Feeding specialists on fatty acid-rich prey have higher gonad weights: Pay-off in Baltic perch?

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Abstract. Individual specialization is a common phenomenon throughout the animal kingdom. Many studies have identified intraspecific competition as one of the main drivers for individual feeding specialization. These studies have mainly considered the quantity of resources, commonly overlooking qualitative aspects of the diet. For example, highly unsaturated fatty acids of the ω-3 class (ω-3 HUFAs) are related to optimal health and growth in consumers. However, little is known on direct fitness consequences for consumers of natural populations that specialize on high-quality resources, such as those rich in ω-3 HUFAs. Despite being such an important qualitative aspect of the diet, it is still unknown whether natural populations show among-individual variation in their choice on prey items that are either rich or poor in HUFAs, and how it affects individual performances. In this study, we investigated whether there is individual feeding specialization and whether it is related to fitness benefits, in a population of perch (*Perca fluviatilis*) in the Baltic Sea. The contribution of pelagic planktivorous fish to the diet varied from 17% to 61% among perch individuals, as depicted by stable isotope mixing models. This variation in diet was also qualitative, as the ω-3 HUFA content differed among prey types. Specialization on the high-quality resource pelagic planktivorous fish was associated with the proportions of ω-3 HUFA in the individuals' muscles and individuals among those with the highest proportions of ω-3 HUFAs had the greatest relative gonad weight (gonadosomatic index, GSI), a proxy for reproductive investment. Thus, our results highlight the function of food quality for individual specialization and its potential to have direct fitness benefits, playing a major role in shaping ecological interactions.

Key words: among-individual diet variation; eggs; fatty acid composition; female investment; food quality; ω-3 HUFAs.

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INTRODUCTION

In their common quest for resources, individuals within a population may differ in their specialization on specific prey items, and such variation in resource use have been found even among individuals of a given age and sex (Araújo et al. 2011). Individual specialization is widespread in the animal kingdom, occurring at all trophic levels within a food web (Bolnick et al. 2003), and has profound implications for ecology and evolution (Quevedo et al. 2009, Bolnick et al. 2011, Skúlason et al. 2019). While the degree of individual specialization depends on several ecological, behavioral, and physiological factors, intraspecific competition for food has been identified as the main driver (Bolnick et al. 2003, Svanbäck and Persson 2004, Araújo et al. 2011). Most studies have focused on the sheer quantity of prey organisms available, showing that the

degree of individual specialization is density-dependent (e.g., Venne and Magnan 1995, Schindler et al. 1997, McLaughlin 2001). However, small quantities of highly nutritious food may be as valuable as large amounts of food of lower quality (Müller-Navarra 2008). Yet, the quality aspects of resources have been largely neglected in attempts to identify the ultimate causes of individual diet specialization.

The quality of food can be defined in different ways, such as palatability, toxicity, or as the proportion composed of physiologically important organic compounds, which includes several fatty acids (Giusti et al. 2008, Müller-Navarra 2008). Fatty acids are parts of lipids, involved in signaling pathways, regulating several cellular functions, and being crucial components of cell membranes (Arts and Kohler 2009, Parrish 2009). Especially, highly unsaturated fatty acids (HUFAs) of the ω-3 class (20:5-ω-3, EPA and 22:6ω-3, DHA) are linked to optimal health and fitness in consumers (Brett and Müller-Navarra 1997, Twining et al. 2016). For example, studies of aquacultured fish show that the quality of the mother's food, especially its content of ω-3 HUFAs, influences the offspring's fitness (Mourente and Odriozola 1990, Abi-ayad et al. 1997, Bell et al. 1997). However, most studies have been conducted under controlled laboratory conditions with domesticated taxa, and little is known about how high-quality diet affects fitness of individuals in natural populations. Thus, we lack a general understanding of fitness benefits for individuals in natural populations specialized on high-HUFA rather than low-HUFA resources (but see Fritz et al. 2017), and how individual diet specialization may contribute to the transfer of parental resources to offspring.

During egg development, gravid females provide propagule resources (e.g., energy and hormones) to the offspring, and the amount and quality of resources allocated to the eggs often profoundly influence the growth and survival of the progeny (Badyaev and Uller 2009). The ovaries of fish are extremely lipid-rich, and fatty acids are incorporated into the yolk of the oocyte to supply the developing embryo with food (Adams 1998). EPA and DHA have been detected in high concentrations in ripe gonads of several teleost fishes, both in males and females (Tocher and Sargent 1984), being involved in optimal growth and tissue differentiation during early ontogeny (Sargent et al. 1999, Ballantyne et al. 2003, Tocher 2010). Furthermore, elevated DHA levels have been associated with a higher sperm motility that can lead to a higher hatching success (Vassallo-Agius et al. 2001). Specialization on resources with a high level of ω-3 HUFAs may therefore promote a higher reproductive success, leading to a substantial fitness benefit in both sexes.

Here, we studied the extent of individual specialization on diets with different quality and its relation to fitness benefits, in a population of Eurasian perch (*Perca fluviatilis*) located in the Forsmark area of the Baltic Sea. Perch is a well-studied example showing individual diet variations in natural conditions. In lakes, perch individuals specialize in feeding on either pelagic zooplankton or littoral prey types, such as benthic invertebrates and fish (Svanbäck and Eklöv 2002, Svanbäck et al. 2008, Quevedo et al. 2009). Besides being ubiquitous in freshwater systems throughout Europe, perch is further the most common coastal predatory fish in the Baltic Sea (Ådjers et al. 2006, HELCOM 2018). Less is known about diet specialization of perch in the Baltic Sea, but there is some evidence indicating that the use of resources differs between pelagic and littoral perch (Mustamäki et al. 2014). However, whether this reflects individual specialization or is an effect of opportunistic feeding on spatially variable resources is unclear. Generally, perch in the Baltic Sea feed on zooplankton and benthic invertebrates, but fish prey, consisting of benthic and planktivorous fish species form a dominant part of the diet (Lappalainen et al. 2001, Sandström and Karås 2002, Jacobsen et al. 2019). To date, specialization patterns occurring on the individual preference on benthic and planktivorous fish prey have not been investigated. In addition, the prey types perch in the Baltic Sea are of very different levels of ω-3 HUFAs. Generally, benthic fish and invertebrates have a lower level of ω-3 HUFAs compared to pelagic fish (Litzow et al. 2006, Lau et al. 2012, Strandberg et al. 2015, Scharnweber et al. 2016*b*). Perch in the Baltic Sea therefore provides an excellent study system to understand the direct implications of individual specialization and diet quality on fitness in natural populations.

We quantified diet of perch using stable isotope mixing models, and we also evaluated their fatty acid content. We then compared the proportion of fatty acid-enriched prey consumed by perch to their fatty acid content. Finally, we studied how individual diet specialization might affect fitness using relative gonad weight (gonadosomatic index, GSI), a proxy for reproductive investment. Specifically, we hypothesized that individual specialists feeding on pelagic planktivorous fish (that are rich in ω-3 HUFAs) would have a higher proportion ω-3 HUFAs in their muscle tissue and a higher GSI.

MATERIAL AND METHODS

Field sampling

In 9-10 August 2017, we collected perch caught in the annual coastal monitoring (Ådjers et al. 2006, Söderberg 2008) under the ethical permit number C139/13. Sampling locations were close to the shore (<100 m) at water depths between 1 and 3 m (Fig. 1). Two linked multi-mesh survey gillnets (35 m long, 3 m deep), each with five mesh sizes (17, 22, 25, 33, and 50 mm), were deployed overnight.

All fish caught were identified to species and measured for total length (TL ± 1 cm). A length-stratified subsample of perch were immediately selected and processed for subsequent stable isotope and fatty acid analyses. We only chose perch that had red gills. These perch were sexed, measured (TL ± 1 mm), and weighed (total weight and gutted weight, measured to nearest 1 g), and the weights of their gonads were obtained (to nearest 0.01 g) as well as the maturation status on a 4-grade scale (HELCOM 2015). The gonadosomatic index (GSI) was calculated as the proportion of gonad weight to the total gutted weight (somatic weight). We sampled 55 females and 21 males, with TL ranged from 131 to 346 mm (mean 215 mm ± 49 standard deviation [SD]) and total weight ranged from 27 to 534 g (mean 145 g ± 109 SD). We then dissected two small pieces of the dorsal muscle tissue, one for the fatty acid analyses and one for subsequent stable isotope analyses. We collected tissues sample of potential fish prey for stable isotope and fatty acid analyses. These specimens were collected during perch sampling or when found intact in the stomachs of the dissected perch.

These sampled prey species were mostly littoral and benthivorous (roach, *Rutilus rutilus*, $N = 2$, ruffe, *Gymnocephalus cemua*, $N = 4$, bream, *Abramis brama*, $N = 1$) but also included planktivorous species, three-spined stickleback (*Gasterosteus aculeatus*, $N = 1$) and herring (*Clupea harengus*, $N = 2$), which also dwell more pelagically. Potential invertebrate resources were sampled in September 2017, as well as in June and September the subsequent year (Appendix S1: Table S1). Variation in stable isotope values ($\delta^{13}C$ and $\delta^{15}N$) of organismal groups was not significantly different between years (Mann–Whitney U-test, $P > 0.05$) so we pooled samples from both years for the analyses. At each gillnet station, zooplankton and benthic invertebrates were sampled. Zooplankton samples were collected using a zooplankton net (100 μm mesh size; 0.25 m diameter) deployed over multiple vertical 1-m hauls to obtain enough biomass (11 samples were analyzed for stable isotopes N_{iso}, among which 4 were also analyzed for fatty acids, N_{FAcid}). Benthic invertebrates were collected from stones and with a sweep net. We allowed several hours for gut clearance and sorted them in major taxonomic groups (*Gastropoda* $N_{iso} = 18$, $N_{FAcid} = 10$; *Gammaridae* $N_{iso} = 9$, $N_{FAcid} = 4$; *Idotea* $N_{iso} = 3$, $N_{FAcid} = 1$; *Chironomidae* $N_{iso} = 2$, $N_{FAcid} = 1$; *Trichoptera* $N_{iso} = 3$, $N_{FAcid} = 0$; *Tabanidae* $N_{iso} = 4$, $N_{FAcid} = 0$; *Coleoptera* $N_{iso} = 1$, $N_{FAcid} = 0$; *Turbellaria* $N_{iso} = 1$, $N_{FAcid} = 0$; *Zygoptera* $N_{iso} = 1$, $N_{FAcid} = 0$; and *Anisoptera* $N_{iso} = 1$, $N_{FAcid} = 0$). All samples (perch and putative prey) collected for stable isotope analyses were over-dried at 60°C, while those for fatty acid analyses were stored at −20°C for less than 6 months.

Because maturation status and gonadal weight vary seasonally, we also compared GSI of the sampled perch to GSI of perch caught in other seasons and years (in August in 2003, 2017 and 2018; in August, October and December in 2015), sampled at the same stations with the same method.

Stable isotope analysis and Bayesian mixing model

Oven-dried tissues samples were ground to a fine powder using a mortar and pestle, and approximately 1 mg of powder was put into tin capsules. Elemental and stable isotope analyses
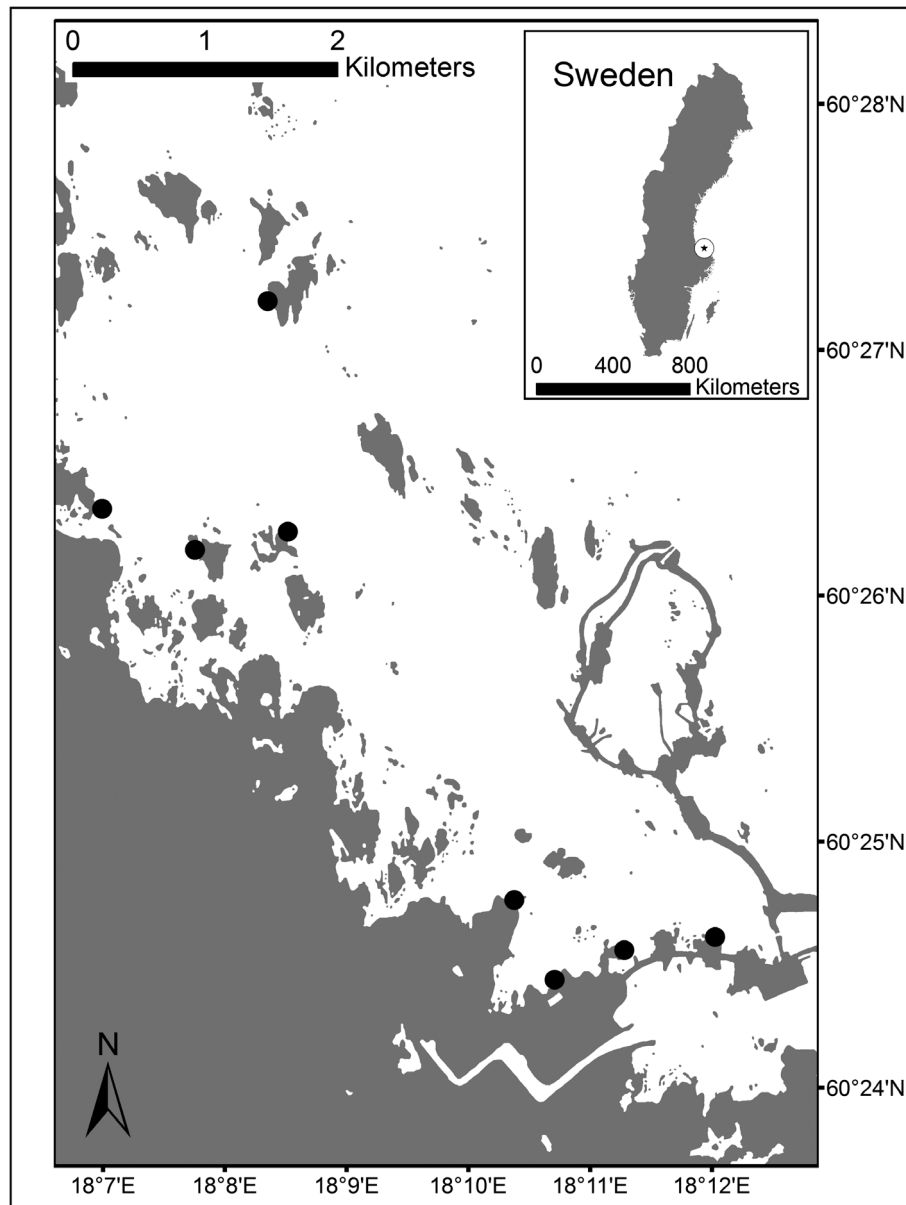
Fig. 1. Map of sampling sites. Black dots represent the eight net locations. © Landmäteriet.

of carbon and nitrogen were conducted at the University of California, Davis Stable Isotope Facility, California, USA, using a PDZ Europa ANCA-GSL elemental analyzer coupled to a PDZ Europa 20-20 isotope ratio mass spectrometer (Sercon, Cheshire, UK). As in all samples, C/N was low (3.84 ± 0.82; mean ± SD), and no lipid normalization was performed (Kiljunen et al. 2006). Results are expressed using the δ notation,

referring the ratios of samples to the international standards (Vienna Pee Dee Belemnite and Air for carbon and nitrogen, respectively). Measurement error was 0.2‰ for ^{13}C and 0.3‰ for ^{15}N.

To estimate the long-term contribution of the different prey to the diet of the individual perch, the stable isotope signatures were analyzed using Bayesian mixing models in MixSIAR

version 3.1.10 (Stock et al. 2018). Invertebrates (Gastropoda, Isopoda, Amphipoda, Diptera, Turbellaria, Coleoptera, and Odonata; $N = 43$), benthivorous (common bream, roach, ruffe), and pelagic planktivorous fish (herring, three-spined stickleback) were used as distinct end-members in the model (Appendix S1: Table S1), using a fractionation factor of 0.4‰ ± 1.3 SD for $\delta^{13}C$ and 3.4‰ ± 1.0 SD for $\delta^{15}N$ based on Post (2002). We refrained from including zooplankton as potential prey because their isotopic composition laid outside the mixing polygon (Fig. 1) and because they are usually not found in stomachs of perch of the sizes investigated herein (Jacobsen et al. 2019). For the Bayesian model, we used uninformative priors and perch individuals were set as a fixed factors with a residual only error structure (Stock and Semmens 2016; see Data S1 for MixSIAR script).

Fatty acid analysis

Fatty acid analyses were performed following the approach described by Scharnweber et al. (2016*b*). Lipids were extracted by submerging 100–200 mg of fish tissue in a solution of chloroform/methanol (2/1 by volume). Lipid extraction was enhanced by using an additional ultrasound bath (10 min). Non-lipids were removed using an aqueous solution of 0.88% potassium chloride, and this procedure was repeated twice. Organic phases were subsequently pooled and evaporated under nitrogen stream. Lipids were dissolved in hexane and then transmethylated at 90°C for 90 min using 1% H_2SO_4 as catalyst. Analyses of fatty acid methyl esters (FAMEs) were conducted at Uppsala University using an Agilent 6890 N Gas Chromatographer (Agilent Technologies, Santa Clara, California, USA) equipped with a DB-23 column (length 30 m, ID 0.25 mm, film thickness 0.25 μm; Agilent). We applied a split injection (20:1) with an initial temperature of 180°C for 8 min, which was then increased by 2°C min^{-1} to 210°C, and this temperature was finally maintained for 2 min. Helium was used as a carrier gas with an average velocity of 34 cm/s. Peaks of FAMEs were identified using mass spectra and retention times, and a heneicosanoic acid (Nu-Chek Prep. Elysian, Minnesota, USA) was used as an internal standard. Concentrations of fatty acids were calculated based on calibration curve of known FAME mixtures (Nu-Chek Prep). To obtain proportions of ω-3 HUFAs, we summed the proportions of EPA (20:5ω-3) and DHA (22:6ω-3).

Statistical analysis

We used non-parametric Kruskal–Wallis test with Bonferroni-adjusted Dunn's pairwise comparisons to analyze differences between proportions of ω-3 HUFAs in different perch prey.

Data on the contribution of pelagic planktivorous fish were transformed using a reflection (i.e., each score was subtracted from a constant that is larger than the largest score) to remove negative skewness, and an additional log-transformation was applied to reduce (positive) skewness. We used multiple regression model to analyze variation of the proportion of ω-3 HUFAs in muscle tissue of perch. In the model, we included the contribution of pelagic planktivorous fish to the diet (reflected and log-transformed data), sex (with data coded as females = 0; males = 1), and TL as predictors and included all possible two-way interactions. A second multiple regression model was used to analyze variation of GSI in perch. We included the contribution of pelagic planktivorous fish to the diet (reflected and log-transformed data), sex (with data coded as females = 0; males = 1), ω-3 HUFAs, TL, and all possible two-way interactions as predictors. We tested our hypothesis by using a stepwise backward model procedure excluding non-significant interactions, while keeping all main effects. The assumptions of normal distribution and homogeneities of variances were met for regression analyses. IBM SPSS statistics V25 was used for all frequentist analyses.

RESULTS

The isotopic composition of prey groups was distinct and showed typical patterns. Specifically, pelagic planktivorous fish were ^{13}C-depleted compared to benthic resources, and fish had higher $\delta^{15}N$ values compared to lower trophic levels (benthic invertebrates and zooplankton; Fig. 2). The $\delta^{15}N$ and $\delta^{13}C$ values of perch varied from 9.9‰ to 12.5‰ and from −21.2‰ to 17.2‰, respectively (Fig. 2). This indicated that among-individual differences in diet mainly occurred through the use of benthic vs. pelagic resources.
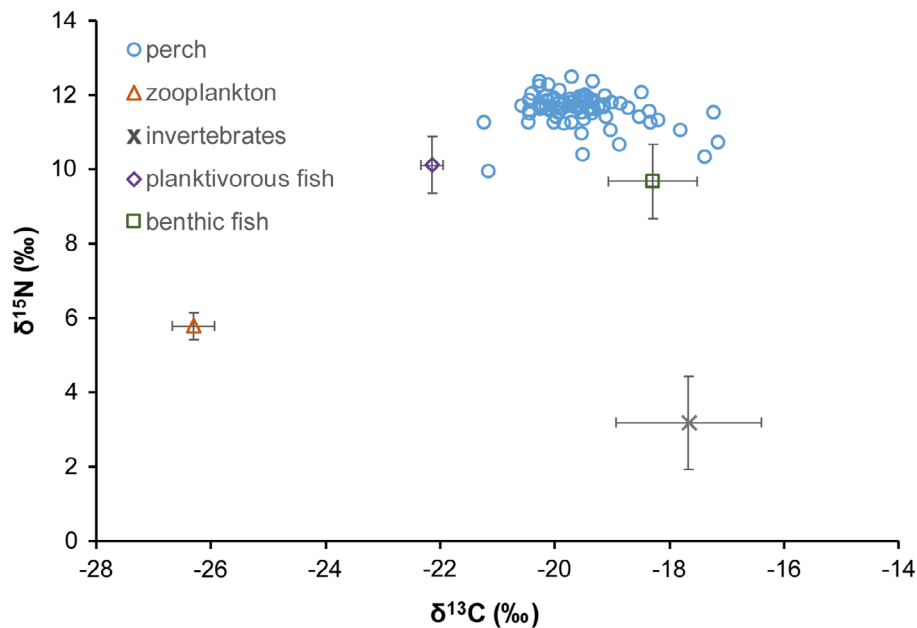
Fig. 2. Isotope biplot of $\delta^{15}N$ and $\delta^{13}C$ values of individual perch from the Baltic Sea and their potential resources (mean ± SD).

As revealed from the Bayesian mixing model, perch fed mostly on fish (average contribution 91.2% ± 2.5). The contribution of pelagic planktivorous fish to the diet of perch varied between 16.7% (95% Bayesian credibility interval [CI] 3.5–37.2%) and 60.7 (95% CI 18.4–89.4%).

We identified 35 and 32 fatty acids in perch and invertebrate samples, respectively. Proportions of ω-3 HUFAs differed significantly between prey groups (Kruskal–Wallis: $H_2 =$ 16.07 $P < 0.001$; all pairwise comparisons between prey groups $P < 0.05$). Proportions of ω-3 HUFAs were much lower in benthivorous prey fish (1.57% ± 0.51 SD) and benthic invertebrates (5.21% ± 2.62 SD), compared to pelagic planktivorous prey fish (46.37% ± 2.55 SD). This highlights the elevated quality of pelagic planktivorous prey fish (Appendix S1: Fig. S1).

The contribution of pelagic fish to the diet of perch and sex had a significant effect on the proportion of ω-3 HUFAs in perch ($t = -4.77$, $P < 0.001$ and $t = -3.85$, $P < 0.001$, respectively) and explained 32.1% of the variation (Appendix S1: Table S2a). Specifically, the proportion of ω-3 HUFAs was higher in females compared to males, and it was also positively associated with the contribution of pelagic fish to the diet of perch (Fig. 3). Body length did not explain the proportion of ω-3 HUFAs in perch (Table 1). Sex and the proportion of ω-3 HUFAs were significantly associated with GSI ($t = -2.75$, $P = 0.008$ and $t = 2.24$, $P = 0.029$, respectively) and explained 24.0% of the variation (Appendix S1: Table S2b). GSI was higher for females compared to males and was also positively associated with increasing proportion of ω-3 HUFAs (Fig. 4). While the highest GSI are found among the individuals with clearly highest proportions of ω-3 HUFA, we note that variation in GSI is high (ranging 0.25–2.8 in females) and that we find no relationship between proportion ω-3 HUFA proportion and GSI among individuals with GSI < 2.0 ($P > 0.05$). The contribution of pelagic fish to the diet of perch and body length had no effect on GSI (Table 1).

DISCUSSION

Our results suggest that perch show individual specialization with respect to the degree to which they incorporate pelagic planktivorous fish into their diet. While all studied perch in this Baltic Sea area had a fish-based diet, the contribution from pelagic planktivorous fish, such as herring,
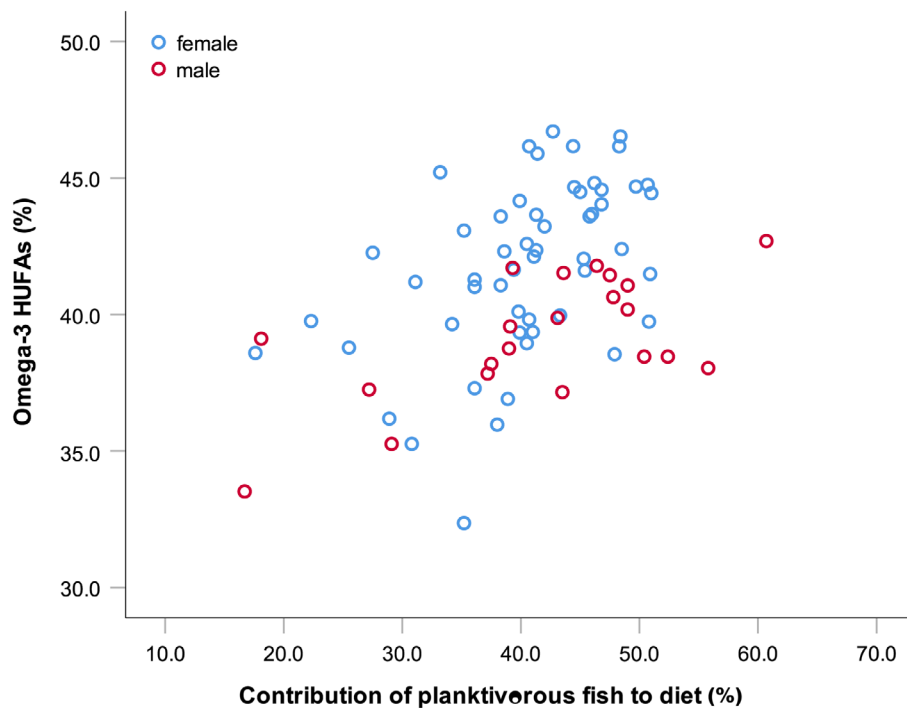
Fig. 3. Relationship between the contribution of pelagic planktivorous fish to the diet of female and male Baltic perch and their ω-3 HUFAs muscle content (%).

Table 1. Results of multiple regression models explaining variation of (a) proportion of ω-3 HUFAs and (b) gonadosomatic index (GSI) of perch.

Model	Predictor	Coefficient	Standard error	t	P
(a) ω-3 HUFAs	**(constant)**	**45.77**	**1.77**	**25.92**	**<0.001**
	Sex	**−2.78**	**0.72**	**−3.85**	**<0.001**
	Contribution planktivorous fish (log reflect)	**−49.07**	**10.29**	**−4.77**	**<0.001**
	TL	<0.01	<0.01	−3.85	0.74
(b) GSI	(constant)	−0.87	0.88	−0.99	0.327
	Sex	**−0.34**	**0.12**	**−2.75**	**0.008**
	Contribution planktivorous fish (log reflect)	−0.41	1.82	0.23	0.821
	TL	<0.01	<0.01	0.66	0.510
	Proportion ω-3 HUFAs	**0.04**	**0.02**	**2.24**	**0.029**

Notes: Bold font depicts significant predictors. Note that in the data, sexes were coded as females = 0 and males = 1.

varied between individuals. In freshwater fish, including perch inhabiting many lakes in Sweden, intraspecific variation in resource use along the benthic–pelagic axis is relatively common, oftentimes accompanied by a divergence in body morphology (Skúlason and Smith 1995). However, this pattern is usually connected to the feeding on either invertebrates or zooplankton, rather than the source of the fish prey (Svanbäck

and Eklöv 2002, Svanbäck et al. 2008, Quevedo et al. 2009). Individual feeding specialization in general reduces intraspecific competition (e.g., in perch, Svanbäck et al. 2008). Specializing on particular types of prey could also have other fitness benefits, due to their quality. For example, pelagic planktivorous fish species are rich in ω-3 HUFAs (see also Litzow et al. 2006, Lau et al. 2012, Strandberg et al. 2015, Scharnweber et al.
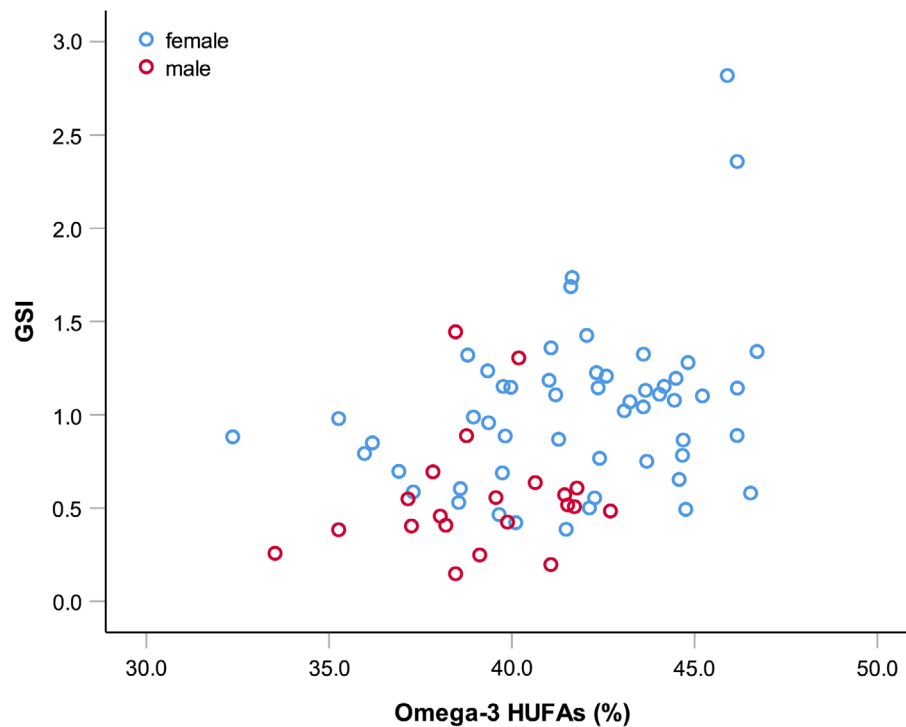
Fig. 4. Relationship between proportions of ω-3 HUFAs in female and male Baltic perch muscle tissues and the gonadosomatic index (GSI).

2016*b*) and specializing on them may thus provide benefits. Our results show a positive relationship between the dietary contribution of pelagic planktivorous fish (fatty acid-enriched) and the proportions of ω-3 HUFAs in muscle tissue of male and female perch. In this study, proportions of ω-3 HUFAs in perch inhabiting a brackish water area varied between 32% and 47%. Thus, it exceeded values of 27–43% reported for freshwater perch (Scharnweber et al. 2016*a*) and the 22–33% in the closely related Yellow perch (*Perca flavescens*; Happel et al. 2015). This might be due the higher proportion of ω-3 HUFA-rich fish prey in the diet of Baltic Sea perch, compared to the diets of lake perch that is mainly composed of ω-3 HUFA-poor invertebrates (Happel et al. 2015, Scharnweber et al. 2016*a*).

Furthermore, the proportions of ω-3 HUFAs in perch were positively associated with GSI in perch of both sexes (although in females found only for individuals with GSI > 2.0), which could lead to a higher fecundity through either the production of more or bigger eggs in

females or more sperm in males. Formation of gonads depends on the provision of lipids, and female eggs are particularly HUFA-enriched (Adams 1998, Pickova et al. 1999, Tocher 2003). For instance, Strandberg et al. (2018) reported a six times higher amount of DHA in vendace roe (*Coregonus albula*) compared to that in muscle tissue. HUFAs are selectively transferred and catabolized from different tissues and organs, including muscles, to be accumulated in gonadal tissue, following seasonal dynamics (Henderson et al. 1984, Schwalme et al. 1993, Tocher 2003). However, specific processes involved as well as the rates and timing of fatty acid mobilization and translocation have not been identified for perch. In this study, we did not measure HUFAs of the gonadal tissue and future research is needed to explore the seasonal dynamics of fatty acid composition of different tissues. Our regression model explained only 32.1% of the variation in GSI, and mobilization processes could be one of the factors explaining the remaining variation in GSI of Baltic Sea perch.

The potential connection between HUFA-rich diets and high fecundity is in line with previous studies on perch raised in aquaculture. These show increased larval survival and stress resistance when broodstock females were fed with DHA- and EPA-enriched diets (Abi-ayad et al. 1997, Henrotte et al. 2010). Similarly, a ω-3-rich diet of the broodstock males resulted in increased sperm functionality, especially the motility (Vassallo-Agius et al. 2001, Lahnsteiner et al. 2009). However, all previous studies have been conducted under controlled laboratory conditions and using artificial diets. Our documentation of fitness benefits associated with individual specialization on high-quality food resources, occurring on a natural scale in a wild population is therefore an important contribution to the discussion of the factors leading to individual specialization. Our results suggest that individual specialization may provide direct physiological benefits when targeted to high-quality prey, benefits that could result in increased reproductive output.

Our study is one of the very few that directly associate the consumption of HUFA-rich resources with general fitness advantages, for example, fecundity, in natural populations. To our knowledge, only two more studies exist on this topic: Twining et al. (2018) showed that the breeding success in Tree swallows (*Tachycineta bicolor*) is strongly influenced by the availability of aquatic insects rich in HUFAs, and Fritz et al. (2017) demonstrated a higher immune response in wolf spiders (*Tigrosa georgicola*) inhabiting wetland habitats, where HUFA-rich aquatic resources are common, compared to spiders living in upland habitats.

While our multiple regression model provided significant effects of the predictors sex and the proportion of ω-3 HUFAs on GSI, the majority of 76% of the variation in GSI remained unexplained by our model, suggesting that other factors unrelated to the ones addressed in this study may also affect GSI. Differences in the gonadal development may also depend on water temperature (Miller et al. 2015), pollution (Segner 2011), parasite load (Šimkova et al. 2005), or potential genetic effects. Furthermore, the positive association to high GSI we observed was not found in individuals with low GSI (<2.0; Fig. 4). This may be because of the seasonal build-up of gonadal size, which is important to account for when comparing GSI values among individuals. At our study site, perch gonad build-up starts after summer and progresses until spawning in late April to early June (Appendix S1: Fig. S2, see www.slu.se/institutioner/akvatiska-resurser/databaser/kul/ for data). At the time of sampling in our study (i.e., early August), gonads were far from their final size, as observed when comparing these GSI values to those of perch captured later in the growing season (Appendix S1: Fig. S2). Thus, the perch individuals with highest GSI (Fig. 4) are likely not general outliers; rather, their specialization on ω-3 HUFA-rich prey may have enabled them to start their seasonal gonadal build-up earlier than the other sampled individuals. Obviously, future studies need to confirm the generality of our results, as only one perch population was sampled, and we can show associative relationships based on rather few individuals, while only suggesting an underlying cause. We therefore encourage multi-seasonal sampling, including the ω-3 HUFAs content in gonads and experiments to further study the link between individual diet specialization on ω-3 HUFA-rich prey and fitness benefits.

In accordance with previous studies (Fritz et al. 2017, Twining et al. 2018), our results are part of the growing evidence that ω-3 HUFAs are not only necessary for optimal growth and health of consumers, but also may lead to a substantial fitness advantage. Specialization on HUFAs-rich prey could therefore potentially alter ecological interactions. It may even promote patterns of populations divergence and thus organismal evolution, as individual specialization within populations can be viewed as one of the very early stages of speciation (Hendry 2009). Focusing on qualitative aspects of trophic interactions and within-population variation in such interactions may therefore also open new avenues for future research on ecological speciation.

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