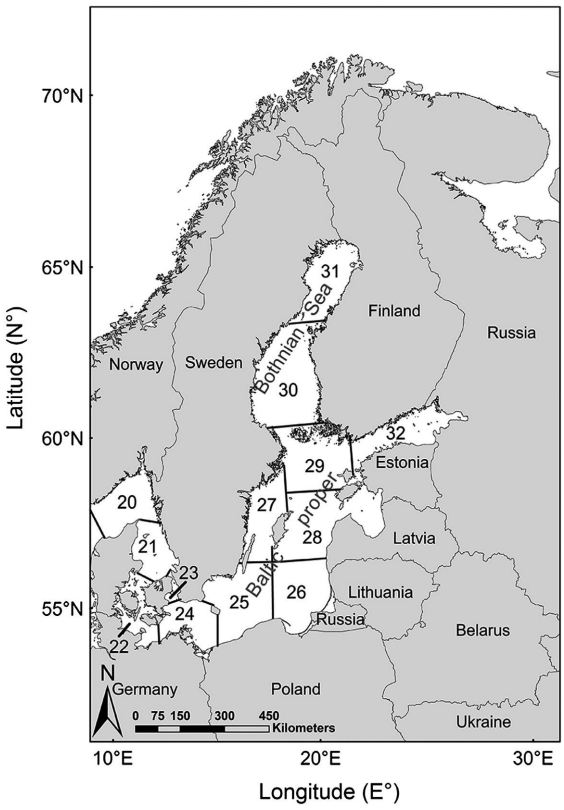

Fig. 1. Map of the Baltic Sea and its surrounding countries showing the International Council for the Exploration of the Sea subdivisions (SDs) 20–32. SDs 24–29 constitute the Baltic Proper and SDs 30–31 the Bothnian Sea and Bothnian Bay, respectively.

Salmon predation window

To assess the size-dependency of the interaction between salmon and its prey, we estimated the minimum, mean, and maximum prey:predator size ratio from the stomach data. We estimated the prey:predator size ratios by fitting linear regression relationships (with intercept 0) to the minimum, mean, and maximum total prey lengths consumed by salmon in 10-cm length classes, for the size range 30–120 cm. We used linear regression because prey size increases linearly with predator size for members of the subfamily Salmoninae, including Atlantic salmon (Mittelbach and Persson 1998, Keeley and Grant 2001). We excluded the maximum prey size of the two largest length classes of salmon, length class 100–110 and 110–120 cm, when fitting the regressions as they were smaller than observed in smaller salmon length classes. The latter can be explained by the fact that sprat never and herring rarely reach lengths over 27 cm, meaning almost all prey fish stay within the consumable

size range of a ≥ 100-cm salmon (Appendix S2: Fig. S2). Also, we do not expect such a decrease in maximum prey size to be due to any morphological constrains of Baltic salmon, as the gape size most likely does not decrease after reaching a body length ≥100 cm.

Size-specific relative attack rate of salmon

The attack rate, that is, the number of successful attempts to capture a prey during a given time, depends on the predator's ability to localize and capture a prey which in turn depends on the size of both the predator and the prey (Claessen et al. 2002). To calculate the size-specific relative potential attack rate of Baltic salmon, we used the tent-function equation by Claessen et al. (2002) and applied this on the prey:predator size ratios estimated from the salmon stomach data, that is, the predation window:

$$\mathrm{AR}(l_\mathrm{p}, l_\mathrm{s}) = \begin{cases} A l_\mathrm{s}^{\alpha} \frac{l_\mathrm{p} - \delta l_\mathrm{s}}{(\varphi - \delta) l_\mathrm{s}} & : \textit{if } \delta l_\mathrm{s} < l_\mathrm{p} \leq \varphi l_\mathrm{s} \\ A l_\mathrm{s}^{\alpha} \frac{\varepsilon l_\mathrm{s} - l_\mathrm{p}}{(\varepsilon - \varphi) l_\mathrm{s}} & : \textit{if } \varphi l_\mathrm{s} < l_\mathrm{p} < \varepsilon l_\mathrm{s} \\ 0 & : \text{otherwise} \end{cases} \quad (1)$$

in which AR is the potential attack rate of a salmon with length (l_s) on a prey with length (l_p), A is the maximum attack rate on an optimal-sized prey, α is the allometric exponent of maximum attack rate, δ is the minimum size ratio below which the prey fish is too small, φ is the mean size ratio, and ε is the maximum ratio of prey to salmon body length above which the prey for a specific salmon body length is too large (Fig. 3a). We set the maximum attack rate A and the allometric exponent α to 1.6 and 0.6, respectively, following Claessen et al. (2000) and van Leeuwen et al. (2013), as these are the only estimates of size-specific piscivorous attack rate currently available. The maximum attack rate A has, however, no influence on our results as we converted the attack rate into a relative scale with the potential attack-rate estimate of a 105-cm salmon set to 1. The allometric scaling exponent, α, which governs the relative differences in attack rate between differently sized predators on identically sized prey, is based on attack-rate experiments using piscivorous perch, *Perca fluviatilis* L. As 0.6 is the only published value of α based on piscivory, we used it in our analysis to enable comparisons between differently sized piscivorous salmon. To test the robustness of our results, we performed a sensitivity analysis using lower and higher α values, from a range based on Englund et al. (2011; Appendix S5). We calculated the relative potential attack rate of salmon ranging from 0 to 120 cm on prey lengths of 0–50 cm with a length interval of 0.5 cm.

Basin- and size-specific prey availability for salmon

We calculated the SSP for Baltic salmon for each of SDs 25–29 as these are the SDs we have prey data from, collected in the BIAS. We derived the SSP of prey of length l_p for differently sized (l_s) salmon using the following equation:

$$\mathrm{SSP}(l_\mathrm{p}, l_\mathrm{s}) = \sum (\mathrm{AR}(l_\mathrm{p}, l_\mathrm{s}) \times W(l_\mathrm{p})) \quad (2)$$

in which AR is the potential attack rate of a salmon of a specific length (l_s) from Eq. 1 and W is the biomass (in grams) of prey in length class (l_p). To enable comparisons of the SSP for differently sized salmon, we converted SSP into a relative scale, varying from −1 to +1, where +1 corresponds to the highest amount of suitable-sized prey observed in the time period 1984–2015 across salmon size classes and SDs and −1 corresponds to the lowest amount of suitable-sized prey.

Explaining salmon diet

We tested whether the total prey biomass or the SSP could best explain the observed diet of salmon caught in SDs 25, 26, and 28, when measured as the observed proportion of sprat biomass in the stomachs relative the total amount of prey biomass (sprat and herring combined). We restricted the analysis to SDs 25, 26, and 28 because these were the three SDs in which the whole size spectrum (30–120 cm) of salmon was caught in sufficient numbers. We used the proportion of sprat in the stomachs as it was the most common prey of Baltic salmon in these SDs during this time period (Fig. 2). We calculated the proportion of sprat in salmon stomachs using the mean of the annual mean sprat proportion in the diet of Baltic salmon at 10-cm length intervals for the time period 1995–1997, for each of SDs 25, 26, and 28 (Appendix S2: Table S1). We excluded year 1994 from the analysis due to a lack of salmon diet data from SD 25 for this particular year. We also excluded length classes with <5 salmon individuals from the analysis (Appendix S2:

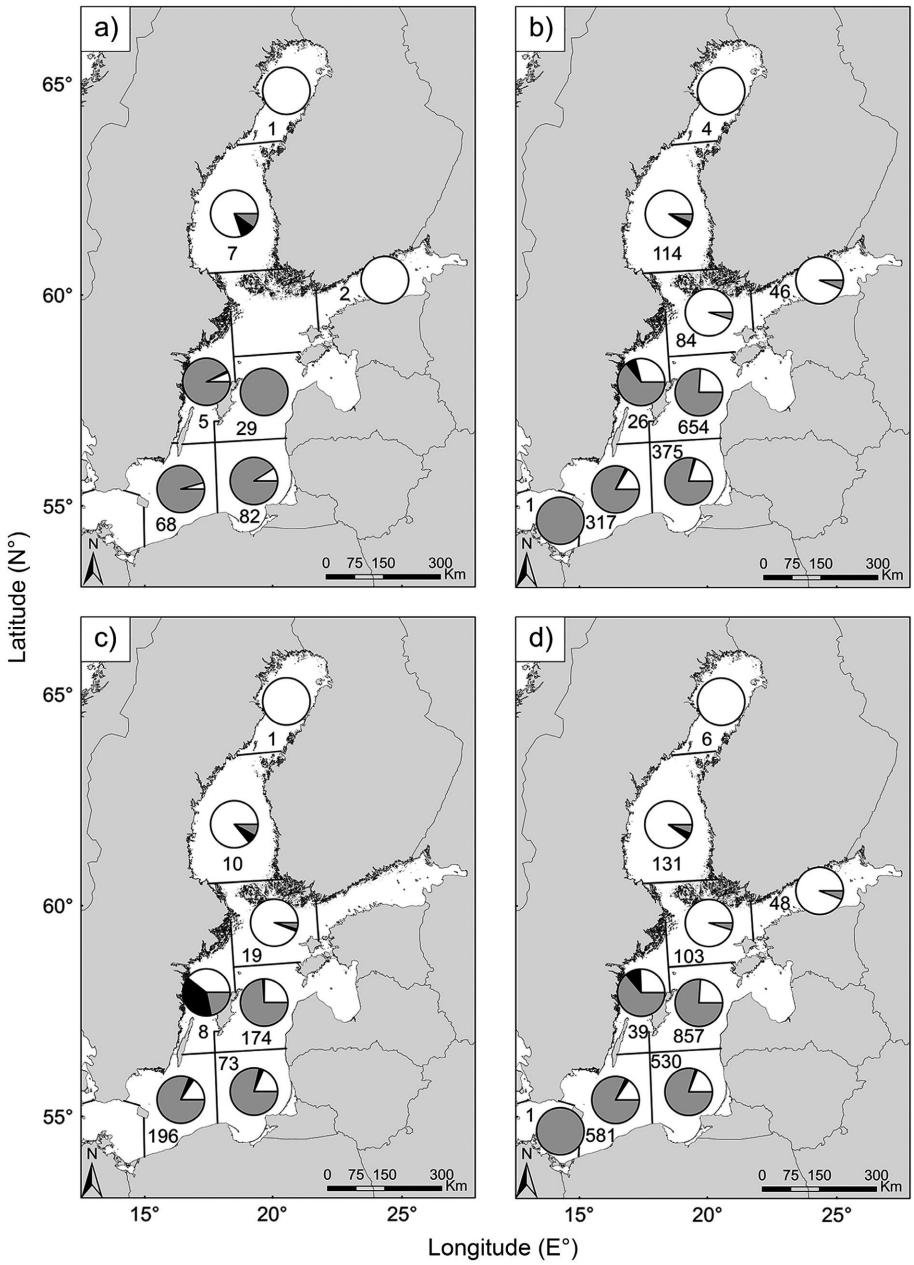

Fig. 2. Diet biomass composition of Baltic salmon (*Salmo salar* L.) during the years 1994–1997, within each of the International Council for the Exploration of the Sea subdivisions (SDs) 24–32, for three different salmon length classes: (a) 30–60 cm, (b) 60–90 cm, and (c) 90–120 cm; and (d) all salmon combined. White indicates herring (*Clupea harengus* L.) biomass, gray indicates sprat (*Sprattus sprattus* L.) biomass, and black indicates three-spined stickleback (*Gasterosteus aculeatus* L.) biomass. Numbers within each subdivision denote the sample size of salmon stomachs.

Table S1). To calculate the SD-specific proportion of the total sprat biomass at sea, we used the mean of the annual total sprat biomass proportion at sea for the same years. To calculate the mean size-specific sprat availability proportion in each SD, we used the annual proportion of suitable-sized sprat biomass derived from Eq. 2. We calculated the proportions of sprat biomass

at sea and the size-specific sprat availability for salmon lengths of 30–120 cm, at 0.5-cm intervals. To test what best explained the observed proportion of sprat biomass in the salmon diet, we used multivariate linear regression models containing salmon length, feeding area (either SD 25, 26, or 28), and either the total sprat biomass at sea or the size-specific sprat availability proportion estimates.

Effects of prey availability on salmon body condition

To get an estimate of the individual body condition of salmon, we used Fulton's condition factor, $K = 100 \times (w_s/l_s^3)$, in which w_s is salmon total weight (g) and l_s is its total length (mm). To investigate whether body condition (K) varied with SSP, we used SSP as the predictor in a piecewise linear regression analysis (Crawley 2012). This allowed us to identify potential threshold values in the effects of prey availability on salmon condition, as their condition could be affected by prey availability at low resource levels but not at high. We first identified the lowest mean squared error of the relationship between K and the SSP (Appendix S3: Fig. S1). Then, we conducted two separate linear regression analyses on the relationship between K and SSP, one on the data points below and another above the identified threshold value (Casini et al. 2009). We also evaluated the effect of body length, SD (25, 26, 28, and 29), and either the SSP or the total prey biomass on salmon body condition using multivariate linear regression analysis both below and above the threshold to determine the strongest explanatory variables. Since there was no recorded weight information for salmon caught in SD 27, we could not calculate K for any salmon caught in this area, which is why we excluded SD 27 from the analysis.

Statistical analysis

We conducted all calculations and statistical analyses using the software R, version 3.2.5 (R Core Team 2016). We assessed model assumptions of homoscedasticity and normally distributed errors visually using Q–Q plots and residual variation vs. fitted values and leverage. We conducted model selection based on the Akaike Information Criterion (AIC), of which the model(s) with the lowest AIC value (± 2 units) were selected.

Results

Size-specific diet and potential attack rate of salmon

The biomass composition of the Baltic salmon diet varied spatially, with sprat being the dominant prey in the southern parts (SDs 24–28) and herring in the northern parts (SDs 29–32) of the Baltic Sea (Figs. 1, 2a–d). Moreover, prey composition varied with salmon size (Fig. 2). In the northern parts (SDs 29–32), herring dominated the diet of all salmon size classes, whereas in the south (SDs 25–28), sprat was the most common prey in the smallest size class of salmon (30–60 cm; Fig. 2a), but became less common with increasing salmon length (Fig. 2b–c). The minimum, mean, and maximum prey size increased with salmon body size (minimum: slope = 0.04, $F_{1,8} = 20.92$, $R^2 = 0.69$, $P = 0.002$; mean: slope = 0.12, $F_{1,\ 13381} = 1.32 \times 10^5$, $R^2 = 0.91$, $P < 0.001$; maximum: slope = 0.35, $F_{1,6} = 755.20$, $R^2 = 0.99$, $P < 0.001$; Fig. 3a). Consequently, the relative potential attack rate varied with salmon body size, and smaller salmon had a narrower range of prey body sizes that they can consume than larger salmon (Fig. 3b).

Size-specific prey availability explains salmon diet

The most parsimonious model explaining salmon diet (i.e., the proportion of sprat biomass in the stomach) included SSP estimates and ICES subdivision (SD; SSP; $P < 0.001$, SD; $P < 0.001$, SSP × SD; $P < 0.001$; Table 1). All models containing the SSP estimates explained a large part of the variation in diet of salmon. In contrast, only two of the models including total prey biomass did (models including also salmon length and the interaction between salmon length and SD; Table 1). Although both predictors (total prey biomass and SSP) vary spatially, only SSP differs among salmon size classes; especially for the smallest salmon, there was a great difference between total prey biomass and SSP (Appendix S1: Fig. S1). The SSP estimates were generally better in explaining the diet of small salmon than large, as the residual deviation from the observed sprat proportion increased with increased salmon size (Appendix S2: Fig. S1). As the proportion of sprat biomass at sea is not affected by salmon size, the predicted diet composition based on total sprat biomass at sea is identical for all salmon size

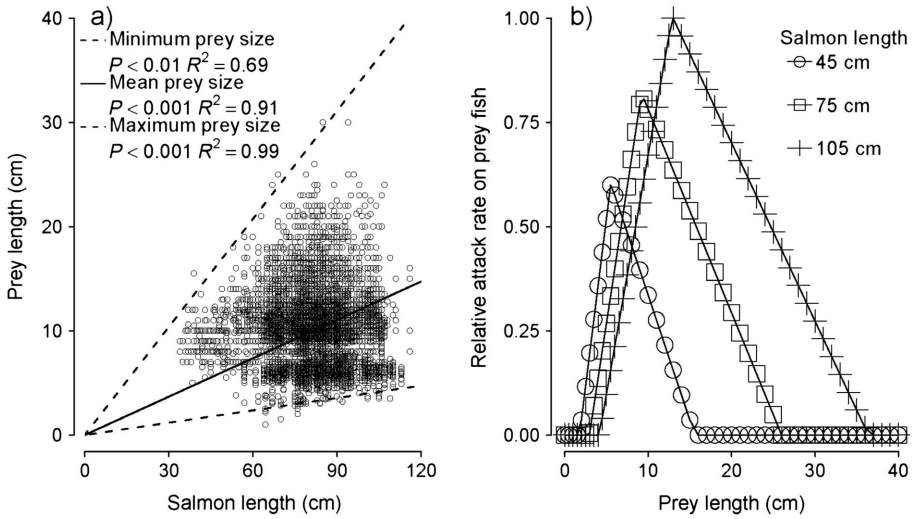

Fig. 3. The size-dependency of Baltic salmon predation on its fish prey: (a) the minimum, mean, and maximum prey:predator size ratio, and (b) the relative attack rate of a 45-, 75-, and 105-cm salmon on differently sized prey fish. Note the relative scale on the y-axis, where 1 equals the maximum attack rate for a 105-cm salmon.

classes, but differed among SDs 25, 26, and 28 (0.53 ± 0.02, 0.79 ± 0.03, 0.81 ± 0.03, mean ± 1 SD, respectively; Fig. 4, gray line). In contrast, the proportion of sprat in the diet predicted using the SSP decreased with salmon size in all SDs as expected, with the largest decrease in SD 25 (Fig. 4, black line, cf. Fig. 2a–c).

Size-specific prey availability affects salmon body condition

Salmon body condition increased with SSP, and more so at low ($y = 0.250x + 1.119$, $F_{1,708} = 70.18$, $R^2 = 0.089$, $P < 0.001$) than at high ($y = 0.105x + 1.018$, $F_{1,\ 1408} = 40.98$, $R^2 = 0.028$, $P < 0.001$) relative SSP (Fig. 5). Also without the threshold, body condition increased with SSP ($y = 0.084x + 1.028$, $F_{1,\ 2118} = 71.15$, $R^2 = 0.032$, $P < 0.001$). Total prey biomass did not explain salmon body condition, as it had either a counterintuitive effect (i.e., decreasing) or no effect (Appendix S4). The models which explained most of the variation in body condition below and above the observed threshold both included SSP, SD, and salmon length (Table 2).

Table 1. Variables, coefficients, and the corresponding AIC of the linear regression models of observed sprat biomass proportions in the diet of Baltic salmon collected during 1995–1997 in ICES subdivisions (SDs) 25, 26, and 28.

Model parameters	AIC	F (df)	R^2	P
SSP	−49.935	9.575 (1,21)	0.281	<0.01
SSP × salmon length	−65.248	15.02 (3,19)	0.657	<0.001
SSP × SD	**−69.429**	**19.28 (3,19)**	**0.714**	**<0.001**
SSP + SD	−56.176	10.83 (2,20)	0.472	<0.001
SSP × salmon length × SD	−64.965	7.96 (7,15)	0.689	<0.001
TBS	−42.078	0.73 (1,21)	−0.013	0.403
TBS × salmon length	−60.569	11.09 (3,19)	0.579	<0.001
TBS × SD	−40.926	0.74 (2,20)	−0.025	0.492
TBS × salmon length × SD	−66.710	11.14 (5,17)	0.697	<0.001

Notes: The model with the lowest AIC value is highlighted in bold. AIC, Akaike Information Criterion; SSP, size-specific prey availability; SD, ICES subdivision; TBS, total prey biomass at sea.

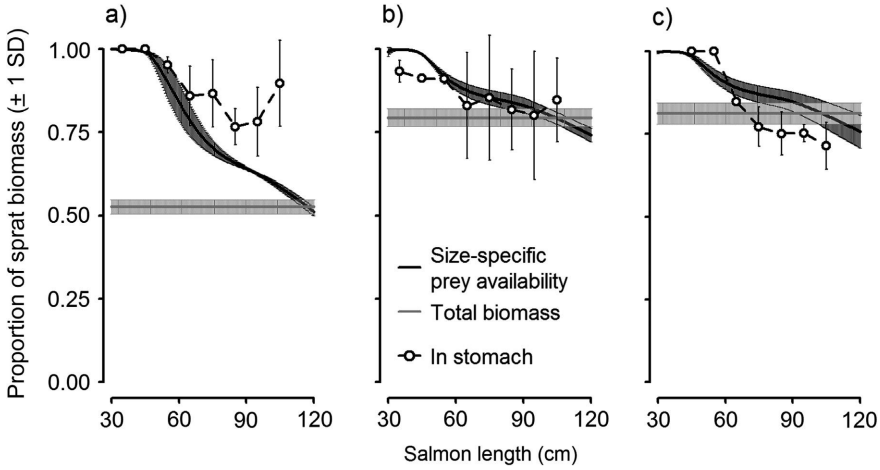

Fig. 4. Mean (± 1 SD) proportion of sprat biomass in salmon stomachs (white dots, shown for 10-cm size classes), predicted mean (± 1 SD) sprat biomass proportion based on either the total prey biomass at sea (gray line) or the size-specific prey availability (SSP) at sea (black line) in International Council for the Exploration of the Sea subdivisions 25 (a), 26 (b), and 28 (c). The total prey biomass and the SSP are estimated for salmon sizes of 30–120 cm, with 0.5-cm intervals.

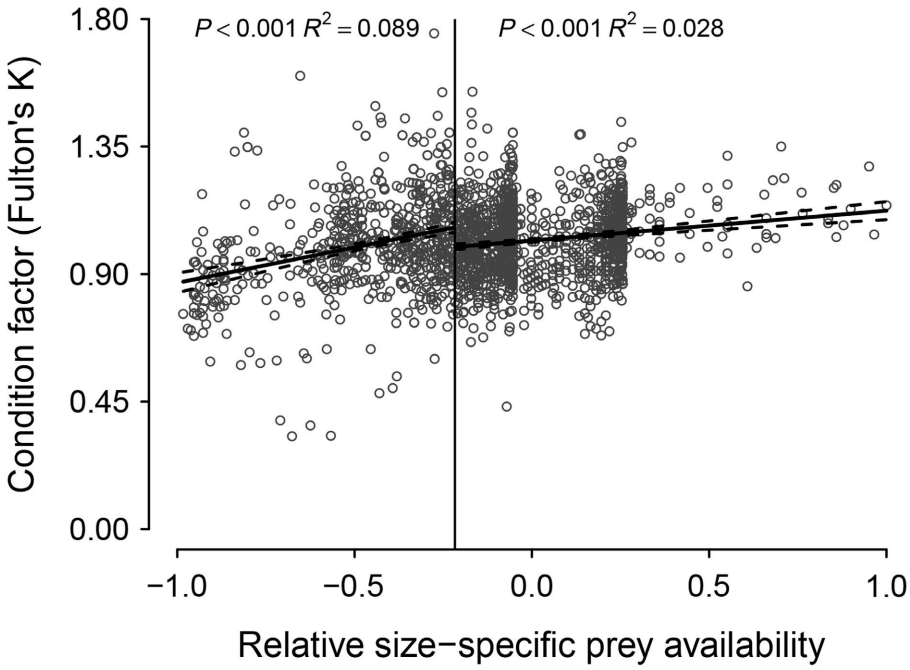

Fig. 5. The relationship between Baltic salmon body condition (Fulton's *K*) and the relative size-specific availability of herring and sprat biomass combined. Regression lines were estimated using piecewise linear regression with dashed lines representing the upper and lower 95% confidence interval limits. The vertical line equals the threshold value, identified using the lowest mean squared error.

Table 2. Variables, coefficients, and the corresponding AIC of the piecewise linear regression models of body condition (Fulton's *K*) of Baltic salmon in ICES subdivisions (SDs) 25, 26, 28, and 29 collected during 1994–1997.

	Below threshold				Above threshold			
Model parameters	AIC	*F* (df)	R^2	*P*	AIC	*F* (df)	R^2	*P*
SSP	−573.755	70.2 (1,708)	0.089	<0.001	−1972.566	40.98 (1,1408)	0.028	<0.001
SSP × salmon length	−621.847	43.02 (3,706)	0.151	<0.001	−2017.617	30.72 (3,1406)	0.06	<0.001
SSP × SD	−587.558	29.89 (3,706)	0.109	<0.001	−1983.364	18.73 (3,1406)	0.036	<0.001
SSP × SD × salmon length	**−641.802**	**23.1 (7,702)**	**0.180**	**<0.001**	**−2049.883**	**19.31 (7,1402)**	**0.083**	**<0.001**

Notes: The model with the lowest AIC value is highlighted in bold. AIC, Akaike Information Criterion; SSP, size-specific prey availability; SD, ICES subdivision.

Discussion

We show, using extensive data on Atlantic salmon diet composition, body size, and SSP, that the interaction between salmon and its prey in the Baltic Sea is highly size-dependent. By accounting for this size-dependency, we can explain the variation in salmon diet composition among salmon individuals in different Baltic Sea basins and of different lengths. The proportion of sprat in the diet decreased with salmon length in all Baltic Sea basins and was better explained by the proportion of sprat in the total amount of suitably-sized prey (which decreases for larger salmon) than by the total proportion of sprat in each basin. Furthermore, we show that the body condition of salmon individuals increased with SSP but was unaffected by an increase in total prey biomass.

Despite the fact that fish body condition varies greatly among individuals and can be affected by multiple factors, such as temperature (Todd et al. 2008), migration duration (Vuorinen et al. 2014), parasites (Krkosek et al. 2013), or selective exploitation (Vainikka et al. 2009), we found a positive effect of SSP on the condition of individual salmon. Salmon condition increased with SSP at both low and high resource levels, with the highest increase at low resource levels. This clearly shows that the performance of individual salmon at sea can be resource-limited. Still, we found no prey dependence of salmon condition when prey size structure was ignored (i.e., when using the total amount of prey biomass), which shows that the resource limitation is size-dependent. As experiments on size-dependent fish feeding of large salmon are lacking, we show that this result of salmon condition being limited by SSP holds for a range of published values for the size-dependence of fish attack rates (0.4–0.8; Englund et al. 2011). In all cases, the large variation in body condition of salmon at sea observed was only partially explained by the SSP, salmon length, and feeding area. This is to be expected, given the many factors that influence an individual's body condition. Previous studies have related salmon performance to other biotic factors, for example, prey quality (Renkawitz et al. 2015) and parasites (Krkosek et al. 2013), as well as abiotic factors, for example, SST (Friedland et al. 2000, Todd et al. 2008). Still, the link between salmon condition and SSP, which we found despite the large variation in body condition among individuals, suggests that this size-dependency between salmon and its prey is also important for understanding salmon performance.

Similar predator–prey relationships have been shown for other piscivorous predators, with changes in prey quality, abundance, or size distributions affecting their performance (Österblom et al. 2006, Øigård et al. 2013, Golet et al. 2015). Given that energy intake affects body growth, energy storage, and reproductive success, the link between size-dependent food availability and the performance of salmon in its growth habitat may be of great importance for understanding variation in survival and spawning success of individual salmon, and therefore also for population-level performance. As salmon cease feeding upon reaching their birth river, individuals are entirely dependent on their stored energy reserves accumulated during feeding at sea to survive the energetically costly river ascent and spawning (Kadri et al. 1995, Jonsson et al. 1997, Vuorinen et al. 2014), and individuals in poor condition are therefore less likely to survive (Todd et al. 2008). Also, recent studies have demonstrated how accounting for individual-level food- and size-dependent processes is essential to understand fish

population- and community dynamics and population responses to changes in productivity and mortality (Ohlberger et al. 2011, Huss et al. 2012, de Roos and Persson 2013). The same may be especially relevant for species characterized by ontogenetic niche shifts that utilize different habitats during the life cycle (van de Wolfshaar et al. 2011, Reichstein et al. 2015), such as salmon. However, such studies are rare and are either purely theoretical or based on small-scale experiments. Our results demonstrate that food- and size-dependent processes indeed can influence the performance of anadromous fish in large marine systems.

The link between individual-level performance and size-dependent foraging has been established for juvenile salmon when still in their river habitat (Wankowski 1979, Wankowski and Thorpe 1979, Keeley and Grant 1997). Our results show that the diet of salmon at sea was better explained by SSP than total prey biomass, especially for small salmon. The proportion of sprat in the diet decreased with increased salmon size, while the variation of sprat in the diet increased among individuals. This could be due to a wider consumable size range of prey with increased salmon size, increasing the potential for salmon to consume both herring and sprat. Also, as the deviation between total sprat biomass and the observed proportion of sprat decreased with salmon size, our results indicate that the diet composition of small salmon is more determined by gape size limitation than of large salmon feeding in the Baltic Sea. Generally, this size-dependency has not been incorporated in studies focusing on the interaction between salmon and its prey at sea. While this is fundamental in order to resolve population and community dynamics (de Roos and Persson 2013), it can also be important for understanding transfer, accumulation, and deficiency of compounds in food webs. Notably, size-dependent predation has commonly not been considered in studies on the importance of prey selection for bioaccumulation of toxic substances in Baltic salmon (Nfon and Cousins 2007) and of thiamine deficiency, which causes high juvenile mortality in salmon offspring (i.e., the M74 disease; Mikkonen et al. 2011, Keinänen et al. 2012).

One potential caveat of our study is the temporal resolution of the prey community. While the salmon diet and performance data as well as the prey data cover the same areas and years, the salmon are caught throughout these years whereas the prey survey was only conducted in the autumn each year. Previous studies have shown that Baltic salmon diet differs across seasons (Karlsson et al. 1999, Hansson et al. 2001), as the proportion of herring increases toward the end of the year. Such within-year diet variation could be due to migration of the prey populations or because individual salmon might feed in different SDs depending on the time of year. However, as we do not have data on actual migrations of the salmon individuals in this study, we could not account for seasonal variation in salmon feeding areas or prey distribution patterns. Still, despite the coarse temporal resolution in prey availability, we successfully link the diet composition of Baltic salmon in different basins as well as the condition of individuals to SSP. Ideally, updated diet data on differently sized salmon feeding in the Baltic Sea would aid quantification of the extent of how changes in both salmon abundance (which has increased 10-fold since 1994–1997 in the Baltic Sea; ICES 2016*b*) and prey community abundance and size distribution (Casini et al. 2010, Östman et al. 2014, Bergström et al. 2015) have affected salmon diet composition and performance in more recent years.

In conclusion, we show how consideration of size- and food-dependent processes is key for understanding large-scale patterns in diet composition and individual-level performance of predatory fish in open aquatic systems. We argue that the size- and food-dependency of Atlantic salmon performance should be included, together with influential environmental factors, in future studies aiming to resolve Atlantic salmon population dynamics. Given the link between food availability, diet composition, individual performance (which has consequences for salmon survival and spawning success), and therefore likely overall population dynamics, we argue that an ecosystem approach including prey species and stretching across river and open sea habitats is needed for successful management of anadromous predatory fish such as salmon.

Acknowledgments

We thank Lars Karlsson, former head of the Swedish Salmon Research Institute, Älvkarleby, for collecting

and keeping the *Baltic Salmon Diet Database* in a format which enabled us to use it 20 years after it was collected. We thank everyone involved in the annual Baltic International Acoustic Survey (BIAS) for their work in sampling the offshore fish community of the Baltic Sea. We also thank the anonymous reviewer for valuable comments on an early version of the manuscript. This work resulted from the BONUS GOHERR project supported by BONUS (Art 185), funded jointly by the EU and the Swedish Research Council Formas. MC was financed by the BONUS INSPIRE project supported by BONUS (Art 185), funded jointly by the EU and the Swedish Research Council Formas.

Literature Cited

Aas, Ø., A. Klementsen, S. Einum, and J. Skurdal. 2011. Atlantic salmon ecology. Wiley-Blackwell, Oxford, UK.

Beaugrand, G., and P. C. Reid. 2012. Relationships between North Atlantic salmon, plankton, and hydroclimatic change in the Northeast Atlantic. ICES Journal of Marine Science 69:1549–1562.

Bergström, U., J. Olsson, M. Casini, B. K. Eriksson, R. Fredriksson, H. Wennhage, and M. Appelberg. 2015. Stickleback increase in the Baltic Sea: a thorny issue for coastal predatory fish. Estuarine, Coastal and Shelf Science 163:134–142.

Casini, M., V. Bartolino, J. C. Molinero, and G. Kornilovs. 2010. Linking fisheries, trophic interactions and climate: Threshold dynamics drive herring *Clupea harengus* growth in the central Baltic Sea. Marine Ecology Progress Series 413:241–252.

Casini, M., J. Hjelm, J. C. Molinero, J. Lövgren, M. Cardinale, V. Bartolino, A. Belgrano, and G. Kornilovs. 2009. Trophic cascades promote threshold-like shifts in pelagic marine ecosystems. Proceedings of the National Academy of Science of the United States of America 106:197–202.

Claessen, D., A. M. de Roos, and L. Persson. 2000. Dwarfs and giants: cannibalism and competition in size-structured populations. American Naturalist 155:219–237.

Claessen, D., C. van Oss, A. M. de Roos, and L. Persson. 2002. The impact of size-dependent predation on population dynamics and individual life history. Ecology 83:1660–1675.

Crawley, M. J. 2012. The R book. Second edition. John Wiley & Sons, Chichester, UK.

Davoren, G. K., and W. A. Montevecchi. 2003. Signals from seabirds indicate changing biology of capelin stocks. Marine Ecology Progress Series 258:253–261.

de Roos, A. M., and L. Persson. 2013. Population and community ecology of ontogenetic development. Princeton University Press, Princeton, New Jersey, USA.

Dixon, H. J., J. B. Dempson, T. F. Sheehan, M. D. Renkawitz, and M. Power. 2017. Assessing the diet of North American Atlantic salmon (*Salmo salar* L.) off the West Greenland coast using gut content and stable isotope analyses. Fisheries Oceanography 26:555–568.

Englund, G., G. Öhlund, C. L. Hein, and S. Diehl. 2011. Temperature dependence of the functional response. Ecology Letters 14:914–921.

Fleming, I. A. 1996. Reproductive strategies of Atlantic salmon: ecology and evolution. Reviews in Fish Biology and Fisheries 6:379–416.

Friedland, K., G. Chaput, and J. Maclean. 2005. The emerging role of climate in post-smolt growth of Atlantic salmon. ICES Journal of Marine Science 62:1338–1349.

Friedland, K., L. P. Hansen, D. A. Dunkley, and J. C. MacLean. 2000. Linkage between ocean climate, post-smolt growth, and survival of Atlantic salmon (*Salmo salar* L.) in the North Sea area. ICES Journal of Marine Science 57:419–429.

Gårdmark, A., M. Casini, M. Huss, A. van Leeuwen, J. Hjelm, L. Persson, and A. M. de Roos. 2015. Regime shifts in exploited marine food webs: detecting mechanisms underlying alternative stable states using size-structured community dynamics theory. Philosophical Transactions of the Royal Society B 370:1–10.

Golet, W. J., N. R. Record, S. Lehuta, M. Lutcavage, B. Galuardi, A. B. Cooper, and A. J. Pershing. 2015. The paradox of the pelagics: why bluefin tuna can go hungry in a sea of plenty. Marine Ecology Progress Series 527:181–192.

Gross, M. R. 1987. Evolution of diadromy in fishes. American Fisheries Society Symposium 1:14–25.

Gross, M. R., R. M. Coleman, and R. M. McDowall. 1988. Aquatic productivity and the evolution of diadromous fish migration. Science 239:1291–1293.

Hansson, S., L. Karlsson, E. Ikonen, O. Christensen, A. Mitans, D. Uzars, E. Petersson, and B. Ragnarsson. 2001. Stomach analyses of Baltic salmon from 1959–1962 and 1994–1997: possible relations between diet and yolk-sac-fry mortality (M74). Journal of Fish Biology 58:1730–1745.

Huss, M., A. Gårdmark, A. van Leeuwen, and A. M. de Roos. 2012. Size- and food-dependent growth drives patterns of competitive dominance along productivity gradients. Ecology 93:847–857.

Huss, M., L. Persson, J. Borcherding, and L. Heermann. 2013. Timing of the diet shift from zooplankton to macroinvertebrates and size at maturity determine whether normally piscivorous fish can persist in otherwise fishless lakes. Freshwater Biology 58: 1416–1424.

ICES. 2016*a*. Second interim report of the Baltic International Fish Survey Working Group (WGBIFS). ICES CM SSGIEOM 07: 591.

ICES. 2016*b*. Report of the Baltic Salmon and Trout Assessment Working Group (WGBAST). ICES CM ACOM 09: 257.

Jonsson, N., B. Jonsson, and L. P. Hansen. 1997. Changes in proximate composition and estimates of energetic costs during upstream migration and spawning in Atlantic salmon *Salmo salar*. Journal of Animal Ecology 66:425–436.

Kadri, S., N. B. Metcalfe, F. A. Huntingford, and J. E. Thorpe. 1995. What controls the onset of anorexia in maturing adult female Atlantic salmon? Functional Ecology 9:790–797.

Karlsson, L., E. Ikonen, A. Mitans, and S. Hansson. 1999. The diet of salmon (*Salmo salar*) in the Baltic Sea and connections with the M74 syndrome. Ambio 28:37–42.

Keeley, E. R., and J. W. A. Grant. 1997. Allometry of diet selectivity in juvenile Atlantic salmon (*Salmo salar*). Canadian Journal of Fisheries and Aquatic Sciences 54:1894–1902.

Keeley, E. R., and J. W. A. Grant. 2001. Prey size of salmonid fishes in streams, lakes, and oceans. Canadian Journal of Fisheries and Aquatic Sciences 58:1122–1132.

Keinänen, M., A. Uddström, J. Mikkonen, M. Casini, J. Pönni, T. Myllylä, E. Aro, and P. J. Vuorinen. 2012. The thiamine deficiency syndrome M74, a reproductive disorder of Atlantic salmon (*Salmo salar*) feeding in the Baltic Sea, is related to the fat and thiamine content of prey fish. ICES Journal of Marine Science 69:516–528.

Klemetsen, A., P.-A. Amundsen, J. Dempson, B. Jonsson, N. Jonsson, M. F. O'Conell, and E. Mortensen. 2003. Atlantic salmon *Salmo salar,* L., brown trout *Salmo trutta* L. and Arctic charr *Salvelinus alpinus* (L.): a review of aspects of their life histories. Ecology of Freshwater Fish 12:1–59.

Krkosek, M., C. W. Revie, P. G. Gargan, O. T. Skilbrei, B. Finstad, and C. D. Todd. 2013. Impact of parasites on salmon recruitment in the Northeast Atlantic Ocean. Proceedings of the Royal Society B 280:20122359.

McCormick, S. D., L. P. Hansen, T. P. Quinn, and R. L. Saunders. 1998. Movement, migration, and smolting of Atlantic salmon (*Salmo salar*). Canadian Journal of Fisheries and Aquatic Sciences 55:77–92.

Mikkonen, J., M. Keinänen, M. Casini, J. Pönni, and P. J. Vuorinen. 2011. Relationships between fish stock changes in the Baltic Sea and the M74 syndrome, a reproductive disorder of Atlantic salmon (*Salmo salar*). ICES Journal of Marine Science 68:2134–2144.

Miller, T. E., and V. H. Rudolf. 2011. Thinking inside the box: community-level consequences of stage-structured populations. Trends in Ecology & Evolution 26:457–466.

Mills, K. E., A. J. Pershing, T. F. Sheehan, and D. Mountain. 2013. Climate and ecosystem linkages explain widespread declines in North American Atlantic salmon populations. Global Change Biology 19: 3046–3061.

Mittelbach, G. G., and L. Persson. 1998. The ontogeny of piscivory and its ecological consequences. Canadian Journal of Fisheries and Aquatic Sciences 55:1454–1465.

Nfon, E., and I. T. Cousins. 2007. Modelling PCB bioaccumulation in a Baltic food web. Environmental Pollution 148:73–82.

Ohlberger, J., Ø. Langangen, E. Edeline, D. Claessen, I. J. Winfield, N. C. Stenseth, and L. A. Vøllestad. 2011. Stage-specific biomass overcompensation by juveniles in response to increased adult mortality in a wild fish population. Ecology 92:2175–2182.

Øigård, T. A., U. Lindstrøm, T. Haug, K. T. Nilssen, and S. Smout. 2013. Functional relationship between harp seal body condition and available prey in the Barents Sea. Marine Ecology Progress Series 484: 287–301.

Österblom, H., M. Casini, O. Olsson, and A. Bignert. 2006. Fish, seabirds and trophic cascades in the Baltic Sea. Marine Ecology Progress Series 323: 233–238.

Östman, Ö., O. Karlsson, J. Pönni, O. Kaljuste, T. Aho, and A. Gårdmark. 2014. Relative contributions of evolutionary and ecological dynamics to body size and life-history changes of herring (*Clupea harengus*) in the Bothnian Sea. Evolutionary Ecology Research 16:417–433.

R Core Team. 2016. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

Reichstein, B., L. Persson, and A. M. de Roos. 2015. Ontogenetic asymmetry modulates population biomass production and response to harvest. Nature Communications 6:6441.

Renkawitz, M. D., T. F. Sheehan, H. J. Dixon, and R. Nygaard. 2015. Changing trophic structure and energy dynamics in the Northwest Atlantic: implications for Atlantic salmon feeding at West Greenland. Marine Ecology Progress Series 538:197–211.

Salminen, M., E. Erkamo, and J. Salmi. 2001. Diet of post-smolt and one-sea-winter Atlantic salmon in the Bothnian Sea, Northern Baltic. Journal of Fish Biology 58:16–35.

Scharf, F. S., F. Juanes, and R. A. Rountree. 2000. Predator size–prey size relationships of marine fish predators: interspecific variation and effects of

ontogeny and body size on trophic-niche breadth. Marine Ecology Progress Series 208:229–248.

Todd, C. D., S. L. Hughes, C. T. Marshall, J. C. MacLean, M. E. Lonergan, and E. M. Biuw. 2008. Detrimental effects of recent ocean surface warming on growth condition of Atlantic salmon. Global Change Biology 14:958–970.

Vainikka, A., A. Gårdmark, B. Bland, and J. Hjelm. 2009. Two- and three-dimensional maturation reaction norms for the eastern Baltic cod, *Gadus morhua*. ICES Journal of Marine Science 66:248–257.

van de Wolfshaar, K. E., R. HilleRisLambers, and A. Gårdmark. 2011. Effect of habitat productivity and exploitation on populations with complex life cycles. Marine Ecology Progress Series 438:175–184.

van Leeuwen, A., M. Huss, A. Gårdmark, M. Casini, F. Vitale, J. Hjelm, L. Persson, and A. M. de Roos. 2013. Predators with multiple ontogenetic niche shifts have limited potential for population growth and top-down control of their prey. American Naturalist 182:53–66.

Vladić, T., and E. Petersson. 2015. Evolutionary biology of the Atlantic Salmon. CRC Press, Boca Raton, Florida, USA.

Vuorinen, P. J., H. Kiviranta, J. Koistinen, O. Pöyhönen, E. Ikonen, and M. Keinänen. 2014. Organohalogen concentrations and feeding status in Atlantic salmon (*Salmo salar* L.) of the Baltic Sea during the spawning run. Science of the Total Environment 468–469:449–456.

Wankowski, J. W. J. 1979. Morphological limitations, prey size selectivity, and growth response of juvenile Atlantic salmon, *Salmo salar*. Journal of Fish Biology 14:89–100.

Wankowski, J. W. J., and J. E. Thorpe. 1979. The role of food particle size in the growth of juvenile Atlantic salmon (*Salmo salar* L.). Journal of Fish Biology 14:351–370.

Werner, E. E., and J. F. Gilliam. 1984. The ontogenetic niche and species interactions in size-structured populations. Annual Review of Ecology and Systematics 15:393–425.

Wilbur, H. M. 1980. Complex life cycles. Annual Review of Ecology and Systematics 11:67–93.

Woodward, G., B. Ebenman, M. Emmerson, J. M. Montoya, J. M. Olesen, A. Valido, and P. H. Warren. 2005. Body size in ecological networks. Trends in Ecology & Evolution 20:402–409.

Supporting Information

Additional Supporting Information may be found online at: http://onlinelibrary.wiley.com/doi/10.1002/ecs2.2081/full