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ORIGINAL PAPER

Trophic plasticity and the invasion of a renowned piscivore: a diet synthesis of northern pike (*Esox lucius*) from the native and introduced ranges in Alaska, U.S.A.

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Abstract The invasion of non-native fishes is a leading cause of extinction and imperilment of native freshwater fishes. Evidence suggests that introduced species with generalist diets have the potential for greatest impacts through competition and predation even though populations are often comprised of specialist individuals. The northern pike (*Esox lucius*), a predatory fish, has been widely introduced outside its native range for recreational fishing purposes, especially in western North America, and it has been implicated in declines and extirpations of native fishes. We synthesized over 2900 individual northern pike diet records across 31 waterbodies from the native and introduced ranges in Alaska to quantify the extent of diet specialization and generalization relative to freshwater prey communities. To control for effects of ontogenetic diet shifts, we separately analyzed major size classes of northern pike and inferred and visualized trophic plasticity from prey-specific abundance indices and ordination. Diet generalization was common in northern pike among waterbodies and usually consisted of individuals consuming macroinvertebrates. However, when available, individual northern pike diets showed specialization on fishes, amphibians, small mammals, and dragonflies. The reliance on macroinvertebrate prey by northern pike from small, isolated lakes in the native and invasive ranges suggests that dietary plasticity facilitates persistence of these predators in the absence of preferred fish prey. Broadly, this synthesis supports the

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hypothesis that trophic plasticity and diet generalization widely occur among invasive and native populations of northern pike which is likely to enhance the probability of introduction success, exacerbate their environmental impacts, and complicate management of this potentially invasive freshwater predator.

Keywords Trophic plasticity · Northern pike · Diet · Community ecology · Trophic ecology · Alaska fishes

> *The greediness of pike knows no bounds*
>
> *- Sergei Aksakov (1847)*

Introduction

Invasive fishes are a leading cause of native fish extinctions and an on-going threat to the ecological function and organization of aquatic communities (Miller et al. 1989; Clavero and García-Berthou 2005). Phenotypic plasticity is widely hypothesized to increase the probability of successful invasions (e.g., Baldwin 1896; Robinson and Dukas 1999) and generally supported empirically (Ruesink 2005; Olden et al. 2006; Fox et al. 2007). Plasticity in trophic ecology, which is often discussed in terms of diet breadth, is a corollary hypothesis for understanding invasion success and predicting community effects (Simon and Townsend 2003). High profile examples of how food webs are affected by nonnative fishes include globally distributed salmonids with trophic plasticity or generalism that disrupt reciprocal trophic exchanges between aquatic and terrestrial environments and compete with and prey upon native fishes and other aquatic organisms (Baxter et al. 2004; Olden et al. 2006; Juncos et al. 2013).

Invasion ecology is closely linked to geography (Davies et al. 2005). Although many invasive fish species have been transplanted among continents, more proximate introductions within continents or bioregions are frequent and impactful (Johnson et al. 2009). For example, the on-going invasion of northern pike (*Esox lucius*), a Holarctic predatory fish valued in recreational fisheries, in southcentral Alaska provides a timely case study of trophic impacts by a predator with implications for invasions elsewhere (Haught and von Hippel 2011; Dunker et al. 2018). Native Alaskan populations presently occur north of the Alaska Range, west to the Bristol Bay area and east to the Canadian border (Dunker et al. 2018). Unconfirmed historical accounts indicate that the invasion of southcentral Alaska started in the 1950s via the unauthorized transplant of northern pike from west of the interior Alaska town of Fairbanks to a lake located south of the Alaska Range. Through invasion and subsequent introductions, northern pike spread to adjacent watersheds including the Kenai Peninsula (Dunker et al. 2018). Northern pike now occupy over 100 Alaskan waterbodies outside their native range, overlapping productive commercial, sport, and subsistence salmon fisheries with concurrently documented species declines in certain areas (Haught and von Hippel 2011; Sepulveda et al. 2013, 2015).

The introduction of northern pike in Alaska is just one case study of the myriad northern pike introductions (McMahon and Bennett 1996; Craig 2008; Johnson et al. 2008; Rypel 2012). In North America, predation by invasive northern pike has been associated with extirpations of small-bodied fish species (Findlay et al. 2000; Patankar et al. 2006; Nicholson et al. 2015), reductions or losses of economically-important recreational fisheries (McMahon and Bennett 1996; Flinders and Bonar 2008; Sepulveda et al. 2013), and has even hindered endangered species recovery efforts (Zelasko et al. 2016). In Europe, both native and introduced northern pike predation can lower preferred prey species abundance in streams (Rincon et al. 1990; Degerman and Sers 1993; Näslund et al. 1998), endanger endemic cyprinids (Elvira and Almodóvar 2001), and extirpate Arctic char (*Salvelinus alpinus*), brown trout, and other fishes (Robinson and Tonn 1989; Byström et al. 2007; Spens and Ball 2008). When fish are gone, remaining prey communities for northern pike often consist of invertebrates (Beaudoin et al. 1999; Haught and von Hippel 2011) and northern pike can persist on mostly invertebrate prey due to generalism (Chapman et al. 1989; Venturelli and Tonn 2005). Thus, to accurately understand the potential breadth of impact northern

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pike have on freshwater communities and aid management responses to ongoing invasions, a comprehensive size-specific diet synthesis comparing northern pike from streams and lakes, including native and nonnative populations, is needed.

In this paper we investigated trophic patterns among native and invasive populations of northern pike in Alaska. We had three objectives: (1) characterize fish prey consumed by northern pike individuals and size-classes, (2) measure the prevalence of specialist and generalist feeding strategies, and (3) test how trophic patterns differ across northern pike populations based on spatial, temporal, and ecological variables. Northern pike are well known piscivores when fish are present, thus, we hypothesized that objective 1 would find fish consumption most prevalent by larger northern pike given ontogenetic diet shifts to piscivory when fish are present (Pedreschi et al. 2015). To the extent that trophic plasticity facilitates successful invasions and is shown in some European northern pike populations (e.g., Pedreschi et al. 2015), we hypothesized that objective 2 would illustrate northern pike as diet generalists at a regional level. Recognizing that northern pike can display high invertebrate consumption and eliminate fishes in small lakes (i.e., Skov et al. 2003; Haught and von Hippel 2011), we expected to see invertebrate-dominated diets in small, invaded lakes, whereas northern pike in invaded rivers with greater connectivity and opportunities for prey movement would have diverse diets including fish (prediction derived from patterns in Sepulveda et al. 2013). Moreover, generalist trophic orientation of northern pike was hypothesized to be focused on highly abundant invertebrate prey, whereas specialist patterns were expected to focus on energy rich prey that could be locally abundant (i.e., fishes when present) or rarer (i.e., opportunistic encounters with fishes, rodents, frogs). Since fish and aquatic communities change with abundance of northern pike depending on waterbody type (Haught and von Hippel 2011; Larsson et al. 2015; Pedreschi et al. 2015), we hypothesized that population-level trophic patterns would be apparent across waterbodies that shared characteristics such as time since invasion, size, and prey taxa consumed.

Methods

Study sites

We analyzed diet data from northern pike sampled from 31 waterbodies throughout the southwest and southcentral regions of Alaska (Fig. 1; Table 1). Sample locations from the native range of northern pike in southwest Alaska comprised: Lake Clark, (31,115 ha, 265 m deep), which drains into Iliamna Lake, Lake Aleknagik, (8000 ha, 100 m deep) which drains into the Wood River about 100 km west of Iliamna Lake, and three small lakes, two of which are adjacent yet disconnected from Iliamna Lake (East Wind, ca. 72 ha, and Stonehouse, ca. 19 ha), and one (Long Bay, ca. 15 ha) that is intermittently connected to Iliamna Lake depending on seasonal rainfall and lake level. The remaining 26 sites were from waterbodies in the invaded range. Two of these sites were streams in the Susitna River basin: Alexander Creek (64 km long, lower velocity with many connected sloughs) and the Deshka River (225 km long, higher velocity with few sloughs). The remaining 23 sites were generally from invaded lakes within the Matanuska and Susitna river drainages and were generally small (< 150 ha), shallow (average maximum depth 10.1 m), and, aside from Rabbit and Scout lakes (the sole waterbody from the Kenai Peninsula), connected to other waterbodies (Haught and von Hippel 2011).

Diet data

Diet data from 2006 to 2016 were synthesized from published and unpublished northern pike studies or eradication efforts around Alaska that used angling, fyke nets, dip nets, gill nets or seines to sample northern pike for their stomach contents during ice-free periods from April through September (Haught and von Hippel 2011; Sepulveda et al. 2013). To control for potential ontogenetic shifts in diets of northern pike ranging from 4 to 102 cm, we separated individuals into three size classes based on observed modes in a pooled length-frequency histogram of all available data (Supplemental material 1). Subsequent analyses were done using fish < 32 cm fork length (FL, small), > 32 cm FL yet < 46 cm FL (medium), and > 46 cm FL (large). Given the disparate nature of data collection we could incorporate seasonal

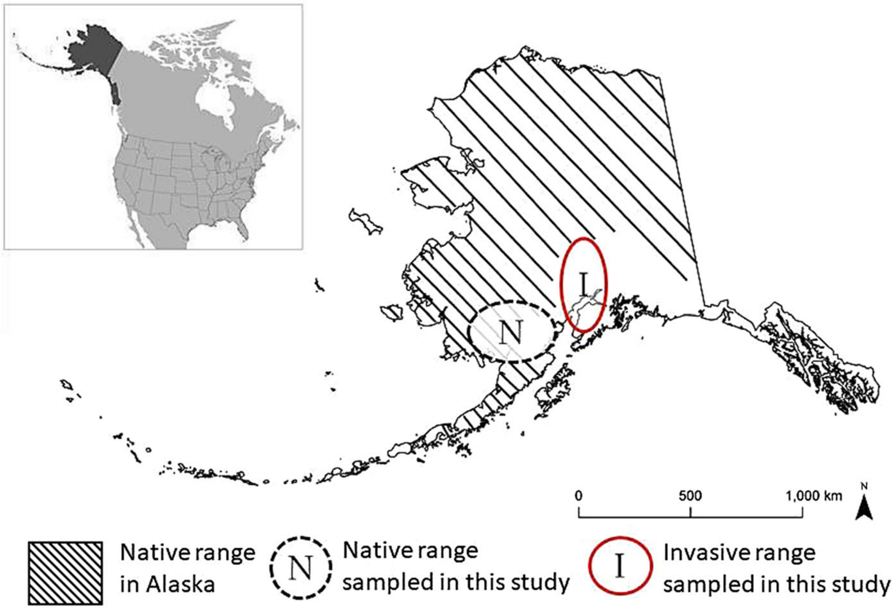

Fig. 1 Native range of northern pike in Alaska and sampled areas from the native and invasive ranges that were included in this study

variation consistently across sites, and thus samples were pooled regardless of date.

Diets were divided into 25 prey taxa categories that allowed for maximum comparisons among datasets. Prey categories included 12 invertebrate, 11 fish, 1 mammal [including shrews (*Sorex* spp.) and red backed voles (*Myodes rutilis*)], and 1 amphibian [wood frogs (*Lithobates sylvaticus*)] (Table 2). Vegetation within diets was omitted under the assumption that it was consumed secondarily during predation. Unidentifiable portions of the diet (extensively digested) found in a fraction of the fish were also omitted from analyses. The taxonomic resolution of prey taxa categories reflected that reported within the original studies. As such, some fish and likely all invertebrate prey categories included multiple species. For example, the salmonid category included species within subfamily Salmoninae (e.g., *Oncorhynchus* spp. and *Salvelinus malma*) and other fish were also grouped by subfamily such as Arctic grayling (*Thymallus arcticus*; subfamily Thymallinae) and whitefish species (subfamily Coregoninae). The stickleback category primarily represented threespine stickleback (*Gasterosteus aculeatus*), but ninespine stickleback (*Pungitius pungitius*) were also potential prey in some areas. The sculpin category was most likely represented by slimy sculpin (*Cottus cognatus*) but could also have included coastrange sculpin (*C. alueticus*), especially in the Bristol Bay waterbodies. The lamprey category potentially included both Pacific (*Entosphenus tridentatus*) and Arctic (*Lethenteron camtschaticum*) lampreys and were not separated. To meet our first objective using fish abundance data from diet samples, we examined fish consumption by waterbody according to each size class and then calculated the percent of fish prey consumed that was comprised by the salmonid category.

Statistical analysis and comparisons

To address our second objective we quantified range-wide northern pike diets in terms of specialization or generalization using prey-specific abundance (PSA) and frequency of occurrence (FO) values. Due to limited samples from native range populations, we aggregated individual diet data separated by size class from native and invasive populations to illustrate PSA patterns of the Alaskan northern pike diets. The PSA value, using mass (prey weight in g), represents how much of a diet a specific prey item constitutes within the group of predators that feed on that prey (Amundsen et al. 1996, from Costello 1990). In the equation, we can view this as PSA (by mass) of prey (h) where S_h equals the abundance of prey h in all stomachs, and S_{th} equals the total abundance of all prey in northern pike that contain prey h:

$$PSA_h = (\Sigma S_h / \Sigma S_{th}) \times 100$$

Table 1 Year of northern pike introduction (? indicates exact year is unsubstantiated) and sample sizes of size classes from native (italicized) and nonnative waterbodies of Alaska

Waterbody	Introduced	Small	Medium	Large	Sampling date
Aleknagik[1]		46	15	11	Jul 2006, 2008
Clark[2]		–	1	8	Sep 2016
East Wind[1]		–	10	–	Jul 2006, 2007
Long Bay[1]		12	5	5	Jul, Aug 2007, 2008
Stonehouse[1]		14	32	14	Jun, Aug 2006–2008
Alexander*[3]	1967	28	120	145	May 2011–2013
Ardaw[4]	1990	3	8	2	Aug 2008
Big[4]	1996	6	10	1	May 2008
Big No Luck[4]	1998	2	5	1	Aug 2008
Charr[4]	1989	4	11	11	Jul 2008
Crystal[4]	2005	6	4	–	Jul 2008
Deshka*[3]	1970	140	156	134	May, Jun, Aug 2011–2013
Frazer[4]	1988	2	4	–	Jul 2008
Jackknife[4]	1989	3	9	–	Jul 2008
James[4]	1992	3	5	1	Jul 2008
Little No Luck[4]	1993	5	20	2	Aug 2008
Long[4]	2000	8	12	5	May 2008
Lynx[4]	1987	2	14	13	Jul 2008
Memory[4]	1987	4	23	1	Apr 2008
Milo[4]	1989	4	13	10	May 2008
Nancy[4]	1987	4	10	3	May 2008
Owl[4]	1991	3	17	9	Jul 2008
Rabbit[4]	1985	–	12	8	Aug 2008
Redshirt[4]	1980	1	13	14	Jul 2008
Scout[4]	2005	3	10	5	Jun 2008
Shell[5]	1970(?)	1058	472	54	May, Jun, Jul, Aug 2012–2016
Shem Pete[4]	1992	5	11	2	Jun 2008
Shirley[4]	1999	6	10	1	Jul 2008
South Rolly[4]	1989	5	18	4	Aug 2008
Sucker[4]	1985	–	2	22	Aug 2007
Tanaina[4]	1988	–	7	1	May 2008

Size classes were separated according to modes of length-frequency histograms for northern pike: small (< 32 cm); medium (32–46 cm); large (> 46 cm)

Asterisks indicate streams; all other waterbodies are lakes

[1]Quinn, unpublished data; [2]Audette, unpublished data; [3]Sepulveda et al. (2013); [4]Haught and von Hippel (2011); [5]Wizik, unpublished data

FO values indicate how often a prey item occurs in a sample of individuals. Viewed as an equation, we see this as the number of fish (S) with a specific prey (h) item divided by the total number of fish in that sample (B):

$$FO = S_h/B$$

Consequently, fish with empty stomachs or those with unknown contents were omitted from our analyses. Using PSA and FO in conjunction facilitates interpretations of trophic specialization or generalization in fishes. For clarity and to interpret generalities, we only illustrate PSA and FO for "common" prey taxa categories that were consumed in > 20% of waterbodies for each size class of fish. PSA values were estimated using prey weights (g) from organisms in northern pike diets from the invaded Alexander and Deshka creeks as well as the native lakes in the Iliamna area (Table 2). These Alaska-specific prey weights were then used as a standard value across all systems that lacked specific measurements, assuming the weights of prey or generally representative.

To address objective 3, we used canonical correspondence analysis (CCA) to distinguish trophic orientations of northern pike populations from each size class and to determine the frequency of generalist

Table 2 Prey taxa and their mean weights of diet items involved in this study

Prey taxa category	Classification	Mean wt (g)
Dragonfly	Anisoptera	0.66
Damselfly	Zygoptera	0.05
Mayfly	Ephemeroptera	0.01
Stonefly	Plecoptera	0.07
Caddisfly	Trichoptera	0.18
Chironomid	Chironomidae	0.02
Beetle	Coleoptera	0.29
Boatmen	Corixidae	0.01
Amphipod	Amphipoda	0.05
Watermite	Hydrachnidia	0.01
Leech	Hirudinea	0.50
Mollusk	Mollusca	0.70
Salmonid	Salmoninae	0.88
Stickleback	Gasterosteidae	1.46
Sculpin	Cottidae	1.20
Alaska blackfish	*Dallia pectoralis*	23.00
Whitefish	Coregoninae	27.01
Northern pike	*Esox lucius*	77.86
Longnose sucker	*Catostomus catostomus*	24.00
Lamprey	Petromyzontidae	1.00
Burbot	*Lota lota*	42.00
Arctic grayling	Thymallinae	31.00
Eulachon	*Thaleichthys pacificus*	5.00
Wood frog	*Lithobates sylvaticus*	8.18
Mammal	Mammalia	11.37

Mean weights of all fishes were generated from diet analyses of fishes from Alexander and Deshka creeks. All other prey item weights were generated from sampling in western Alaska (i.e., lakes Clark, Iliamna, Stonehouse, Eastwind, and Longbay)

predators (vegan package version 2.5-2 in R version 3.5.0; R Development Core Team 2008). Analyses were performed with the dependent diet variables being site-standardized prey taxa category frequency data and the following predictor variables: time since invasion, lake size or stream drainage area in hectares, difference in fish prey taxa categories and invertebrate prey taxa categories consumed (subtract fish prey taxa categories from invertebrate prey taxa categories), and total prey taxa categories consumed. Time since invasion was used as a dummy variable (i.e., extremely high values > 2000 years indicating natural origins) for native waterbodies. Predictor variables were not transformed because significance of CCA findings does not rely on parametric distribution assumptions of predictor variables (Ter Braak 1986; Palmer 1993; Mullen et al. 2011). Rare species (i.e., those consumed in < 20% of waterbodies for each size class) were included in analyses because they contribute to the breadth of taxa consumed by northern pike, potentially inform our findings of species sensitive to invasion, and removal can bias results (Poos and Jackson 2012). Variation of prey in northern pike diets was visualized in the CCA using prey taxa and waterbody (site) scores (i.e., the scores according to significant axis are plotted as X or Y coordinates and interpreted) constrained by predictor variables scaled to relative eigenvalues. The significance of CCA axes and habitat variables were analyzed with permuted ANOVA (Anderson 2001). The first two CCA axes were analyzed with ANOVA and ordination interpretation since little variation was explained if additional axes were included. We performed these analyses in two ways to further investigate responses to invasion: (1) with all native and invaded waterbodies and (2) with only invaded waterbodies.

Results

We analyzed diets of 2914 northern pike, 1584 of which were from Shell Lake (1058 small size class, 472 medium size, and 54 large size). However, due to taxonomic coarseness of invertebrate data for Shell Lake, we only used those data in our first objective. For the rest of the waterbodies, there were 318 small individuals from 25 sites, 587 medium individuals from 30 sites, and 425 large individuals from 26 sites (Table 1).

Large northern pike consumed the greatest prey diversity (25 prey taxa categories) across all waterbodies compared to small (21 prey taxa categories) and medium (22 taxa) northern pike. As expected, mean diet weight was heaviest for large northern pike (20.4 g, ± 31.5 SD), followed by medium (8.8 g, ± 14.9 SD) and small (6.4 g, ± 13.7 SD) northern pike. Relative to our first objective, fish constituted a large portion of the diet in many waterbodies, and aside from the streams and one invaded lake (Lynx), medium and large northern pike consumed more fish than did small northern pike (Fig. 2). Of the individual northern pike and populations that consumed fish,

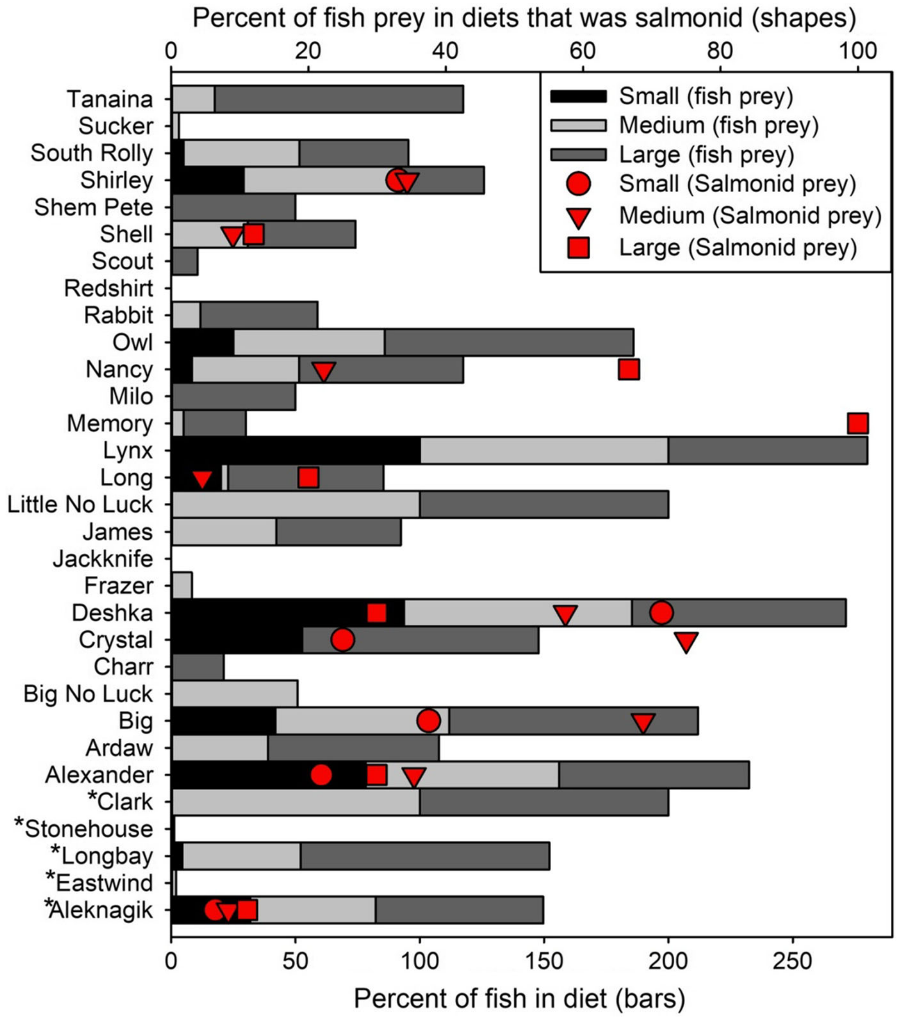

Fig. 2 Stacked bar charts showing the percent of diets containing fish (including salmonids) observed in small, medium, and large northern pike (bars) and percent of diets containing fish that were made up of salmonids (shapes) across waterbodies (locations). Note the bottom axis is additive, meaning each size class has the potential for 100% in each panel, thus each waterbody had the potential to sum to 300% if all fish of all sizes were observed to consume fish. Locations are listed alphabetically in descending order whereas sites in the native range are indicated by an asterisk at the bottom of the figure

diets involved salmonids in a third of the waterbodies (likely due to salmonid availability as prey), but no one size class of northern pike disproportionately consumed salmonids compared to another (Fig. 2). While sample sizes were unbalanced, the only native lake with salmonid consumption (Aleknagik) had similar salmonid composition of fish diets among size classes, yet overall salmonid composition was lower than in other invaded waterbodies with evidence of salmonids consumed.

Statistical analysis and comparisons

Satisfying objective two, prey-specific abundance of common prey taxa categories indicated that generalist trophic strategies were dominant in small northern pike (mean PSA = 25%). In comparison, medium (mean PSA = 40%) and large (mean PSA = 41%) northern pike demonstrated more specialist trophic strategies (Fig. 3). Medium and large northern pike commonly consumed 13 and 10 prey taxa categories, respectively, while small northern pike commonly consumed 8 prey taxa categories. The generalist trophic strategy of medium and large northern pike was characterized by high inter-individual variation in consumption patterns, with individuals specializing on dragonflies and vertebrate prey, including mammal, frog, and other northern pike. Small northern pike fed as generalists on small invertebrate prey but demonstrated individual specialization for mollusks, dragonflies, salmonids and sticklebacks. Cannibalism was a rare occurrence (3% of samples) but, when

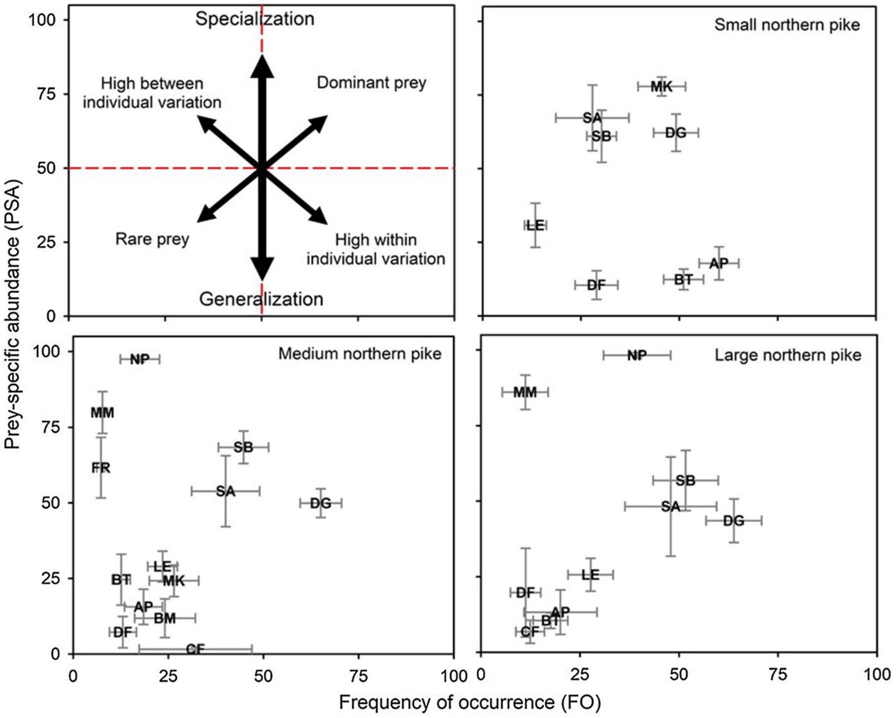

Fig. 3 Prey-specific abundance for common prey items in northern pike diets based on size class. Top left panel is modified from Amundsen et al. (1996) to aid interpretation of panels. Common prey items represent taxa found in greater than 20% of sampled waterbodies per size class. Variance is shown by error bars that indicate standard error of the mean. Prey taxa codes are as follows: DG (dragonfly), DF (damselfly), CF (caddisfly), BT (beetle), BM (boatmen), AP (amphipod), LE (leech), MK (mollusk), SA (salmonid), SB (stickleback), NP (northern pike), FR (wood frog), and MM (mammal)

documented, was most frequent in large individuals (6%) followed by medium fish (2%) and small fish (< 1%). Stickleback, salmonids, and dragonflies were diet items specialized upon by all size classes according to similar PSA values.

Though not shown in the figures, infrequently consumed macroinvertebrate and vertebrate prey taxa (< 20% of waterbodies sampled) had PSA values similar to more commonly consumed taxa categories. Thus, most macroinvertebrates had low PSA and were generally rare prey for pike with generalist feeding strategies whereas dragonfly and vertebrate taxa categories were consumed by pike with specialized feeding strategies as indicated by high PSA (Supplementary material 2-7). Some prey, such as sculpin, were large components in the diets of few populations. Thus, a broad view of northern pike trophic patterns ignores some nuance of rare diet components.

For our third objective, canonical correspondence analysis illustrated the variation in small, medium, and large northern pike diets across all waterbodies and in invaded waters (Fig. 4). The numerical difference between fish and invertebrate prey taxa categories consumed at each waterbody was the most significant variable associated with prey taxa communities per northern pike size class and waterbody type (permuted ANOVA, $P < 0.01$; Table 3). The first two CCA axes were significant for all size classes ($P < 0.01$) across all waterbodies, likely because the differences between native and invaded ranges (i.e., recent invasion compared to historic presence as well as waterbody size). Medium and large northern pike also had a significant third axis ($P < 0.05$) that appeared to illustrate similar patterns as the second axis and were not shown. Alternatively, when only invaded waters were analyzed, each size class had one significant axis and only medium northern pike had a significant second CCA axis.

Although the order of significance varied according to each axis per size class, there were two general axis interpretations used in each ordination plot. First, there was an axis (CCA1) where waterbodies organized according to the difference between invertebrate and fish taxa consumed. This illustrated a gradient of diet composition whereby one direction indicated fish dominated diets (i.e., the invaded streams as well as the native population in Lake Clark) and the opposite direction indicated a diverse diet of macroinvertebrates and other prey items represented by many invaded lakes. Second, there was an axis (CCA 2) that

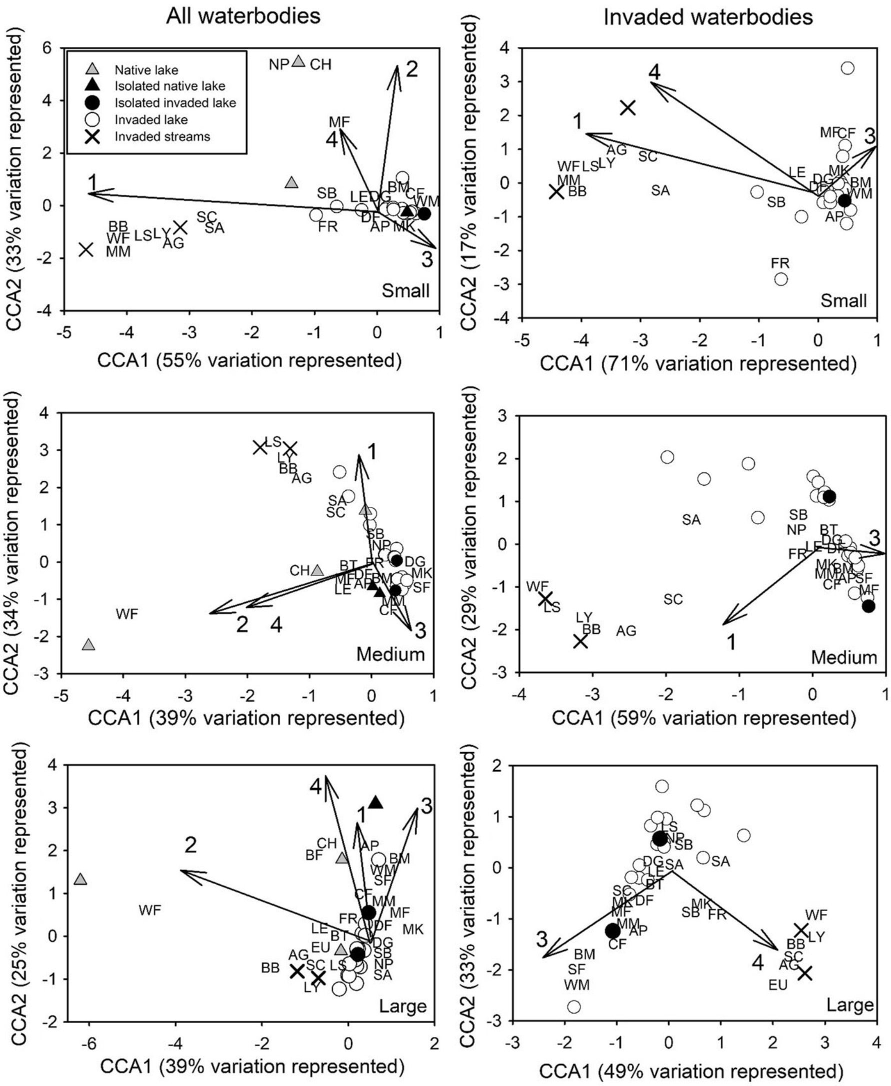

Fig. 4 Canonical correspondence analysis for diets of northern pike separated by size class: small (top panels representing fish < 32 cm); medium (middle panels representing fish greater than or equal to 32 cm but less than 46 cm); and large (bottom panels representing fish > 46 cm). Two-letter text indicates diet items whereas shapes indicate waterbodies. Prey taxa codes are as follows: DG (dragonfly), DF (damselfly), CF (caddisfly), CH (chironomid), SF (stonefly), WM (watermite), BT (beetle), BM (boatmen), AP (amphipod), LE (leech), MF (mayfly), MK (mollusk), SA (salmonid), SB (stickleback), SC (sculpin), NP (northern pike), BF (blackfish) EU (eulachon), BB (burbot), LS (longnose sucker), LY (lamprey), WF (whitefish), AG (Arctic grayling), FR (wood frog), and MM (mammal). Numeric vector labels indicate significant predictor variables: 1 (total prey taxa consumed), 2 (waterbody size), 3 (difference between total fish taxa and total invertebrate taxa consumed), 4 (years since invasion or northern pike introduction)

largely involved total prey taxa consumed (i.e., medium and large northern pike from all waterbodies) or years since northern pike invasion (small northern pike from all waterbodies and only invaded waters), but this axis was more variable and open to additional interpretation per size class and waterbody. Aside from patterns in large northern pike diets that may have been influenced by cannibalism and stickleback presence, diets in isolated lakes grouped relatively tightly for small and medium size classes.

Table 3 *P* values of predictor variables and axes calculated by canonical correspondence analysis of diet data relative to size class (small, medium, and large) of northern pike sampled from 31 Alaskan waterbodies and only invasive populations

Variable	Invasive waters only			All waterbodies		
	Small	Medium	Large	Small	Medium	Large
Years since invasion	**0.002**	**0.002**	**0.003**	**0.009**	**0.001**	**0.002**
Waterbody size	0.252	0.164	0.513	**0.005**	**0.001**	**0.001**
Total prey taxa	**0.001**	0.063	0.086	**0.001**	**0.001**	**0.007**
InvFishDiff	**0.001**	**0.001**	**0.001**	**0.001**	**0.001**	**0.001**
Axis						
CCA1	**0.001**	**0.001**	**0.001**	**0.001**	**0.001**	**0.001**
CCA2	0.196	**0.009**	0.052	**0.002**	**0.001**	**0.001**
CCA3	0.526	0.503	0.76	0.105	**0.005**	**0.005**

Bold indicates variable or axis was significant at $\alpha = 0.05$. Years since invasion for native range lakes was treated as a dummy variable for native waterbodies where it was an extremely high value indicating native range

Discussion

Northern pike trophic orientation differed among size classes but generally indicated specialization toward vertebrate prey, generalization toward macroinvertebrate prey (aside from dragonflies), high inter-individual variability in diet, and seldom consume conspecifics. Whereas others have shown or assumed that northern pike $>$ 85 mm “specialize” on fish prey (i.e., Allen 1939; Frost 1954; Beaudoin et al. 1999), our study suggests a rethinking of northern pike as invertebrate generalists that will specialize on fishes when possible. The extent of invertivore and piscivore-invertivore trophic patterns by northern pike was pronounced in small lakes from both the native and invasive ranges, where individuals consumed macroinvertebrates and occasionally conspecifics or sticklebacks. Results suggest that northern pike diets in isolated lakes in Alaska trend toward invertebrate consumption including dragonflies, amphipods, and leeches. Ordinations also indicated that when fish (e.g., sticklebacks and salmonids) were present in northern pike diets, invertebrates were less likely to be consumed in those waterbodies. Moreover, northern pike showed an ontogenetic shift toward piscivory as they grew larger and, depending on fish community structure, northern pike may have more positive responses in terms of growth and population dynamics when living strictly with prey species such as stickleback or salmonids compared to potential competitors—as long as prey populations are not extirpated (Sánchez-Hernández et al. 2016). High inter-individual variation in northern pike diets creates a spectrum of individual trophic specialization that is also found in other freshwater consumers such as fishes, amphibians, and crustaceans via mechanisms including habitat partitioning and predator density (Werner et al. 1981; Bolnick et al. 2003).

Consistent with Olden et al. (2006), our findings highlighted northern pike as trophic generalists, a trait common among invasive species that can facilitate their ongoing invasion and enhance their impact. While this trophic plasticity may underpin the sentiment of Aksakov’s quote at the opening of this paper, we interpret this pattern to reflect an adaptation for persistence in the diverse, heterogeneous landscapes in the native and invasive ranges of northern pike (sensu Venturelli and Tonn 2006). This strategy results in both predation upon and competition with native species that may create trophic cascades by altering abundance of lower trophic level consumers or of native fish predators (Vander Zanden and Rasmussen 1999; Findlay et al. 2000; Byström et al. 2007). Interestingly, generalist feeding may also enhance survival whereby contrasting prevalence of invertebrate-dominated diets to rare cannibalism could be related to findings that suggest greater prey handling time (i.e., larger prey such as other fishes) exposes northern pike to cannibalistic conspecifics (Nilsson and Brönmark 1999). The fact that the northern pike has such high variation in life history strategy (i.e., spawning time, migration, habitat use) and diet makes it an intriguing focal species in community ecology (Forsman et al. 2015).

Consequences of a predator's trophic patterns can manifest at various scales according to extant community structure. Combining our findings using PSA (objective 2) and ordination (objective 3), we found that prey taxa that were specialized upon such as dragonfly, stickleback, and salmonids represented widespread and strong drivers of diet compared to more infrequently consumed fishes such as burbot (*Lota lota*), whitefish, and Arctic grayling. Stickleback and salmon populations can be sensitive to northern pike presence (Patankar et al. 2006; Sepulveda et al. 2013). The ordinations also exposed a general pattern of habitat overlap by northern pike with many frequently consumed prey taxa in littoral zones rather than other fishes whose behavior make them largely unavailable as prey (i.e., burbot and longnose sucker in deeper, benthic habitats) or whose migratory patterns minimize spatio-temporal overlap (i.e., lamprey and eulachon). Nicholson et al. (2015) showed that northern pike populations may specialize on one prey fish species when available in a lake, but at a broader landscape scale, the deleterious effect of generalist northern pike predation was evident in the extirpation of seven fish species (including members of Cyprinidae, Catostomidae, Cottidae, and Percidae) of various body shapes, sizes, and habitat use patterns across several Canadian lakes. To put this in context with our findings in Alaska, northern pike operate as top predators in littoral zone habitats within isolated lakes (where they can extirpate sticklebacks), rivers (where they can diminish Chinook salmon *O. tshawyctcha* abundance, Sepulveda et al. 2013), and lake–river networks (where they can affect native fishes such as lake-rearing sockeye salmon, Hartman and Burgner 1972). Consequently, their collective effect on fishes in Alaska will be a mosaic according to when and where northern pike invade (or occur). Indeed, CCA illustrated a dichotomy of prey consumption patterns between native and invaded range waterbodies. Within invaded waters only, there was an apparent signal of prey taxa consumption across space and time where connectivity may enhance resilience (prolong presence) of native stream fish communities and isolation trends toward fishless communities over time where invertebrates support northern pike. Thus, while individuals and populations of northern pike could have localized specialization on certain prey taxa (i.e., Beaudoin et al. 1999), their broad scale generalist diet patterns will impact communities at a landscape or regional level.

One of the inherent challenges of synthesis science is to meaningfully bring together data collected with often disparate objectives and approaches. In our case, samples were collected across regions, years, and seasons and consequently we cannot quantitatively assess how prey importance changes among years or seasons, which is undoubtedly important given the ephemeral nature of some prey taxa (e.g., migratory fishes and terrestrial insects). We acknowledge that, summer samples may fail to capture prominent dietary behaviors like cannibalism that may peak during the critical rearing period for young-of-the-year fish by conspecifics within their own cohort or from previous generations (Kipling and Frost 1970; Giles et al. 1986). This may be an especially important food subsidy where northern pike are the only fish present. Despite logistical impediments inherent to any data synthesis, we attempted to minimize variation introduced from disparate datasets. For example, our analyses used weights of prey specific to Alaska, creating more realistic data, information, and inference into northern pike trophic patterns. Sampling protocols in the future should aim to simultaneously maximize the spatiotemporal aspects of northern pike populations with individual level dietary data across longer time frames (i.e., stable isotope analyses), especially from native Alaskan waterbodies that were less plentiful in this study.

Although intraspecific trait variation is ubiquitous within populations, it is lesser known how long-term effects of trophic plasticity may manifest in community structure or dynamics, especially relative to recently invasive species (Bolnick et al. 2011). Applied consequences of invasive northern pike trophic plasticity include a greater challenge and higher cost to restoring native fishes, aquatic habitats, and the economies or livelihoods that depend on native animal communities. Due to the long life span and trophic plasticity of northern pike, management of invasive populations should seek suppression and eradication early in the invasion process as efforts to reintroduce diminished salmonid (or other fish) populations are likely to be impeded by the capacity of northern pike to persist with generalist feeding strategies (Ince and Thorpe 1976; Chapman et al. 1989; Lepak et al. 2012; Sepulveda et al. 2015; Courtney et al. 2018). Therefore, accurately quantifying trophic patterns of northern pike that vary in size and behavior can help predict effects in both native and nonnative ranges that could expand or contract due to climate change, landscape modification, invasion (or introduction), or eradication efforts. The proximity of imperiled or economically-vital species to northern pike throughout Alaska reinforces the need for public engagement strategies to counter current invasions and mitigate impacts.

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