BOREAL ENVIRONMENT RESEARCH 24: 137–153
ISSN 1797-2469 (online)
Helsinki 23 September 2019

Size-dependent diet composition and feeding of Eurasian perch (*Perca fluviatilis*) and northern pike (*Esox lucius*) in the Baltic Sea

Philip Jacobson[1)*], Ulf Bergström[1)] and Johan Eklöf[2)]

[1)] *Swedish University of Agricultural Sciences, Department of Aquatic Resources, Skolgatan 6, SE-742 42 Öregrund, Sweden (*corresponding author's e-mail: philip.jacobson@slu.se)*
[2)] *Stockholm University, Department of Ecology, Environment and Plant Sciences, Svante Arrhenius väg 20 A, SE-114 18 Stockholm, Sweden*

Received 29 Jun. 2018, final version received 25 Jun. 2019, accepted 10 Apr. 2019

Jacobson P., Bergström U. & Eklöf J. 2019: Size-dependent diet composition and feeding of Eurasian perch (*Perca fluviatilis*) and northern pike (*Esox lucius*) in the Baltic Sea. *Boreal Env. Res.* 24: 137–153.

To understand food web dynamics, knowledge about factors influencing trophic interactions is fundamental. Using stomach content analysis, we investigated size-dependent predator-prey relations of two coastal predatory fish in the Baltic Sea: perch (*Perca fluviatilis*) and northern pike (*Esox lucius*). Perch undergo two ontogenetic diet shifts, from zooplankton to macroinvertebrates at ca. 50 mm; and then to fish at ca. 250 mm. For pike, all sizes (103–810 mm) fed almost exclusively on fish. The fish prey of perch and pike was predominantly three-spined stickleback in spring, and gobiids in late summer. The mean and maximum prey:predator size ratio was larger, while the minimum was smaller for pike compared with perch. Perch and pike fed on smaller-sized gobiids, three-spined and nine-spined stickleback compared within the environment. Our results on size-dependent diets of perch and pike is useful for quantitative analyses of food-web interactions and for ecosystem-based management.

Introduction

Knowledge regarding predator-prey interactions forms the very basis for understanding food webs (Cohen *et al.* 1993), population and community dynamics (Estes *et al.* 2011, Rudolf and Lafferty 2011, de Roos and Persson 2013) and eco-evolutionary processes (Post *et al.* 2008, Bolnick *et al.* 2011). Within aquatic systems where fish constitute a key group of predators, predator-prey interactions are size dependent as prey are often swallowed whole and the maximum prey size is therefore limited by predator gape size (Mittelbach and Persson 1998, Nilsson and Brönmark 2000, Scharf *et al.* 2000). Studies on such size dependence have provided new insight into how size-structured populations and communities respond to size-specific predation and changes in resource availability (Ohlberger *et al.* 2011, van Leeuwen *et al.* 2013, Persson *et al.* 2014). Such responses include biomass overcompensation (Schröder *et al.* 2009, 2014), coexistence of competitors via facilitation (de Roos *et al.* 2008) and alterations in trophic interactions (Miller and Rudolf 2011), which can affect community composition to induce alternative stable states (Walters and Kitchell 2001, Persson *et al.* 2007, Estes *et al.* 2011).

Editor in charge of this article: Örjan Östman

In temperate freshwater systems in the northern hemisphere, two of the most common piscivorous fish are the Eurasian perch (*Perca fluviatilis*) and the northern pike (*Esox lucius*) (hereafter referred to as perch and pike, respectively). Both are visual predators that depend on warm water and vegetation during their early developmental stages (Bry 1996, Snickars *et al.* 2010). In lakes, perch undergo two major ontogenetic diet shifts — from zooplankton to macroinvertebrates at lengths from 9–20 cm, and from macroinvertebrates to fish at lengths from 12–20 cm (Horppila *et al.* 2000, Svanbäck and Eklöv 2002, Estlander *et al.* 2010). Northern pike, on the other hand, undergo only one shift — from zooplankton directly to fish, at lengths from 3–10 cm (Mittelbach and Persson 1998). The earlier onset of piscivory in pike is explained by pike having a larger gape relative to their body size, enabling them to consume larger prey (Mittelbach and Persson 1998).

Perch and pike have, since the last glaciation, colonized the Baltic Sea; one of the largest brackish water bodies on Earth. Due to its low salinity and young evolutionary age, the Baltic Sea is a species-poor system with relatively simple food webs (Bonsdorff 2006). Perch and pike are two dominating piscivorous fish in the coastal areas and therefore have major ecological, economical and recreational values (Östman *et al.* 2016, Donadi *et al.* 2017, Hansson *et al.* 2017). Baltic Sea perch undergo the first diet shift (from zooplankton to macroinvertebrates) at the lengths of 4–7 cm (Karås 1984, Hansson 1985, Sandström and Karås 2002). The second diet shift (from macroinvertebrates to fish) has been reported to occur from the sizes of 5–25 cm (Karås 1984, Hansson 1985, 1987, Andersson 1996, Lappalainen *et al.* 2001, Mustamäki *et al.* 2014). The limited data available on the Baltic Sea pike diet indicates that they, in contrast to freshwater pike (which is strictly piscivorous), eat both fish and macroinvertebrates (Karås 1984). Recent studies suggest that abundant perch and pike, by feeding on smaller fish such as the three-spined stickleback (*Gasterosteus aculeatus*), can maintain a trophic cascade that limits the biomass of filamentous algae in shallow Baltic Sea bays (Eriksson *et al.* 2009, 2011, Donadi *et al.* 2017). However, perch and pike populations have declined along parts of the coast (Lehtonen *et al.* 2009, Ljunggren *et al.* 2010, Bergström *et al.* 2016), which negatively impacts the coastal ecosystem and fisheries. Therefore, a better understanding about the size-specific diet of Baltic Sea perch and pike will not only improve our basic understanding about their feeding ecology, which in turn affects their individual growth, maturation, reproduction success and survival (Huss *et al.* 2008, Hixon *et al.* 2014, Persson *et al.* 2014), but it could also increase our understanding of how the ecological function of these predators change over ontogeny. Against this background, the aim of this study was to assess the size-specific diet composition and size-selective feeding of Baltic Sea perch and pike. To this end, we analysed fish stomach content and fish catch data from a large-scale field survey along the central Swedish coast of the Baltic Sea.

Materials and methods

Field Sampling

Perch and pike were sampled in 32 bays along a 360 km stretch of the central Swedish Baltic Sea coast (Fig. 1). Sampling was conducted twice; late spring (5 May–6 June) and late summer (12 August–9 September) in 2014. To ensure sampling from different perch and pike populations, the bays were located ≥ 10 km apart (exceeding the maximum migration distance for most individuals (Saulamo and Neuman 2002)) or separated by natural movement barriers like land or large open-water bodies. In the late spring, fish were caught using Nordic survey gillnets, following the European Union standards for freshwater surveys (https://www.sis.se/api/document/preview/8014404/). The 30 × 1.5 m nets consisted of twelve 2.5 m panels with the following mesh sizes (in correct order): 43, 19.5, 6.25, 10, 55, 8, 12.5, 24, 15.5, 5, 35 and 29 mm knot-to-knot. At each bay, four to five nets were set at 1.5–3 m depth, > 30 m apart and > 10 m from land and bay openings. The nets were set between 16:00–19:00 and lifted between 07:00–09:00 the following morning. All caught fish were counted and measured (total length, to the nearest 1 mm). Second, the

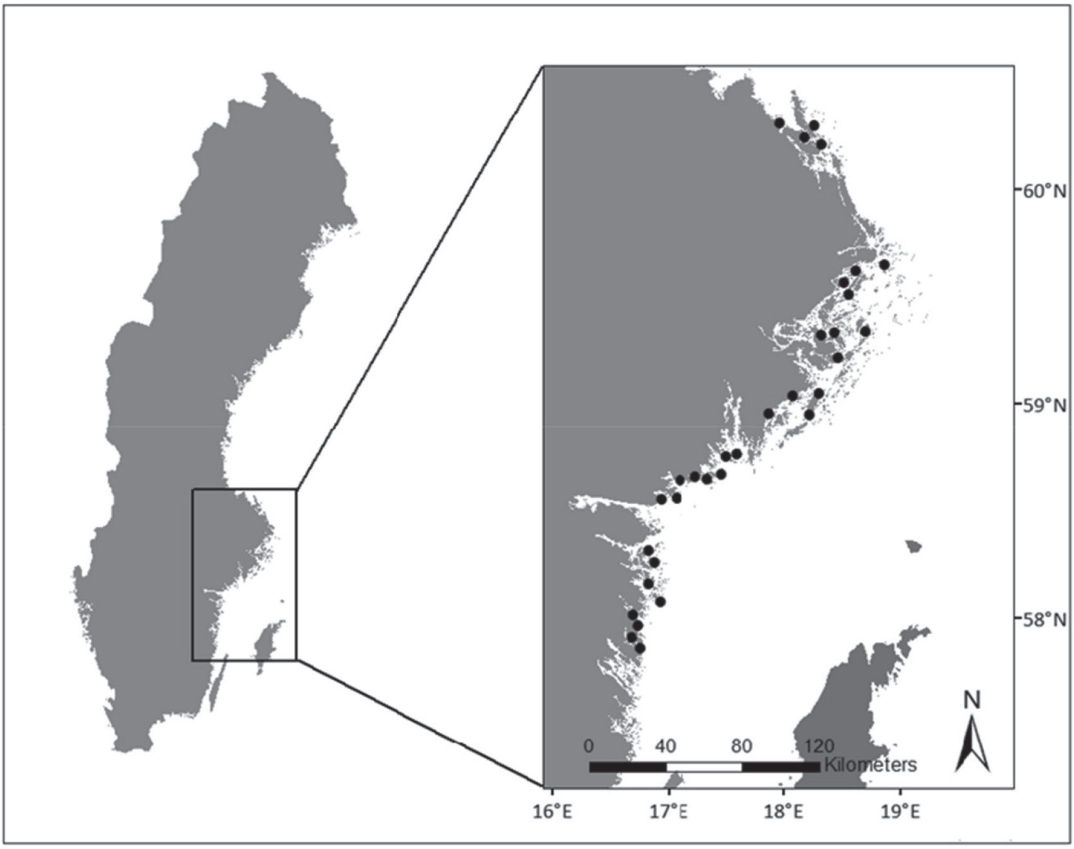


Fig. 1. Map showing the location of the 32 shallow bays (black dots) sampled along the central Swedish Baltic Sea coast.

stomachs of five perch and pike, sorted at 50 mm length classes (e.g., 0–49 mm, 50–99 mm) were dissected, placed in labelled plastic bags, stored on ice during transport, and frozen at –20 °C. The sex and maturation status of each individual was noted. Individuals < 100 mm in length were transported and frozen whole, and the stomachs were dissected in the lab.

In the late summer, fish were sampled in the same 32 bays using low-impact underwater detonations (see Snickars *et al.* 2007 for details). This standardized method is used to sample small young-of-the-year fish, which dominate in late summer but are not caught efficiently using other sampling methods in areas with heterogeneous topography or dense vegetation (Snickars *et al.* 2007). The species of the collected fish were identified and counted, and up to 30 randomly selected individuals were measured (total length, to the nearest 1 mm), stored in 96% ethanol and later studied for stomach content analysis. The fish sampling procedures were approved by the ethical board on animal experiments of the county court of Uppsala, Sweden (permit C 139/13).

Stomach content analysis

Laboratory analyses of perch and pike stomach content were conducted using standard ocular methods (Hyslop 1980). After thawing and extracting all the content from an individual stomach, all food items were identified to the lowest taxonomic level possible. Then, intact prey organisms were measured (total body length, to the nearest 1 mm), counted and sorted together with similar items that include small parts and pieces. All counted food items were then grouped into broader taxonomic groups to enable comparisons between prey groups (Appendix Table A1). For each stomach, the proportion of each prey taxon, determined to the highest taxonomic resolution, was estimated by eye in relation to the stomach fullness (from 0–100% of the surface area of a petri dish). To simplify the graphical presentation of the data, perch and pike individuals were grouped into length classes (25 mm steps for perch and juvenile pike; 100 mm steps for adult pike). For each length class, we divided the proportions for each prey category with the sum of proportions for all prey categories within each length-class to obtain the contribution of each prey category to the total diet.

Predation window

We used the body lengths of whole prey found in stomachs to estimate perch and pike predation windows (i.e., the minimum, mean and maximum prey lengths for a given predator length). We fitted linear regression models to the minimum (1st percentile), mean and maximum (99th percentile) prey size (Scharf *et al.* 1998, 2000), and used the slopes as estimates for the minimum, mean and maximum prey:predator size ratios, respectively.

Size-selective feeding

To test whether perch and/or pike feed on prey fish that are smaller, similar to or larger than the fish in their surrounding environment, we compared the lengths of consumed fish species with the length distribution of the same fish species caught in our gillnets and during detonation fishing (the environment). We compared these lengths (consumed by perch/pike versus length distributions in the environment) for piscivorous perch and pike caught in late spring and for small perch and pike caught in late summer.

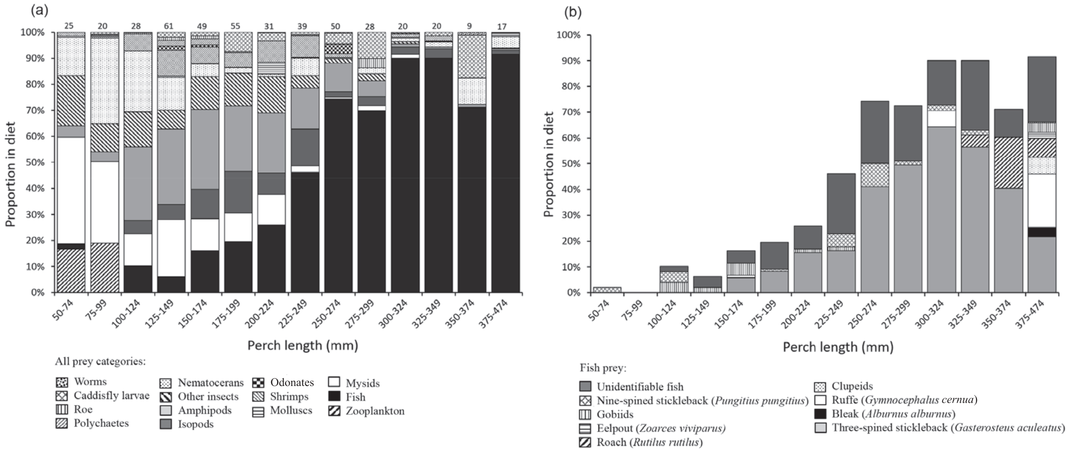
Statistical analyses

All statistical analyses was performed using the software R ver. 3.5.1 (R Core Team 2018). To estimate the minimum and maximum prey:predator size-ratios for perch and pike, quantile regression models were fitted using the *rq()* function of the R-package *quantreg* ver. 5.36 (Koenker 2018). Model assumptions were assessed visually and data transformations were performed when necessary. To test whether perch or pike selectively feed on prey fish of certain sizes, we used one-way ANOVA to compare the length distribution of consumed fish prey species groups ($n \geq 5$ consumed individuals) with their corresponding length distribution in the environment.

Results

Perch diet composition in May–June

Of the 643 perch analysed, 452 (70%) had content in their stomachs (Fig. 2a). Zooplankton was found in stomachs of perch in the two smallest length classes (50–74 mm and 75–99 mm) and the largest perch with zooplankton was 95 mm (Fig. 2a). Meanwhile, fish prey were found in all but one length class (74–99 mm). The proportion of fish in the diet increased with perch length, from 2% in length class of 50–74 mm to 92% in the length class of 375–474 mm, and constituted ≥ 50% of the diet in perch in the size range of 250–474 mm. Eight different prey fish species were found in the stomachs, of which the three-spined stickleback contributed most to the total diet (Fig. 2b). Most fish prey (seven species) was found in stomachs from the largest length class (375–474 mm). Mysids and larger shrimps occurred in length classes between 50–324 mm and 50–349 mm, respectively. Amphipods and isopods were found in stomachs from all length classes and was highest in the intermediate length classes (100–249 mm), constituting 30–42% of the total diet (Fig. 2a). *Gammarus* spp., *C. volutator* and *Idotea* spp. were the most common prey taxa among the amphipods and isopods (Fig. 2c). The categories “other insects” and “nematocerans” also occurred in all length classes and decreased in proportion with increasing perch length (Fig. 2a). The proportion of caddisfly larvae was most common in the length class of 350–374 mm. Finally, odonates, poly-



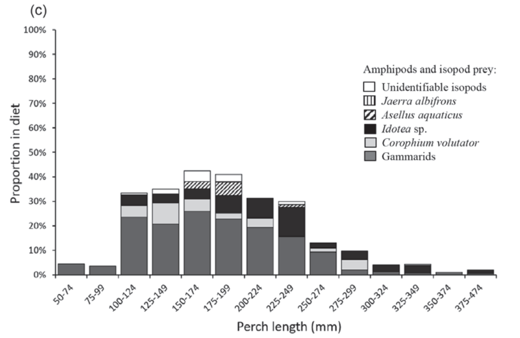


Fig. 2. Diet of Eurasian perch (*Perca fluviatilis*) sampled during May–June 2014 using gillnets. Proportion in diet is the contribution of each food category to the total amount of prey within each length class of perch. Length class is expressed in mm. Number of perch within each length class is shown above each bar.

chaetes, annelids, oligochaetes and roe were the least common food categories recorded (Fig. 2a).

Perch diet composition in August-September

Of the 224 juvenile perch caught using detonation fishing in late summer, 176 (79%) had content in their stomachs. Zooplankton was found in all three length classes but the contribution to diet decreased from 93% to 11% with increasing perch length (from 42–99 mm). In the length class of 50–74 mm, the proportion of zooplankton was 50% and the remaining 50% was a mix of fish, mysids and nematocerans (Fig. 3a). Fish prey were recorded in the two largest length classes (50–74 and 75–99 mm), and increased with length from 13% to 37%. Two fish taxa were found: gobiids (*Gobiidae* spp.), constituting 12% and 21% of the diet of the two length classes; and three-spined stickleback, constituting 0.44% of the total diet in length class of 75–99 mm (Fig. 3b). Mysids, amphipods and isopods were also recorded in the two largest length classes (50–74 mm and 75–99 mm) and increased from 14% to 29% with length. Of the amphipods and isopods, gammarids were the most common prey (Fig. 3a and 3c). Nematocerans were recorded in all three length classes (42–49 mm, 50–74 mm and 75–99 mm) and varied from 2% to 6%. “Other insects”, molluscs, odonates and polychaetes only occurred sporadically (Fig. 3a).

Pike diet composition in May-June

Of the 34 stomachs of adult pike analysed, 26 (76%) had content. The lower catches of pike compared with perch was most likely explained by a lower population density in combination with a lower catchability of pike in gillnets (Kinnerbäck 2001). Fish completely dominated the

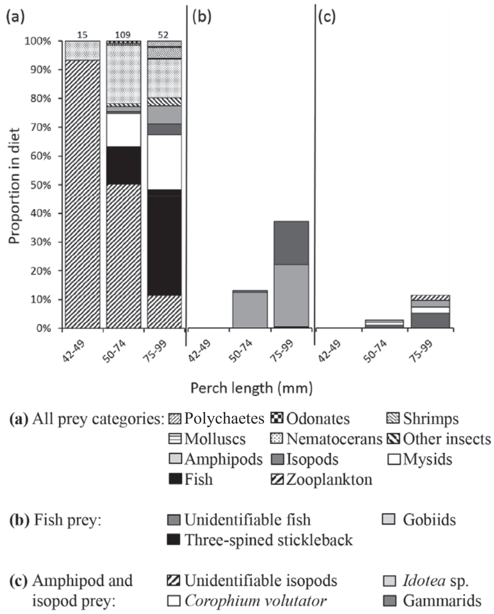


Fig. 3. Diet of Eurasian perch (*Perca fluviatilis*) sampled during August–September 2014 using underwater detonations. The proportion in diet is the contribution of each food category to the total amount of prey within each length class of perch. Length class is expressed in mm. Number of individuals within each length class is shown above each bar.

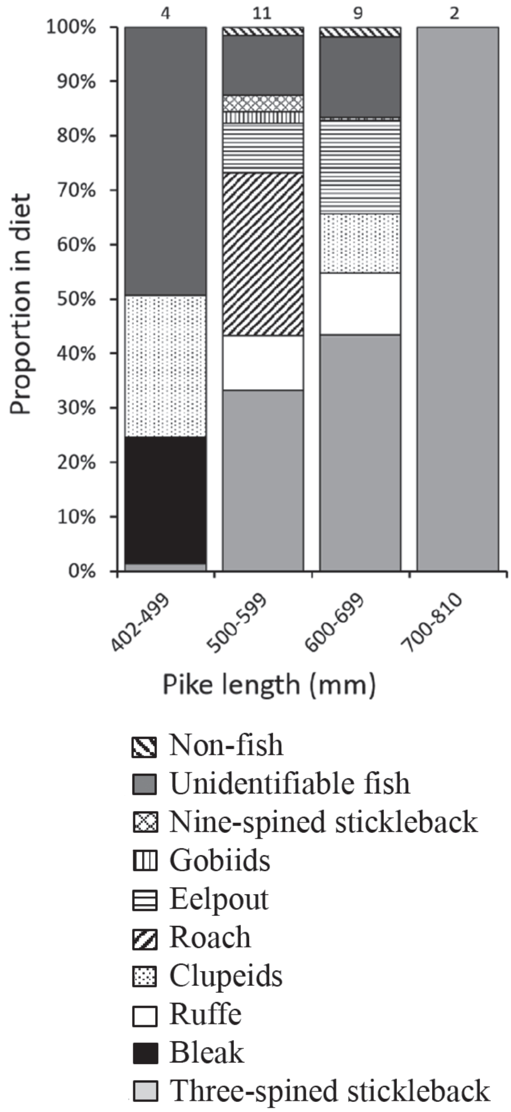


Fig. 4. Diet of northern pike (*Esox lucius*) sampled during May–June 2014 using gillnets. Proportion in diet is the contribution of each food category to the total amount of prey within each length class of pike. Length classes are expressed in mm. Number of individuals within each length class is shown above each bar. The non-fish diet category includes mysids, amphipods, molluscs and odonates.

diet in all length classes (Fig. 4). In total, eight different fish prey species were found in the pike stomachs. Three-spined stickleback was the most common prey in the three largest length classes, and increased from 33% to 100% in the diet with pike length. Other prey items than fish were rare (< 1.8% of the total diet; Fig. 4).

Pike diet composition in August-September

The stomachs of 79 juvenile pike were analysed, of which 64 (81%) had content. Fish were the main prey in all length classes (83–100% of total content), and four prey fish species were recorded (Fig. 5a). Gobiids were the most common fish prey (found in all five length classes, varying from 32% to 81% of the total diet), followed by clupeids (0–45%), nine-spined stickleback (0–7%) and three-spined stickleback (0–4%) (Fig. 5b). Zooplankton was recorded in only one stomach in the smallest length class (103–124 mm). Isopods were found in the three smallest length classes, constituting 1–13% of the diet. Shrimps were recorded in the size range of 125–174 mm, constituting 3–5% of the total diet, while amphipods, molluscs, nematocerans

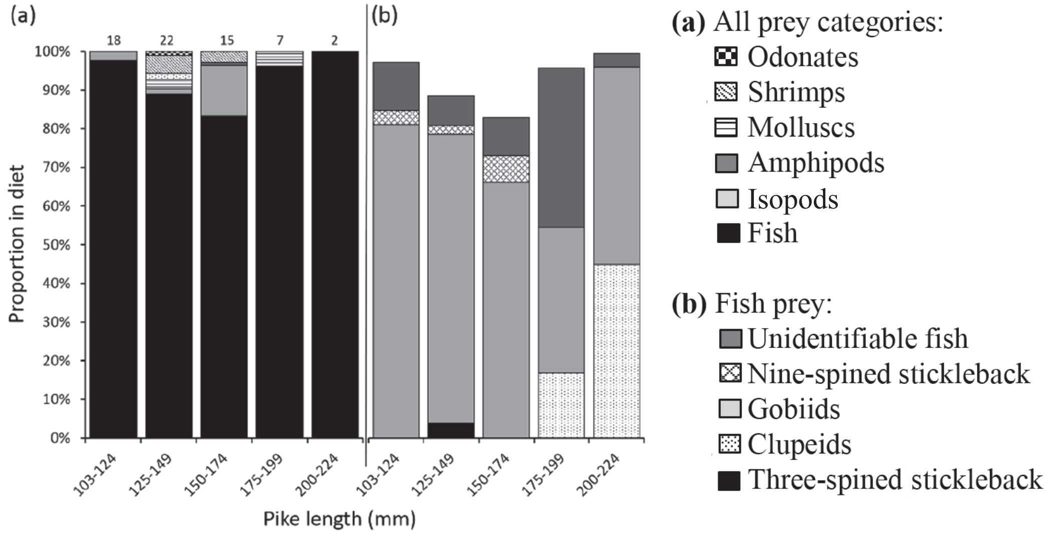


Fig. 5. Diet of northern pike (*Esox lucius*), sampled during August–September 2014 using underwater detonations. Proportion in diet is the contribution of each food category to the total amount of prey within each length class of pike. Length classes are expressed in mm. Number of individuals within each length class is shown above each bar.

and odonates constituted a minor proportion (0–5%) of the total diet (Fig. 5a).

Predation window

In perch, the minimum, mean and maximum prey:predator size ratio were 2.2% ($SE = 0.0014$, $p < 0.05$), 6.5% ($SE = 0.0024$, $p < 0.05$) and 30.2% ($SE = 0.027$, $p < 0.05$), respectively (minimum: $y = 0.022x - 1.60$; mean: $y = 0.065x + 0.65$; maximum: $y = 0.302x - 4.04$) (Fig. 6a). In pike, the minimum prey:predator size ratio was –0.23% ($SE = 0.0032$, $p = 0.46$) while the mean and maximum prey:predator size ratio were 9.8% ($SE = 0.010$, $p < 0.05$) and 36.5% ($SE = 0.050$, $p < 0.05$) respectively (minimum: $y = -0.0023x + 3.32$; mean: $y = 0.098x + 4.78$; maximum: $y = 0.365x + 12.49$) (Fig. 6b).

Size-selective feeding

The consumable biomass of the prey fish community increased with perch and pike size (Appendix Figs. A1 and A2). When comparing the lengths of consumed prey with prey in the environment, perch caught in late spring fed on smaller individuals of three-spined stickleback (one-way ANOVA: $F_{1,\,14073} = 771.4$, $p < 0.001$) and nine-spined stickleback (one-way ANOVA: $F_{1,\,464} = 90.01$, $p < 0.001$), while there was no difference for ruffe (one-way ANOVA: $F_{1,\,903} = 2.35$, $p = 0.126$) (Fig. 7a). Pike also fed on smaller three-spined stickleback than in the environment (one-way ANOVA: $F_{1,\,13888} = 32.99$, $p < 0.001$) (Fig. 7b). Due to small sample sizes ($n < 5$), comparison of consumed and caught fish prey was not assessed for any of the other consumed fish prey groups (Fig. 7a, and 7b). In late summer, perch fed on smaller gobiids (one-way ANOVA: $F_{1,\,1411} = 88.62$, $p < 0.001$, log-transformed lengths to fulfil the assumption of normal-distributed residuals) (Fig. 7c). Pike also fed on smaller gobiids (one-way ANOVA: $F_{1,\,1488} = 115.5$, $p < 0.001$, log-transformed lengths to fulfil the assumption of normal-distributed residuals), while there was no difference when feeding on clupeids (one-way ANOVA: $F_{1,\,615} = 0.61$, $p = 0.44$) compared to in the environment (Fig. 7d).

Discussion

Perch and pike constitute the two dominating piscivorous fishes in coastal areas of the Baltic

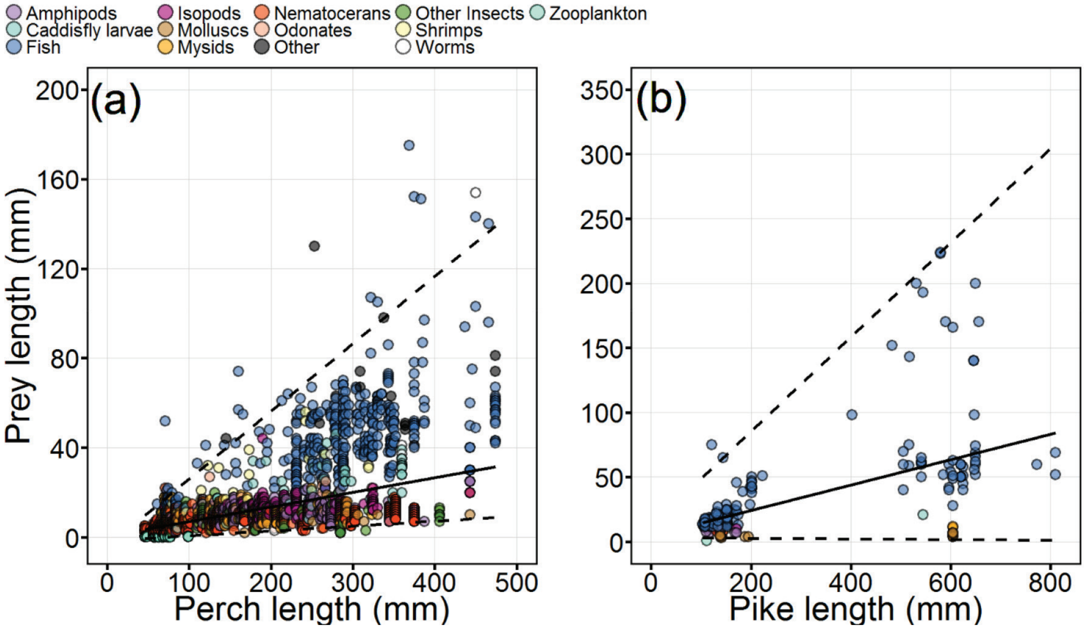


Fig. 6. Predation window of (**a**) Eurasian perch (*Perca fluviatilis*) and (**b**) northern pike (*Esox lucius*) in the Baltic Sea. Dotted lines show the minimum and maximum prey:predator size ratios and the solid line represents the mean prey:predator size ratio. Minimum and maximum lines are quantile regression models fitted to the 1st and 99th quantile, respectively, while the mean solid line is fitted using a linear regression model.

Sea. Yet, knowledge about their size-specific diet composition and prey preference is scarce. Using data from 868 perch and 113 pike caught in 32 bays along a 360 km coastal stretch, we show that Baltic Sea perch undergo two ontogenetic diet shifts, from zooplankton to macroinvertebrates, and from macroinvertebrates to fish, while pike feed predominantly on fish in all size classes investigated (100–810 mm in length). The maximum prey size increased with predator size (30.2% and 36.5% for perch and pike, respectively), while the minimum prey size increased with 2.2% for perch but did not change with increased body size for pike. Consequently, the consumable part of the prey fish community increase with predator body size. In addition, perch and pike feed relatively more on smaller prey individuals of three of the most common fish prey than what appears to be available to them; three- and nine-spined sticklebacks and gobiids.

Baltic Sea perch fed on 14 taxa from a wide variety of organism groups. However, the contribution of each of the taxa to the total diet changed considerably with perch size. In perch caught in late spring, zooplankton constituted a minor proportion of the total diet in the two smallest length classes (size range 50–99 mm). For perch caught in late summer, zooplankton dominated the diet for lengths < 50 mm while constituting a minor part of the diet in the length class of 75–99 mm, indicating that perch switch from zooplankton to invertebrates in the size-range of 50–74 mm. This size range corresponds well with those previously reported for Baltic Sea perch (Karås 1984, Hansson 1985, Sandström and Karås 2002, Mustamäki *et al.* 2014), but is considerably lower than the size range reported for freshwater perch of 90–200 mm (Horppila *et al.* 2000, Svanbäck and Eklöv 2002, Estlander *et al.* 2010). The reasons for this marked difference in size thresholds between Baltic and freshwater perch may be explained by differences in the available macroinvertebrate prey assemblages and the amount of zooplankton available for perch to feed on. In lakes, perch macroinvertebrate diet is dominated by insect larvae and isopods (Horppila *et al.* 2000,

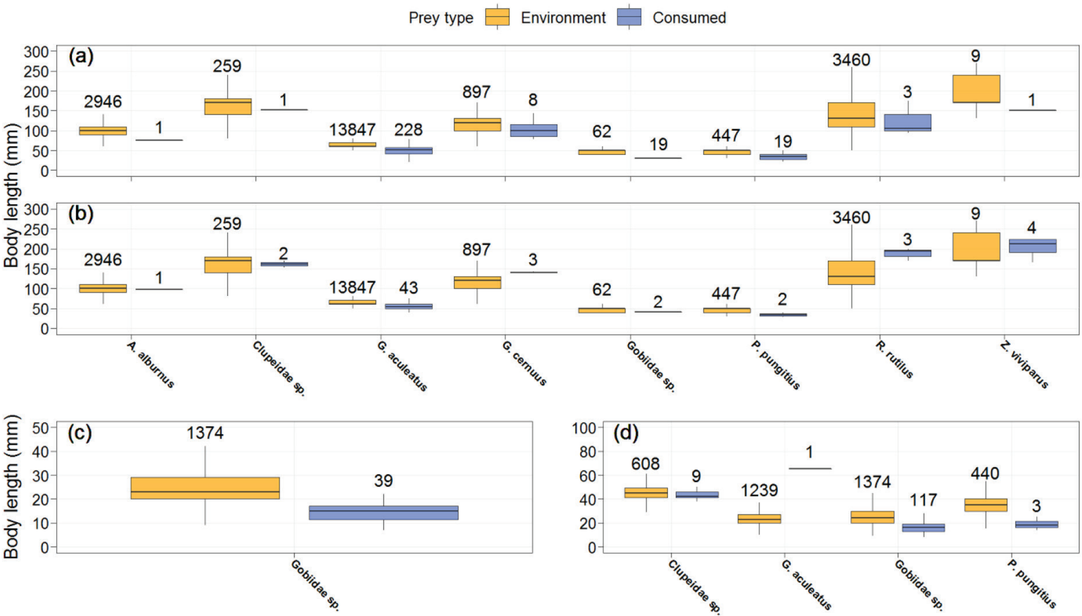


Fig. 7. Size-distribution of each consumed fish species or groups caught in 32 shallow bays along the central Swedish Baltic Sea coast (orange boxes) and consumed (blue boxes) by (**a**) piscivorous (≥ 250mm) Eurasian perch (*Perca fluviatilis*) caught in May–June, (**b**) large (≥ 402 mm) northern pike (*Esox lucius*) caught in May–June, (**c**) small perch (42–99 mm) caught in August–September and (**d**) small northern pike (103–224 mm) caught in August –September. The number above each box denote the number of measured individuals for each fish prey species or group. The black line denotes the median body size, the box range denote the 25th and 75th percentile of the size-range and whiskers denote values < 25th and > 75th percentile.

Svanbäck and Persson 2004, Estlander *et al.* 2010), while in the Baltic Sea, also mysids and amphipods are an important part of the diet (see Results). Lower zooplankton densities in the coastal region of the Baltic Sea compared with freshwater lakes, and higher densities of mysids and amphipods, could therefore explain the earlier shift to macroinvertebrate prey in the Baltic Sea (Mustamäki *et al.* 2014). It is possible that the higher diversity of potential prey items for Baltic Sea perch could increase consumer fitness (Lefcheck *et al.* 2013).

The second ontogenetic diet shift in perch (from macroinvertebrates to fish) occurred at a length of 250 mm (even though fish prey were also recorded in smaller length classes). This size threshold was larger compared with those found in freshwater perch; 100–200 mm (Horppila *et al.* 2000, Svanbäck and Eklöv 2002, Estlander *et al.* 2010, Svanbäck *et al.* 2015), but concurs with some Baltic Sea studies (Karås 1984, Andersson 1996, Lappalainen *et al.* 2001). Meanwhile, Hansson (1985, 1987) and Mustamäki *et al.* (2014) reported the shift to occur at smaller lengths in other areas of the Baltic Sea; 75–175 mm (northern Bothnian Bay, Gulf of Finland, southern Bothnian Sea, northern and central Baltic Proper), 150–210 mm (northern, central and southern Bothnian Bay) and 50–74 mm (Åland Islands), respectively. The perch in our study are larger at the onset of piscivory compared with perch found in freshwater and in some regions of the Baltic Sea, which could be explained by differences in the size, abundance and diversity of both macroinvertebrate and fish prey. If macroinvertebrates constitute a large part of the available prey biomass, a shift to piscivory might not be needed to sustain a high energy intake at lengths ≤ 250 mm. Instead, lake studies suggest that omnivory (feeding on a mixed diet of zoobenthos and fish) reduces intra- and interspecific competition and significantly increases piscivore population sizes and control over smaller fish (Vander Zander *et al.* 2005). Consequently, macroinvertebrate diversity and density in relation to fish prey diversity and density may influence the size at which the two major dietary shifts occur (see also Karås 1984, Mustamäki *et al.* 2014). In summary, even though there is a clear sequence of shifts in the dominating prey type over perch ontogeny, macroinvertebrates constitute an important prey for Baltic Sea perch of intermediate length classes (100–250 mm).

In contrast to perch, the Baltic Sea pike fed almost exclusively on fish and had already undergone a dietary shift from zooplankton to fish at the smallest size caught (100 mm). This piscivorous diet is similar to that reported from both freshwater areas and in the Baltic Sea (Karås 1984, Mittelbach and Persson 1998). Adult pike fed on a range of different fish species, but the diet was dominated by the three-spined stickleback. Previous experimental studies have shown that pike, when given a choice, fed primarily on other fish species than three-spined stickleback (Hoogland *et al.* 1956, Nilsson 2010). Here, the dominance of three-spined sticklebacks as a pike prey most likely reflects the very high densities of stickleback during the spring spawning period (Bergström *et al.* 2015, Byström *et al.* 2015), potentially making sticklebacks the most energetically efficient prey to feed on. The contribution of three-spined stickleback in the diet was higher in the largest length classes of pike compared with smaller length classes, despite that other, larger fish prey were available for pike to consume (Appendix Figs. A1 and A2). Also, pike fed on smaller three-spined stickleback individuals compared within the environment. That predominantly small three-spined stickleback individuals were fed upon by large pike could be due to the morphological defences of sticklebacks, which can restrict predation from perch, pike (Hoogland *et al.* 1956) and rainbow trout (*Oncorhynchus mykiss*) (Lescak and von Hippel 2011), potentially making smaller stickleback individuals easier to consume than large ones. Also, these findings indicate that the spines of sticklebacks could be easier to handle for large pike. Similar results have been shown for Baltic salmon feeding at sea, indicating that large salmon feed more on sticklebacks than small salmon (Jacobson *et al.* 2018). Also, pike keeps feeding on small prey as they become large, which has been reported for northern pike in North America (Gaeta *et al.* 2018). Consequently, given that the minimum prey:predator size ratio for pike decreased with increasing size, and that three-spined stickleback was common as prey for adult pike, small fish prey species seem to constitute an important resource for adult pike in our study area.

For small pike and perch (which were predominantly caught in late summer), gobiids was the most common fish prey. This difference (compared to stickleback being a dominant prey in late spring) most likely reflects the seasonality of available prey and morphological differences between three-spined sticklebacks and gobiids. Gobiids and sticklebacks were the two smallest (Fig. 7c and 7d) and most abundant fish prey species in late summer (Appendix Table A3) available for perch and pike to consume (Fig. 7c and 7d). Gobiids lack protective body armour and are therefore easier to feed upon than three-spined stickleback by small juvenile perch and pike (Hoogland *et al.* 1956, Reist 1980, Lescak and von Hippel 2011).

The minimum and maximum predator-prey relationships of perch (2.2% and 30.2%, respectively) were smaller than those assumed based on feeding experiments (6% and 45%; Claessen *et al.* 2000), while only the minimum was smaller and the maximum in the same range as in one other field study (minimum: 10–30%; maximum: 20–50% in Dörner and Wagner 2003). This difference could be explained by differences in consumed prey species, as the assumed predation window from Claessen *et al.* (2000) was estimated on the prey size of cannibalistic perch, while the prey sizes and species here included both fish, macroinvertebrates, insects and zooplankton. Moreover, the field-based diet study of perch by Dörner and Wagner (2003) was dominated by roach (*Rutilus rutilus*), pike-perch (*Sander lucioperca*) and perch. Here, we show a smaller maximum prey size of perch despite large fish prey being available as potential prey. The minimum predator-prey size relationship estimate for pike (–0.23%) was smaller compared to other studies, while the maximum estimate (36.5%) was smaller than most studies (maximum: 20–42% in Wahl and Stein 1993; minimum: ~2.5%; maximum: 50% in Pierce *et al.* 2001; maximum: 38–45% in Gaeta *et al.*

2018). Second, pike had a larger mean and maximum prey-predator size ratio compared to perch (9.8% and 36.5% vs. 6.5% and 30.2%, respectively), showing that pike consume larger prey compared to equally-sized perch. Also, as pike grow larger than perch, large pike can feed on a larger proportion of the entire prey fish community (Appendix Figs. A1 and A2). This suggests that the range of consumable prey sizes increase with perch and pike body size and that large perch and pike have more available fish prey biomass to feed upon than small individuals.

Cannibalism is relatively common in freshwater perch and pike populations (Smith and Reay 1991, Mehner *et al.* 1996, Claessen *et al.* 2000) but was not recorded in this study (a similar result was observed in Mustamäki *et al.* 2014). A potential reason could be the abundant and diverse fauna of small fish prey in shallow Baltic Sea bays (Fig. 7, Appendix Figs. A1, A2 and Table A3), reducing the likelihood to feed on conspecifics (see also Mehner *et al.* 1996).

Conclusion

Our results demonstrate that both prey species composition and prey size (within taxa) change with perch and pike body size. Moreover, there is a clear diversification of prey sizes with increasing body size, such that large individuals feed on a mix of small, medium and large prey organisms. This indicates that the ecological role of these predators depend not only on prey community composition, but also on predator and prey size distributions. As both perch and pike predation can strongly influence the structure and functioning of the Baltic Sea coastal ecosystem (Donadi *et al.* 2017), our results contribute to a better understanding of how the abundance and size structure of these predator populations may affect food web configuration and function. Such knowledge is important for ecosystem-based management aimed at maintaining both fisheries and healthy habitats.

Acknowledgements: We thank; the property and fishing right owners around each bay for facilitating the field work; G. Johansson, G. Lilliesköld Sjöö, E. Mörk, S. Skoglund, M. van der Snoek, M. van Regteren, V. Thunell, S. Donadi, Å. Austin-Nilsson, J. P. Hansen, G. Sundblad, B.K. Eriksson and J. Sagerman for excellent assistance in the field; S. Skoglund for assisting with the stomach content analysis; and L. Laikre, A. Andersson and K. Tahvanainen for lending lab-space and material when needed; two reviewers for their valuable comments on the previous version of the manuscript. This study is a product of project Plant-Fish (http://www.plantfish.se) and was funded by Formas (grant 2013-1074) and in kind support from Groningen University (Netherlands).

References

Andersson J. 1996. *Provfiske Gamlebyviken 1996* (Master's Thesis; in Swedish). Kalmar University.

Bergström L., Heikinheimo O., Svirgsden R., Kruze E., Ložys L., Lappalainen A., Saks L., Minde A., Dainys J., Jakubavičiūtė E., Ådjers K. & Olsson J. 2016. Long term changes in the status of coastal fish in the Baltic Sea. *Estuar. Coast. Shelf Sci.* 169: 74–84.

Bergström U., Olsson J., Casini M., Eriksson B.K., Fredriksson R., Wennhage H. & Appelberg M.2015. Stickleback increase in the Baltic Sea — A thorny issue for coastal predatory fish. *Estuar. Coast. Shelf Sci.* 163: 134–142.

Bolnick D.I., Amarasekare P., Araujo M.S., Burger R., Levine J.M., Novak M., Rudolf V.H., Schreiber S.J., Urban M.C. & Vasseur D.A. 2011. Why intraspecific trait variation matters in community ecology. *Trends Ecol. Evol.* 26: 183–192.

Bonsdorff E. 2006. Zoobenthic diversity–gradients in the Baltic Sea: Continuous post-glacial succession in a stressed ecosystem. *J. Exp. Mar. Biol. Ecol.* 330: 383–391.

Bry C. 1996. Role of vegetation in the life cycle of pike. *Pike* Springer, Netherlands: 45–46.

Byström P., Bergström U., Hjälten A., Ståhl S., Jonsson D. & Olsson J. 2015. Declining coastal piscivore populations in the Baltic Sea: Where and when do sticklebacks matter? *Ambio* 44: 462–471.

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

Cohen J.E., Pimm S.L., Yodzis P. & Saldaña J. 1993. Body sizes of animal predators and animal prey in food webs. *J. Anim. Ecol.* 62: 67–78.

de Roos A.M. & Persson L. 2013. *Population and Community Ecology of Ontogenetic Development*. Monographs in Population Biology, Princeton University Press, Princeton, New Jersey, USA.

de Roos A.M., Schellekens T., van Kooten T. & Persson L. 2008. Stage–specific predator species help each other to persist while competing for a single prey. *Proceedings of the National Academy of Sciences* 105: 13930–13935.

Donadi S., Austin Å.N., Bergstrom U., Eriksson B.K., Hansen J.P., Jacobson P., Sundblad G., van Regteren M. & Eklof J.S. 2017. A cross-scale trophic cascade from large predatory fish to algae in coastal ecosystems. *Proc. R. Soc. B* 284: 20170045.

Dörner H. & Wagner A. 2003. Size-dependent predator-prey relationships between perch and their fish prey. *J. Fish Biol.* 62: 1021–1032.

Eriksson B.K., van Sluis C., Sieben K., Kautsky L. & Raberg S. 2011. Omnivory and grazer functional composition moderate cascading trophic effects in experimental Fucus vesiculosus habitats. *Mar. Biol.* 158: 747–756.

Eriksson B.K., Ljunggren L., Sandström A., Johansson G., Mattila J., Rubach A., Råberg S. & Snickars M. 2009. Declines in predatory fish promote bloom–forming macroalgae. *Ecol. Appl.* 19: 1975–1988.

Estes J.A., Terborgh J., Brashares J.S., Power M.E., Berger J., Bond W.J., Carpenter S.R., Essington T.E., Holt R.D., Jackson J.B.C., Marquis R.J., Oksanen L., Oksanen T., Paine R.T., PikitchE.K., Ripple W.J., Sandin S.A., Scheffer M., Schoener T.W., Shruin J.B., Sinclair A.R.E., Soulé M.E., Virtanen R. & Wardle D.A. 2011. Trophic downgrading of planet earth. *Science* 333: 301–306.

Estlander S., Nurminen L., Olin M., Vinni M., Immonen S., Rask M., Ruuhijarvi J., Horppila J. & Lehtonen H. 2010. Diet shifts and food selection of perch *Perca fluviatilis* and roach *Rutilus rutilus* in humic lakes of varying water colour. J. Fish Biol. 77: 241–256.

Gaeta J.W., Ahrenstorff T.D., Diana J.S., Fetzer W.W., Jones T.S., Lawson Z.J., McInerny M.C., Santucci V.J., Jr. & Vander Zanden M.J. 2018. Go big or ... don't? A field-based diet evaluation of freshwater piscivore and prey fish size relationships. *PLoS One* 13: e0194092.

Hansson S. 1985. Local growth differences in perch (*Perca fluviatilis* L.) in a Baltic archipelago *Hydrobiologia* 121: 3–10.

Hansson S. 1987. Effects of pulp and paper mill effluents on coastal fish communities. *Ambio* 16: 344–348.

Hansson S., Bergström U., Bonsdorff E., Härkönen T., Jepsen N., Kautsky L., Lundström K., Lunneryd S.G., Ovegård M., Salmi J., Sendek D. & Vetemaa M. 2017. Competition for the fish–fish extraction from the Baltic Sea by humans, aquatic mammals, and birds. *ICES J. Mar. Sci.*

Hixon M.A., Johnson D.W. & Sogard S.M. 2014. BOFFFFs: on the importance of conserving old-growth age structure in fishery populations. *ICES J. Mar. Sci.* 71: 2171–2185.

Hoogland R., Morris D. & Tinbergen N. 1956. The spines of sticklebacks (*Gasterosteus* and *Pygosteus*) as means of defence against predators (*Perca* and *Esox*). *Behaviour* 10: 205–230.

Horppila J., Ruuhijarvi J., Rask M., Karppinen C., Nyberg K. & Olin M. 2000. Seasonal changes in the diets and relative abundances of perch and roach in the littoral and pelagic zones of a large lake. *J. Fish Biol.* 56: 51–72.

Huss M., Byström P., Strand Å., Eriksson L.O. & Persson L. 2008. Influence of growth history on the accumulation of energy reserves and winter mortality in young fish. *Can. J. Fish. Aquat. Sci.* 65: 2149–2156.

Hyslop E.J. 1980. Stomach contents analysis — a review of methods and their application. *J. Fish Biol.* 17: 411–429.

Jacobson P., Gårdmark A., Östergren J., Casini M. & Huss M. 2018. Size-dependent prey availability affects diet and performance of predatory fish at sea: a case study of Atlantic salmon. *Ecosphere* 9: e02081.

Karås P. 1984. The food selection among fish in the Biotest basin, Forsmark, during 1978–83. *Statens Naturvårdsverk Meddelande* 1913: 1–33 (in Swedish).

Kinnerbäck A. 2001. Stratified random fish sampling using standardised multi–mesh gillnets. *Fiskeriverket informerar* 2: 34 (in Swedish).

Koenker R. 2018. quantreg: *Quantile Regression*.

Lappalainen A., Rask M., Koponen H. & Vesala S. 2001. Relative abundance, diet and growth of perch (*Perca fluviatilis*) and roach (*Rutilus rutilus*) at Tvärminne, northern Baltic Sea, in 1975 and 1997: responses to eutrophication? *Boreal Environ. Res.* 6: 107–118.

Lefcheck J.S., Whalen A.M., Davenport T.M., Stone P.J. & Emmet Duffy J. 2013. Physiological effects of diet mixing on consumer fitness: a meta–analysis. *Ecology* 94: 565–572.

Lehtonen H., Leskinen E., Selén R. & Reinikainen M. 2009. Potential reasons for the changes in the abundance of pike, *Esox lucius*, in the western Gulf of Finland, 1939–2007. *Fish. Manage. Ecol.* 16: 484–491.

Lescak E.A. & von Hippel F.A. 2011. Selective predation of threespine stickleback by rainbow trout. *Ecol. Freshwat. Fish* 20: 308–314.

Ljunggren L., Sandström A., Bergström U., Mattila J., Lappalainen A., Johansson G., Sundblad G., Casini M., Kaljuste O. & Eriksson B.K. 2010. Recruitment failure of coastal predatory fish in the Baltic Sea coincident with an offshore ecosystem regime shift. *ICES J. Mar. Sci.* 67: 1587–1595.

Mehner T., Schultz H., Bauer D., Herbst R., Voigt H. & Benndorf J. 1996. Intraguild predation and cannibalism in age-0 perch (*Perca fluviatilis*) and age-0 zander (*Stizostedion lucioperca*): Interactions with zooplankton succession, prey fish availability and temperature. *Ann. Zool. Fenn.* 33: 353–361.

Miller T.E. & Rudolf V.H. 2011. Thinking inside the box: community–level consequences of stage-structured populations. *Trends Ecol. Evol.* 26: 457–466.

Mittelbach G.G. & Persson L. 1998. The ontogeny of piscivory and its ecological consequences. *Can. J. Fish. Aquat. Sci.* 55: 1454–1465.

Mustamäki N., Cederberg J. & Matilla J. 2014. Diet, stable isotopes an morphology of Eurasian perch (*Perca fluviatilis*) in littoral and pelagic habitats in the northern Baltic Proper. *Environ. Biol. Fishes* 97: 675–689.

Nilsson K. 2010. Större gädda (*Esox lucius*) konsumerar inte storspigg (*Gasterosteus aculeatus*): är taggarna ett problem eller är spiggen för liten? (Master's Thesis; in Swedish). *Linnaeus University*

Nilsson P.A. & Brönmark C. 2000. Prey vulnerability to a gape-size limited predator: behavioural and morphological impacts on northern pike piscivory. *Oikos* 88: 539–546.

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

Östman Ö., Eklöf J., Eriksson B.K., Olsson J., Moksnes PO. & Bergström U. 2016. Top–down control as important as eutrophication effects in North Atlantic coastal ecosystems. *J. Appl. Ecol.* 53: 1138–1147.

Persson L., van Leeuwen A. & de Roos A.M. 2014. The ecological foundation for ecosystem–based management of fisheries: mechanistic linkages between the individual-, population-, and community-level dynamics. *ICES J. Mar. Sci.* 71: 2268–2280.

Persson L., Amundsen P.A., de Roos A.M., Klemetsen A., Knudsen R. & Primicerio R. 2007. Culling prey promotes predator recovery- alternative states in a whole-lake experiment. *Science* 316: 1743–1745.

Pierce C.L., Sexton M.D., Pelham M.E., Liao H. & Larscheid J.G. 2001. Dynamics of the littoral fish assemblage in Spirit lake, Iowa, and implications for prey availability for piscivores. *N. Am. J. Fish. Manage*. 21: 884–896.

Post D.M., Palkovacs E.P., Schielke E.G. & Dodson S.I. 2008. Intraspecific variation in a predator affects community structure and cascading trophic interactions. *Ecology* 89: 2019–2032.

R Core Team 2018. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. Available at: http://www.R-project.org/

Reist J.D. 1980. Selective predation upon pelvic phenotypes of brook stickleback, *Culaea inconstans*, by northern pike, *Esox lucius*. *Canadian Journal of Zoology* 58: 1245–1252.

Rudolf V.H. & Lafferty K.D. 2011. Stage structure alters how complexity affects stability of ecological networks. *Ecol. Lett.* 14: 75–79.

Sandström A. & Karås P. 2002. Effects of eutrophication on young-of-the-year freshwater fish communities in coastal areas of the Baltic. *Environ. Biol. Fishes* 63: 89–101.

Saulamo K. & Neuman E. 2002. Local management of Baltic fish stocks — significance of migrations. *Fiskeriverket informerar* 9: 19.

Scharf F.S., Juanes F. & Sutherland M. 1998. Inferring ecological relationships from the edges of scatter diagrams: Comparison of regression techniques. *Ecology* 79: 448–460.

Scharf F.S., Juanes F. & Rountree R.A. 2000. Predator size – prey size relationships of marine fish predators: interspecific variation and effects of ontogeny and body size on trophic-niche breadth. *Mar. Ecol. Prog. Ser.* 208: 229–248.

Schröder A., Persson L. & de Roos A.M. 2009. Culling experiments demonstrate size–class specific biomass increases with mortality. *Proceedings of the National Academy of Sciences* 106: 2671–2676.

Schröder A., van Leeuwen A. & Cameron T.C. 2014. When less is more: positive population-level effects of mortality. *Trends Ecol. Evol.* 29: 614–624.

Smith C. & Reay P. 1991. Cannibalism in teleost fish. *Rev. Fish Biol. Fish.* 1: 41–64.

Snickars M., Sandström A., Lappalainen A. & Mattila J. 2007. Evaluation of low impact pressure waves as a quantitative sampling method for small fish in shallow water. *J. Exp. Mar. Biol. Ecol.* 343: 138–147.

Snickars M., Sundblad G., Sandström A., Ljunggren L., Bergström U., Johansson G. & Mattila J. 2010. Habitat selectivity of substrate–spawning fish: modelling requirements for the Eurasian perch *Perca fluviatilis. Mar. Ecol. Prog. Ser.* 398: 235–243.

Svanbäck R. & Eklöv P. 2002. Effects of habitat and food resources on morphology and ontogenetic growth trajectories in perch. *Oecologia* 131: 61–70.

Svanbäck R. & Persson L. 2004. Individual diet specialization, niche width and population dynamics: implications for trophic polymorphisms. *J. Anim. Ecol.* 73: 973–982.

Svanbäck R., Quevedo M., Olsson J. & Eklöv P. 2015. Individuals in food webs: the relationships between trophic position, omnivory and among–individual diet variation. *Oecologia* 178: 103–114.

Wahl D.H. & Stein R.A. 1993. Comparative population characteristics of muskellunge (*Esox masquinongy*), northern pike (*E. lucius*), and their hybrid (*E. masquinongy* × *E. lucius*). *Can. J. Fish. Aquat. Sci.* 50: 1961–1968.

Walters C. & Kitchell J.F. 2001. Cultivation/depensation effects on juvenile survival and recruitment: implications for the theory of fishing. *Can. J. Fish. Aquat. Sci.* 58: 39–50.

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

Vander Zander M.J., Essington T.E. & Vadeboncoeur Y. 2005. Is pelagic top-down control in lakes augmented by benthic energy pathways? *Can. J. Fish. Aquat. Sci.* 62: 1422–1431.

Appendix

Table A1. Classification of food items found in stomachs of Baltic Sea perch (*Perca fluviatilis*) and northern pike (*Esox lucius*).

Broad group	Medium group	Food item	Observed in perch	Observed in pike
Amphipods	*Corophium volutator*	*Corophium volutator*	X	
	Gammarids	*Gammarus* spp.	X	X
Fish	Bleak	*Alburnus alburnus*	X	X
	Clupeids	*Clupeidae* spp.	X	X
	Eelpout	*Zoarces viviparous*	X	X
	Gobiids	*Gobiidae* spp.	X	X
		Pomatoschistus minutus	X	
	Nine-spined stickleback	*Pungitius pungitius*	X	X
	Roach	*Rutilus rutilus*	X	X
	Ruffe	*Gymnocephalus cernua*	X	X
	Three-spined stickleback	*Gasterosteus aculeatus*	X	X
	Unidentifiable fish	Fish	X	X
Isopods	*Asellus aquaticus*	*Asellus aquaticus*	X	X
	Unidentified isopods	*Isopoda* spp.	X	X
	Idotea	*Idotea* spp.	X	
	Jaera albifrons	*Jaerra albifrons*	X	
Molluscs	Bivalves	*Bivalvia*	X	
		Cardium sp.	X	X
		Mya arenaria	X	
		Mytilus edulis	X	X
		Parvicardium hauniense	X	
	Gastropods	*Bithynia tentaculata*	X	X
		Hydrobia neglecta	X	
		Hydrobia sp.	X	X
		Potamopyrgus antipodarum		X
		Theodoxus fluviatilis	X	
Mysids	Mysids	*Mysidae*	X	X
Nematocerans	Chironomids	*Chironomidae* spp.larvae	X	
		Chironomidae spp.pupae	X	
	Nematocera	*Nematocera* larvae	X	X
		Nematocera pupae	X	
Odonates	Odonata	*Anispotera* nymph	X	
		Odonata	X	
		Zygoptera nymph	X	X
Polychaetes	*Polychaeta*	*Polychaeta* spp.bristles	X	
Roe	Roe	Roe	X	
Shrimps	Shrimps	*Caridea* spp.	X	X
		Palaemon adspersus	X	
Caddisfly larvae	*Trichoptera*	*Trichoptera* spp.	X	X
		Phryganea striata	X	
		Trichoptera spp. house	X	
		Trichoptera spp. larvae	X	X
		Trichoptera spp. pupae	X	
Worms	*Annelida*	*Annelida* spp.	X	
	Oligochaeta	*Oligochatea*	X	
Zooplankton	*Cladocera*	*Cladocera*	X	X
	Copepoda	*Copepoda*	X	

Table A1. (*continued*)

Broad group	Medium group	Food item	Observed in perch	Observed in pike
Other insects	*Hemiptera*	*Corixa* sp.	X	
		Corixa sp. nymph	X	
		Ilyocoris cimicoides	X	
	Unidentified insects	*Diptera* larvae	X	
		Diptera pupae	X	
		Insecta adults	X	
		Insecta larvae	X	
		Insecta pupae	X	
Other	Gastric fluid	Fluid of different colors	X	X
	Non-food	Rock	X	
		Sand	X	
		Unknown black tissue	X	
		White parasitic flatworm	X	X
	Vegetation material	*Fucus vesiculosus*	X	
		Leaf parts	X	
		Plant material	X	
		Rhodophyta	X	
		P. pectinatus	X	
		Vegetation parts	X	
Empty	Empty	Empty	X	X

Note: X = observed in ≥ 1 stomach

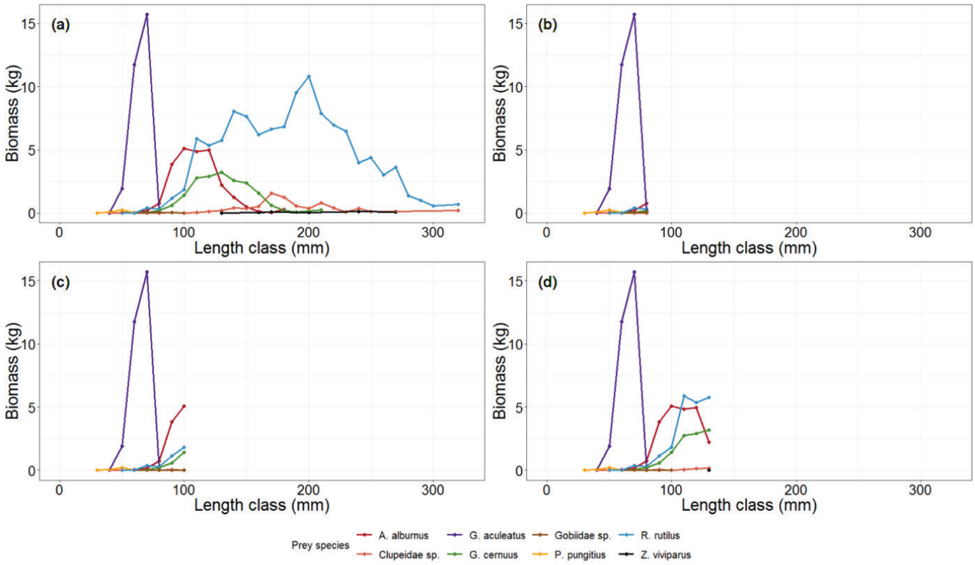


Fig. A1. The biomass (converted using length-weight relationships; Appendix Table A2) and size-structure of prey fish species consumed by perch, caught in 32 shallow bays sampled in late spring (May–June) of 2014, along the central Swedish Baltic Sea coast. (**a**) Biomass and size-structure of all prey fish species; (**b**) consumable biomass of all prey fish species for a 300 mm perch; (**c**) consumable biomass of all prey fish species for a 375 mm perch; (**d**) consumable biomass of all prey fish species for a 474 mm perch. Maximum prey size for perch was calculated using the quantile regression model (prey length = 0.302 × perch length – 4.04) from the predation window of perch (Fig. 6a).

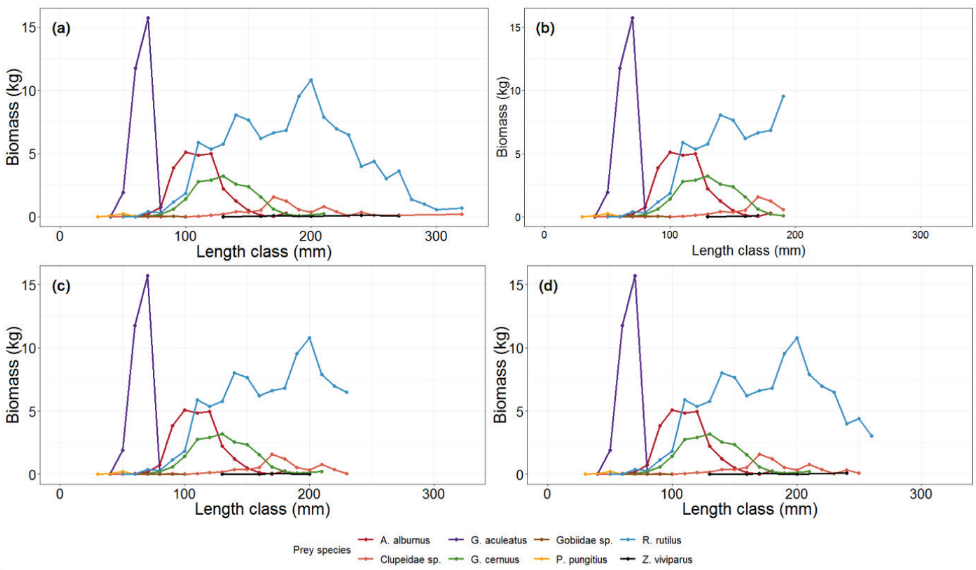


Fig. A2. The biomass (converted using length-weight relationships; Appendix Table A2) and size-structure of prey fish species consumed by northern pike, caught in 32 shallow bays sampled in late spring (May–June) of 2014, along the central Swedish Baltic Sea coast. (**a**) Biomass and size-structure of all prey fish species; (**b**) consumable biomass of all prey fish species for a 499 mm pike; (**c**) consumable biomass of all prey fish species for a 599 mm pike; (**d**) consumable biomass of all prey fish species for a 699 mm pike. Maximum prey size for pike was calculated using the quantile regression model (prey length = 0.365 × pike length + 12.49) from the predation window of pike (Fig. 6b).

Table A2. Length–weight conversion constants for the 8 prey groups consumed by Baltic sea perch and northern pike derived from the Swedish national database on coastal fish (KUL), used for converting lengths into biomass using the formula: W = aL^b, where W is the weight (in grams), *a* and *b* are species-specific constants and *L* (cm) is the individuals' length.

Prey groups	Constants	
	a	*b*
A. alburnus	0.006	3.0695
Clupeidae sp.	0.0057	3.02253
G. aculeatus	0.00571	3.09
G. cernua	0.009	3.1011
Gobiidae sp.	0.005	3.1335
P. pungitus	0.0098	2.7507
R. rutilus	0.005	3.2166
Z. viviparus	0.00184	3.25475

Table A3. Number of bays in which each recorded fish species were caught using underwater detonations in late summer (August–September) in 2014 at 32 different bays in the Baltic Sea.

Species	Scientific name	Number of bays
Perch	*Perca fluviatilis*	29
Sand/Common goby	*Pomatoschistus minutus/microps*	29
Three-spined stickleback	*Gasterosteus aculeatus*	24
Nine-spined stickleback	*Pungitius pungitius*	20
Bleak	*Alburnus alburnus*	16
Roach	*Rutilus rutilus*	16
Pike	*Esox lucius*	12
Sprat	*Sprattus sprattus*	12
Baltic herring	*Clupea harengus*	9
White bream/Bream	*Blicca bjoerkna/Abramis brama*	8
Tench	*Tinca tinca*	8
Black goby	*Gobius niger*	6
Ruffe	*Gymnocephalus cernua*	3
Minnow	*Phoxinus phoxinus*	2
Straightnose pipefish	*Nerophis ophidion*	2
Crucian carp	*Carassius carassius*	2
Pike-perch	*Sander lucioperca*	1
Smelt	*Osmerus eperlanus*	1
Turbot	*Psetta maxima*	1
Sprat or Baltic herring	*Sprattus sprattus/Clupea harengus*	1