

Top-down control of invertebrates by Ninespine Stickleback in Arctic ponds

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Abstract: Despite their widespread presence in northern-latitude ecosystems, the ecological role of Ninespine Stickleback *Pungitius pungitius* is not well understood. Ninespine Stickleback can occupy both top and intermediate trophic levels in freshwater ecosystems, so their role in food webs as a predator on invertebrates and as a forage fish for upper level consumers probably is substantial. We introduced Ninespine Sticklebacks to fishless ponds to elucidate their potential effects as a predator on invertebrate communities in Arctic lentic freshwaters. We hypothesized that Ninespine Stickleback would affect freshwater invertebrate communities in a top-down manner. We predicted that the addition of Ninespine Sticklebacks to fishless ponds would: 1) reduce invertebrate taxonomic richness, 2) decrease overall invertebrate abundance, 3) reduce invertebrate biomass, and 4) decrease average invertebrate body size. We tested our hypothesis at 2 locations by adding Ninespine Stickleback to isolated ponds and compared invertebrate communities over time between fish-addition and fishless control ponds. Ninespine Sticklebacks exerted strong top-down pressure on invertebrate communities mainly by changing invertebrate taxonomic richness and biomass and, to a lesser extent, abundance and average invertebrate size. Our results supported the hypothesis that Ninespine Stickleback may help shape lentic food webs in the Arctic.

Key words: Ninespine Stickleback, top-down, food webs, predation, addition experiment, Arctic

Fish can shape the structure and composition of aquatic communities through top-down control on their invertebrate prey (Power 1990, Carpenter and Kitchell 1993). Despite the clear capacity for fishes to drive top-down effects, isolating the role of individual fish species or trophic levels is difficult given the complexity of aquatic food webs (e.g., Winkelmann et al. 2011, Helenius et al. 2015). Direct effects of predation may be masked or modified by other members of the food web, confusing specific trophic relationships (Polis 1994, Batzer et al. 2000). Also, the relative position of fish predators in a food web may affect predator–prey interactions at lower trophic levels or alter interspecific interactions (Jonsson et al. 2007). The indirect effects of predators on invertebrate communities (e.g., shifts in invertebrate behavior) may dilute the effect of direct consumption, masking important interactions (Batzer et al. 2000, Jonsson et al. 2007). Furthermore, predator effects are often reduced or altered by the spatial complexity of habitat (e.g., macrophytes),

which can provide refuge for invertebrate prey (Gilinsky 1984, Zimmer et al. 2000, Hornung and Foote 2006). We are better able to describe specific interactions and the nature and pattern of the effect of specific fish species within their food webs via the use of experiments and studies comparing fishless to fish-inhabited systems (Power 1992, Polis 1994, Batzer et al. 2000, Lepori et al. 2012).

The presence of fish may change the composition, richness, abundance, biomass, or size of taxa in the invertebrate community relative to fishless systems (e.g., Gilinsky 1984, Knapp et al. 2001, Parker et al. 2001, Hornung and Foote 2006, Winkelmann et al. 2011). Consumption of a nonrandom subset of prey taxa by newly introduced fish can change richness or composition of invertebrate taxa (Gilinsky 1984, Winkelmann et al. 2011, Helenius et al. 2015). Often, within gape limitations, fish predators preferentially consume large-bodied individuals or taxa, leading to a decrease in the overall size of invertebrates or to a community composed of

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smaller-bodied species (Brooks and Dodson 1965, Carlisle and Hawkins 1998, Knapp et al. 2001). This preference may alter the abundance or standing crop of invertebrates as fish predators consume invertebrate prey.

Small-bodied fish species are often a link in food webs that allows energy to flow laterally across habitat boundaries before it flows up the food chain (Schindler and Scheuerell 2002, Vander Zanden and Vadeboncoeur 2002, Solomon et al. 2011). For example, Vander Zanden and Vadeboncoeur (2002) found that benthic production indirectly supported >35% of the diet of 3 piscivorous fishes because their small-bodied fish prey relied on benthic food sources. One such group of small-bodied fishes are the sticklebacks, Family Gasterosteidae, which, by virtue of their omnivorous dietary habits, often serve this intermediate role in aquatic food webs (Morrow 1980, Delbeek and Williams 1988, Hornung and Foote 2006). McFarland (2015) found that Ninespine Stickleback *Pungitius pungitius* are a valuable food resource for Arctic Grayling *Thymallus arcticus* and accounted for 88% of prey biomass consumed in a study on the Arctic Coastal Plain of Alaska. However, to date, no investigators have published studies on the influence of Ninespine Stickleback predation on invertebrate communities. The few related studies are limited to observation or comparisons with other sticklebacks or Arctic Char *Salvelinus alpinus* (Delbeek and Williams 1988, Gallagher and Dick 2011, McFarland 2015).

This paucity of information on the ecological role of Ninespine Stickleback is surprising given their circumpolar distribution and dominance in Arctic lakes (Morrow 1980, Haynes et al. 2014, Laske et al. 2016). In terms of catch-per-unit-effort, the average numerical ratio of Ninespine Stickleback to other sympatric fish species in lakes of the central Arctic Coastal Plain of Alaska is ~800 : 1 (SML, unpublished data), indicating they make up a large proportion of fish biomass and probably play a substantial role in food webs. Considering the rapid metabolism and dietary flexibility of Ninespine Stickleback (Cameron et al. 1973) and the associated high demand for food resources, they are likely to affect their invertebrate prey. In experiments on related species, total invertebrate abundance increased in the presence of Threespine Stickleback *Gasterosteus aculeatus* because predation pressure on large crustaceans released small-bodied microzooplankton from predation or competition and caused their numbers to rise (Helenius et al. 2015). Brook Stickleback *Culaea inconstans* competed with large-bodied predatory invertebrates for food, which led to depletions of predatory and noninsectivorous invertebrate biomass and functional replacement of invertebrate predators by Brook Stickleback (Hornung and Foote 2006).

Ninespine Stickleback have the potential to transfer energy along multiple trophic pathways (Gallagher and Dick 2011) because of their relative position in local food webs as either the top fish predator (when found as the sole pred-

atory fish) or as an intermediate predator (when found with additional predatory fishes). They can mediate the transfer of energy from littoral habitats to predatory fish in the pelagic zone or indicate changes in the primary source of energy production (phytoplankton vs periphyton; Gallagher and Dick 2011). However, their precise role in Arctic food webs may be difficult to describe in natural habitats where ecosystem interactions are complex. The ponds and lakes that routinely contain populations of Ninespine Stickleback are structurally diverse, with open water, shallow weed margins, submerged vegetation, and areas of flooded tundra (Cameron et al. 1973), all of which may provide different cover and habitats for invertebrate prey. Furthermore, limnology differs between ponds and lakes (surface area [SA] > 0.1 km²). Lakes tend to be deeper, cooler, and less productive than ponds (Rautio et al. 2011) and the presence of predatory fishes in lakes may confound or mute the direct effects of Ninespine Stickleback on the invertebrate community. Zooplankton are larger and more abundant in fishless systems than in lakes or ponds with fish (Rautio and Vincent 2006), but discerning the role of individuals in a multiple-predator environment is complex (Sih et al. 1998). Therefore, attributing influence solely to Ninespine Stickleback would be difficult. Thus, initial explorations of their ecosystem role may be best examined in simple, isolated pond systems.

The goal of our study was to investigate the role of Ninespine Stickleback as a predator in lentic freshwater food webs in Arctic Alaska via an addition–control experiment to detect top-down effects on invertebrate community structure. This experimental approach provided information on the direction and breadth of effects while controlling for external factors (e.g., waterbody type, invertebrate composition, and fish density). Essentially, we took the first step in establishing foodweb patterns that could be driven by the presence of Ninespine Stickleback in Arctic ponds and lakes. We predicted that the addition of Ninespine Stickleback to previously fishless ponds would have the following top-down effects: 1) reduce invertebrate taxonomic richness, 2) lower overall invertebrate abundance, 3) reduce invertebrate biomass, and 4) decrease average invertebrate body size. We repeated our experiment in small, isolated ponds over sequential years at 2 locations with differing climate, physiography, and geology (Jorgenson and Grunblatt 2013) to investigate the potential effect of local conditions on the role of Ninespine Stickleback in aquatic food webs.

METHODS

We selected trough ponds from 2 locations (hereafter, North and South) on the Arctic Coastal Plain, Alaska, in which to conduct our experiment (Fig. 1A–C). The low-relief tundra is underlain by thick, continuous permafrost,

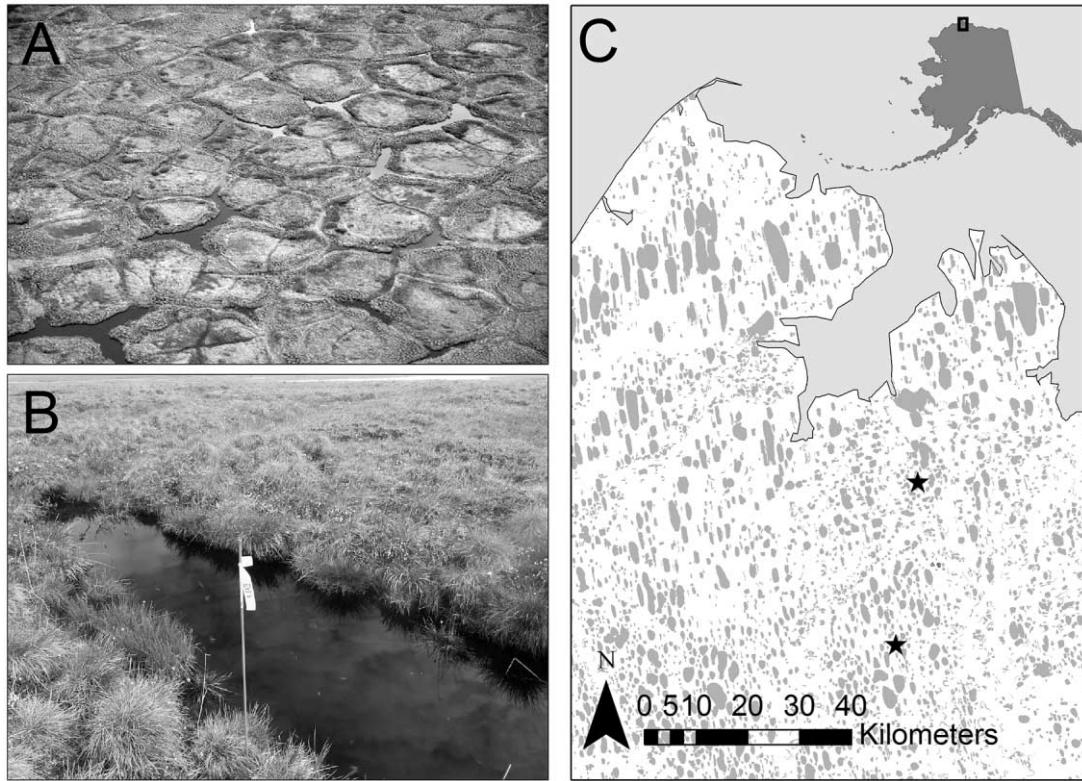


Figure 1. Aerial view of trough ponds (A), an on-site view of 1 experimental pond (B), and maps showing the 2 study locations (North and South; indicated by stars) and the site location in Alaska (C).

which inhibits subsurface drainage and leads to formation of various thermokarst water bodies. Troughs form in the cracks between polygonal ground formations and deepen as the ice beneath melts. These ponds measured $\sim 1\text{--}2$ m wide and 0.5 m deep, with an average pond surface area of 25 m^2 (Table 1). Trough ponds have limited submerged vegetative cover for invertebrates or fish to use, and most cover consists of overhanging grasses or flooded grass margins. Water in the ponds comes from snowmelt in June and is maintained through subsurface flows and precipitation events until refreezing by October (Koch et al. 2014). North is underlain with peat and has more standing surface water than South, which is underlain by sand. The location of ponds in upland areas and lack of surface water connections provided aquatic habitats naïve to fish prior to our experiment.

At each location, we collected Ninespine Stickleback from 1 lake adjacent to the ponds (<1 km from the pond site). We set fyke nets with 6.4-mm mesh overnight to capture fish for transport to ponds. We moved fish in 19-L buckets, and supplied them with air with the aid of battery-operated aquarium pumps (Penn Plax Silent-Air B10, Hauppauge, New York). Fish ranged in size from $\sim 30\text{--}60$ mm total length. We did not keep any fish considered less than age-1 and assumed that no size-based diet differences would exist

based on published diet data for adults (Cameron et al. 1973, Delbeek and Williams 1988). We added Ninespine Stickleback to ponds based on a previously reported mean value of 11 g/m^2 (Cameron et al. 1973), adjusting the number of fish added to attain the correct biomass given pond area. We counted the fish once we attained the desired biomass (Table 1). We added fish to 5 ponds at North (2013) and 6 ponds at South (2012). We selected an equal number of control ponds at each location.

One to 2 d prior to adding Ninespine Stickleback, we used a $243\text{-}\mu\text{m}$ -mesh D-frame dip net with an opening of 604 cm^2 to sample nektonic and benthic invertebrates in all ponds. We moved the net in a J-shaped motion that began with the net grazing the bottom, then passed the net horizontally along the bottom and up through the water column. We collected 2 replicate dip-net samples from each pond and noted the depth of the water at each sweep location. Replicate net samples increased the opportunity to capture rare taxa, and we did not compare within-pond variation based on these 2 samples. We examined taxa rarefaction curves before adding fish to assess whether collection was adequate (Fig. S1; Gotelli and Colwell 2001). At North, we sampled invertebrates in the same way 1, 3, and 6 wk post-introduction. At South, we sampled invertebrates 1, 2, and 8 wk post-introduction. We stored invertebrate sam-

Table 1. Pond location, addition treatment, and surface area (SA). The biomass (g) and number (*n*) of fish stocked are given for fish-addition ponds. ID = identifier.

Location	Addition treatment	Pond ID	SA (m ²)	Fish added (g)	Fish added (<i>n</i>)
North	Control	N2	19.0	–	–
		N4	45.0	–	–
		N5	36.0	–	–
		N6	70.0	–	–
		N9	20.8	–	–
	Fish-addition	N1	10.5	116	103
		N3	58.0	396	393
		N7	35.0	385	344
		N8	54.6	601	551
		N10	38.0	418	353
South	Control	3	26.0	–	–
		4	19.6	–	–
		7	7.2	–	–
		8	5.3	–	–
		9	18.9	–	–
		11	18.1	–	–
	Fish-addition	1	15.2	167	153
		2	6.5	70	60
		5	11.1	122	101
		6	8.7	96	93
		10	4.3	47	34
		12	22.3	245	303

ples in 95% ethanol for later processing. On post-introduction sampling days, we recaptured Ninespine Stickleback with unbaited minnow traps (23-cm diameter × 44.5-cm length, two 2.5-cm openings, 6-mm steel mesh) and sampled the stomach contents by gastric lavage with a 22-gage intravenous catheter attached to a syringe. We flushed stomachs with 3 to 5 mL of filtered pond water and stored stomach contents in 95% ethanol. We sampled 6 (North) or 5 (South) individuals at each fish-addition pond (total = 30 fish/location on each sampling date). We then released fish back to the pond. At North, we also sampled stomach contents 1 d post-introduction.

In the laboratory, we identified all invertebrates from dip-net collections and stomach contents to the lowest practical taxonomic level and assigned a life stage (larva, pupa, or adult). For example, macroinvertebrates were identified to family, but Ostracoda were identified no lower than to class. From the dip-net samples, for each pond and sampling period, we captured images of up to 20 individuals of each taxon with a Leica DFC425 (Leica Microsystems, Buffalo Grove, Illinois) camera mounted on a dissection microscope. We digitally measured invertebrate lengths with ImageJ (version 1.48; imagej.nih.gov). We used length–mass regression equations from the literature to estimate biomass

of invertebrates (Dumont et al. 1975, Pace and Orcutt 1981, Culver et al. 1985, Benke et al. 1999, Sabo et al. 2002, Gruner 2003, Miyasaka et al. 2008, Rennie and Evans 2012).

Statistical analyses

Invertebrates We compared number of invertebrate taxa, abundance, biomass, and size of invertebrates in control and fish-addition ponds at each sampling time to assess whether invertebrate assemblage characteristics changed in the presence of Ninespine Stickleback. Number of invertebrate taxa was the number of unique invertebrate taxa found in each pond. Rarefaction was not possible because drastic differences in invertebrate abundance among addition treatments (e.g., post-addition at South: average count in control ponds = 4713 individuals, average count in fish-addition ponds = 118 individuals) rendered standardized measures of richness incomparable. At each pond and sampling time, we divided the number of invertebrates by the sweep depth of the 2 samples to calculate abundance (number of invertebrates/cm depth swept). To obtain biomass, we multiplied the number of invertebrates by the average biomass on a taxon-specific basis from length–mass equations (referenced above), and divided by the depth of the

sweep to obtain biomass/cm of depth swept. We used mean weighted length calculations (following methods by Helenius et al. 2015) to estimate differences in overall invertebrate size between control and fish-addition ponds at each sampling time. We tested for effects of addition treatment and time while accounting for location (fixed effect) and pond (random effect) based on linear mixed-effects models in R package *nlme* (version 3.1-126; R Project for Statistical Computing, Vienna, Austria) and accounted for temporal autocorrelation with a 1st-order autoregressive structure for all models except our model for number of invertebrate taxa, which was based on compound symmetry (model selection based on lowest Akaike Information Criterion for small samples [AICc] score; R package *AICcmodavg*, version 2.0-4). Log(*x*)-transforming abundance and biomass values prior to analysis improved normality.

We used multivariate approaches to examine changes in invertebrate community composition caused by the addition treatment, time, and addition-treatment × time interaction. We standardized abundances of individual taxa to species maxima and omitted taxa captured only once during the course of the study. We visually examined a non-metric multidimensional scaling (NMDS) plot (R package *vegan*, version 2.3-4) at 2 and 3 dimensions to assess which yielded the lowest stress. We then used repeated-measures multivariate analysis of variance (PERMANOVA) based on dissimilarities using Bray–Curtis distances (function *adonis*; R package *vegan*, version 2.3-4) to estimate the proportion of variation explained by location (North vs South), addition treatment, time, and the addition-treatment × time interaction in permutation tests (1000 iterations). We repeated these analyses on the mass of invertebrates to assess predation effects on invertebrate biomass.

Stomach contents For each invertebrate taxon at all post-addition sampling times, we calculated frequency of occurrence as the number of fish in which the taxon occurred divided by the total number of fish with food in their stomachs. To calculate the mean proportion of diet items by number, we summed the invertebrates in the stomach contents of the 5 or 6 sampled fish (fish were pseudo-replicates within ponds) at each sampling time and calculated the numerical proportions for all taxa standardized to the total. We assessed the influence of time since introduction on the mean proportion of diet items by number in Ninespine Stickleback stomach contents with PERMANOVA on commonly consumed items (frequency of occurrence > 20%). This function allowed us to partition sources of variation and account for the pond effect in the permutation tests (1000 iterations). We then calculated similarity percentage (SIMPER; *vegan*) between diets, by numeric proportion, at the beginning and end of the experiment using dissimilarity matrices. At South, we compared diets at week 1 to week 8, and at North, we compared diets at day 1 to week 6 and di-

ets at week 1 to week 6. Furthermore, we estimated the contributions of potentially influential taxa (mean contribution to dissimilarity > 10%) to dietary differences.

RESULTS

Invertebrates

Our prediction that introducing Ninespine Stickleback to ponds would decrease invertebrate richness was supported. Addition of Ninespine Stickleback reduced the number of invertebrate taxa in fish-addition ponds at both locations by an average of 21.7% compared to control ponds (North: $t = -2.60$, $df = 45$, $p = 0.01$; South: $t = -3.11$, $df = 45$, $p = 0.003$; Fig. 2A, B). Richness attenuated over the season at all ponds, but the reduction was greatest in fish-addition ponds. Compared to control ponds, richness in fish-addition ponds was reduced by an average of 4 taxa (31.2%) at North and 1 taxon (10.5%) at South. After the initial decrease, number of taxa did not differ detectably over time (post-addition; North: $t = 0.20$, $df = 45$, $p = 0.84$; South: $t = -0.77$, $df = 45$, $p = 0.44$) or by location ($t = -1.95$, $df = 45$, $p = 0.06$).

Support for our prediction that introducing Ninespine Stickleback would decrease invertebrate abundance was limited (Fig. 2C, D). Abundance initially decreased but then increased at North (addition treatment × time interaction: $t = 3.61$, $df = 40$, $p < 0.001$) but remained lower at South (addition treatment: $t = -8.88$, $df = 18$, $p < 0.001$). After an immediate decrease (week 1), abundance stayed low throughout all sampling periods at South (time: $t = 1.05$, $df = 40$, $p = 0.30$). Fish-addition ponds at South contained 98% fewer invertebrates/cm depth swept than their control-pond counterparts, but at North, fish addition interacted with time to confound the influence of fish introduction on invertebrate abundance. Abundance rebounded after an initial 84% decrease (compared to control ponds). By the 6th wk post-addition, abundance of invertebrates in fish-addition ponds exceeded control-pond values by 23%. This increase in abundance was not accompanied by an increase in biomass (Fig. 2C, E).

At both locations, fish addition decreased invertebrate biomass (North: $t = -3.06$, $df = 18$, $p = 0.007$; South: $t = -5.13$, $df = 18$, $p < 0.001$; Fig. 2E, F), providing support for our hypothesis. As with abundance at South, after an initial decrease in biomass, invertebrate losses stabilized and did not continue through time. At all post-addition sampling times, invertebrate biomass was ~90% lower in fish-addition than in control ponds.

Our prediction that introduction of Ninespine Stickleback would decrease the overall size of invertebrates in the ponds was not supported. At both locations, fish addition did not affect mean weighted size of invertebrates (North: $t = -1.36$, $df = 45$, $p = 0.18$; South: $t = -1.13$, $df = 45$, $p = 0.26$; Fig. 2G, H). At North, length tended to diverge over time between addition treatments (addition-

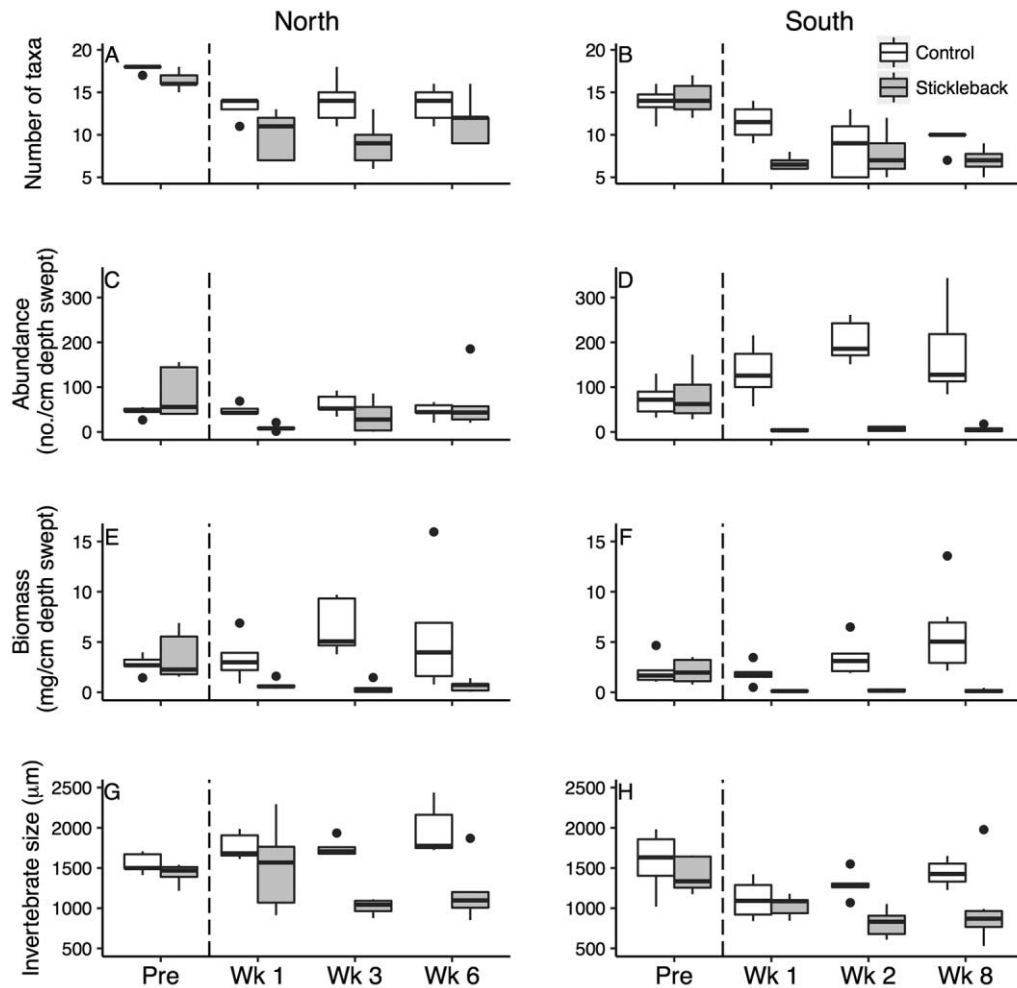


Figure 2. Box-and-whisker plots for the number of taxa (A, B), abundance (C, D), biomass (E, F), and size (G, H) of invertebrates before and after Ninespine Stickleback addition to ponds in the North (A, C, E, and G) and South (B, D, F, and H) locations. Lines in boxes are medians, box-ends are quartiles, whiskers are $1.5 \times$ inter-quartile range, and dots show outliers. The vertical dashed line separates pre-addition and post-addition sampling dates. No. = number, Wk = week, pre = pre-addition.

treatment \times time interaction: $t = -1.90$, $df = 45$, $p = 0.06$), but sampling time and the addition-treatment \times sampling time interaction were not significant at South, though the pattern of mean weighted lengths over time was similar for North and South ponds (Fig. 2G, H).

NMDS plots showed the relative similarity of samples (centroids of all ponds in the addition-treatment-time group) for location, addition treatment, and time (Fig. 3A–F). Three dimensions reduced stress (0.16) and provided better fit for the data than 2 dimensions. Plots based on the first 2 dimensions (NMDS1 vs NMDS2; Fig. 3A, D) showed strong separation of samples by addition treatment and location and showed that pre-addition communities were more similar to communities in control than in fish-addition ponds. Proximity among samples suggested that fish addition had a greater influence than time on commu-

nity structure. Plots based on the 1st and 3rd dimensions (NMDS1 vs NMDS3; Fig. 3B, E) showed separation by addition treatment along the 1st axis. Evaluation of the 2nd and 3rd dimensions (NMDS2 vs NMDS3; Fig. 3C, F) showed separation by location.

PERMANOVA supported the trends visible in the NMDS plot. Fish addition was an important factor in shaping invertebrate communities at North and South regardless of whether dissimilarities were based on abundance ($R^2 = 0.38$, $p < 0.001$) or biomass ($R^2 = 0.35$, $p < 0.001$). Time accounted for little of the variation in biomass among communities ($R^2 = 0.02$, $p = 0.02$). Time and the addition-treatment \times time interaction accounted for little of the variation in abundances among communities (time: $R^2 = 0.02$, $p = 0.02$; addition-treatment \times time interaction: $R^2 = 0.01$, $p = 0.05$). The amounts of variation in biomass

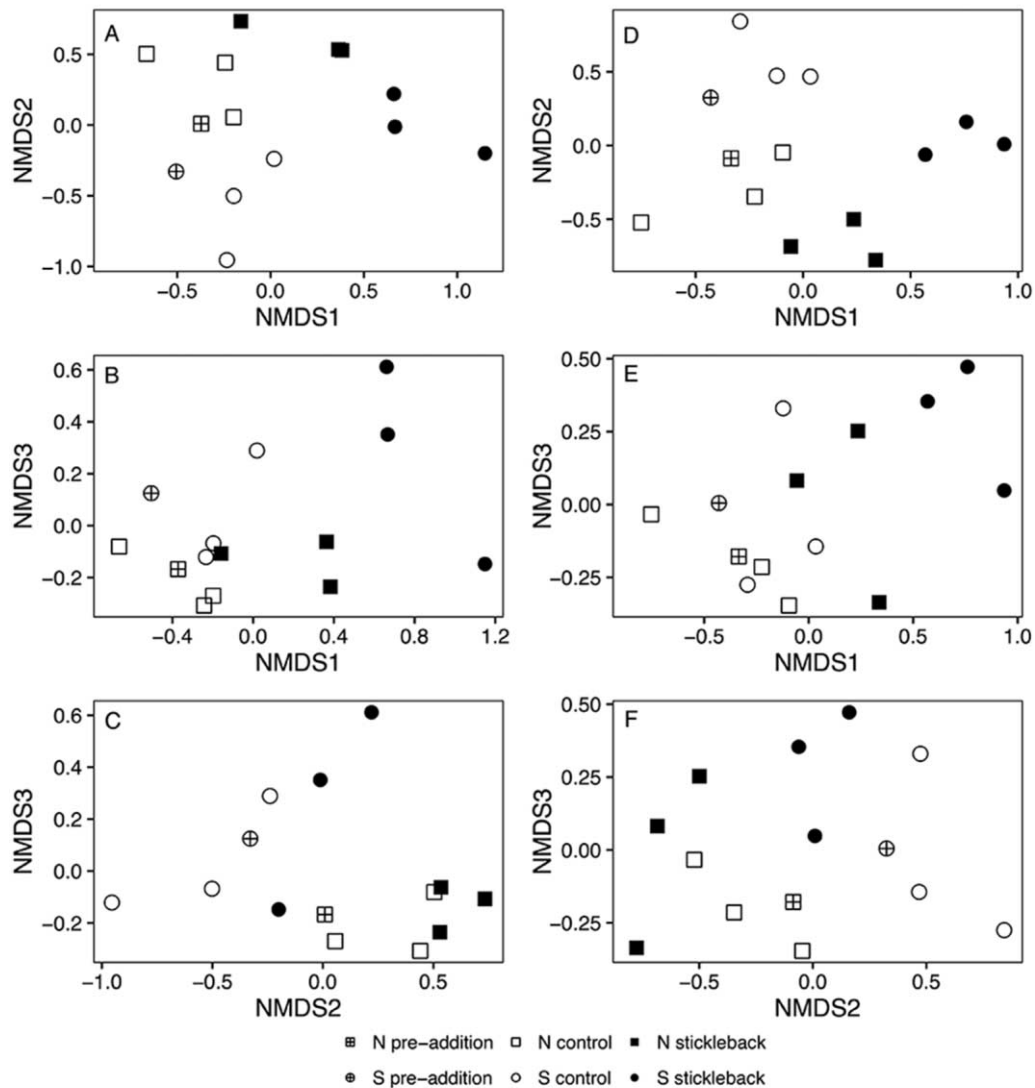


Figure 3. Nonmetric multidimensional scaling (NMDS) plots for invertebrate communities based on abundance (A–C) and biomass (D–F). Individual points represent the centroids of invertebrate communities for North (N) and South (S) pre-addition, control, and stickleback addition ponds at each sampling time. Proximity indicates similarity among communities.

or abundance among communities explained by sampling time (the repeated-measure) were $\leq 2\%$. Location, which appeared distinctly in our NMDS plots, was a secondary source of variation in abundance ($R^2 = 0.20$, $p < 0.001$) and biomass ($R^2 = 0.22$, $p < 0.001$) among communities.

Stomach contents

Based on frequency of occurrence, the diets of Ninespine Stickleback were more diverse at North than South (Tables 2, 3). Three taxa occurred regularly in the diets of Ninespine Stickleback at both North and South. At South, Chironomidae (larva and pupa), Cyclopoida, and Harpacticoida had a frequency of occurrence $>30\%$ at each sam-

pling time. At North, Chironomidae (larvae and pupae) and Cyclopoida had a frequency of occurrence $>30\%$ at all time periods and Harpacticoida had a frequency of occurrence $\geq 30\%$ at wk 3 and wk 6. Harpacticoida, Chydoridae, and Ostracoda increased in frequency of occurrence (Tables 2, 3) and numeric proportion in fish stomach contents (Fig. 4) after the abundance of large-bodied prey declined. Chironomidae frequency of occurrence was consistent throughout the experiment (Tables 2, 3), and the numeric proportion of all Diptera (larvae and pupae), including Chironomidae, in the diets was relatively consistent (Fig. 4). We saw a shift from larger prey (e.g., Daphniidae) to small-bodied prey (e.g., Harpacticoida) at both locations (Fig. 4). Consumption of Daphniidae and Baetidae

Table 2. Frequency of occurrence (% of Ninespine Stickleback with a given taxon in stomach contents) at North 1 d (d1), 1 wk (wk1), 3 wk (wk3), and 6 wk (wk6) post-addition.

Taxon	Frequency of occurrence (%)			
	d1	wk1	wk3	wk6
Chironomidae	77	40	80	77
Daphniidae	63	7	0	0
Chaoboridae	43	0	0	0
Cyclopoida	43	67	47	77
Baetidae	37	0	0	0
Unknown Diptera	33	93	37	40
Dytiscidae	20	20	3	0
Harpacticoida	10	23	30	73
Ostracoda	10	23	23	20
Hydrachnidia	10	7	0	3
Calanoida	10	0	3	3
Terrestrial	7	23	60	13
Chydoridae	7	3	23	50
Ceratopogonidae	7	0	3	7
Dixidae	3	7	0	3
Unknown Trichoptera	3	7	0	0
Tipulidae	3	3	0	0
Copepod nauplii	3	0	0	17
Collembola	0	13	23	13
Physidae	0	13	3	0
Nematoda	0	7	0	7
Unknown Cladocera	0	3	0	0
Unknown Ephemeroptera	0	3	0	0
Unknown Copepoda	0	0	3	0

occurred only within the 1st wk after introduction, and differences in abundance indicated that these taxa were removed from the invertebrate communities of fish-addition ponds (Fig. 5A, B).

Given the differences in invertebrate communities by location, we analyzed the numeric proportion of diet contents separately for North and South. At both locations, we observed a change in stomach contents over time (PERMANOVA, North: $R^2 = 0.16$, $p = 0.005$; South: $R^2 = 0.24$, $p < 0.001$). The dissimilarity matrix indicated changes in both proportion of diet items and identity of prey. Diets differed by 82% from week 1 to week 8 at South (SIMPER), primarily because of changes in Harpacticoida, Daphniidae, and Cyclopoida, with mean contributions to diet dissimilarity of 23 ± 16 (SD), 17 ± 19 , and $15 \pm 14\%$, respectively. At North, diets differed by 81% from day 1 to week 6 and by 68% from week 1 to week 6. From day 1, Daphniidae and Harpacticoida drove these differences, with mean contributions to diet dissimilarity of 26 ± 15 and $13 \pm 11\%$, respectively. From week 1, Ostracoda and Harpacticoida

supported these differences, with mean contributions to diet dissimilarity of 17 ± 19 and $12 \pm 12\%$, respectively.

DISCUSSION

We found support for our hypothesis that Ninespine Stickleback exert top-down controls on invertebrate communities of small Arctic ponds common across the Alaskan Arctic landscape. The effects of fish on the invertebrate community occurred rapidly and persisted throughout the short growing season, and communities quickly shifted from pre-addition and control values. Selective feeding by Ninespine Stickleback (e.g., Ingram et al. 2011, Helenius et al. 2015) targeted specific taxa. This preferential feeding resulted in complete losses of large-bodied, nektonic taxa like Daphniidae and Baetidae, providing evidence that top-down effects can be strong enough to drive local extinctions. By the end of the experiment, Ninespine Stickleback consumption had shifted toward benthic prey like harpacticoid copepods. Behavioral differences between nektonic

Table 3. Frequency of occurrence (% of Ninespine Stickleback with a given taxon in stomach contents) at South 1 wk (wk1), 2 wk (wk2), and 8 wk (wk8) post-addition.

Taxon	Frequency of occurrence (%)		
	wk1	wk2	wk8
Cyclopoida	59	85	70
Daphniidae	52	4	0
Harpacticoida	48	44	93
Chironomidae	33	67	57
Copepod nauplii	30	15	0
Empididae	11	15	0
Hydrachnidiae	11	4	7
Ostracoda	7	22	47
Dytiscidae	7	0	0
Collembola	0	11	7
Dixidae	0	7	0
Limnephilidae	0	4	0
Oligochaeta	0	4	0
Tardigrada	0	0	3
Terrestrial	0	4	3

and benthic taxa probably contributed to the order in which these prey were consumed. Active prey or those swimming in the water column, like Baetidae and Daphniidae, may have a higher risk of encounter with fish predators (Wellborn et al. 1996) and might have been more likely to be consumed than taxa that use cover (e.g., tuft-weaving or tube-building midges; Gilinsky 1984, Power et al. 1992). By selecting specific taxa from the available pool (Delbeek and Williams 1988), Ninespine Stickleback effectively altered the community of invertebrates. Our experimental approach was useful for discerning the potential effects of fish on lower trophic levels because it controlled for confounding factors, including differences arising from location, shifts in diet composition over time, and changes in invertebrate communities unrelated to fish predation (e.g., emergence).

Location of the experimental ponds was a secondary source of variation for invertebrate abundance and biomass, but experimental outcomes demonstrated the importance of Ninespine Stickleback presence across spatial gradients of climate or physiography. Initial invertebrate communities at North and South varied before introducing Ninespine Stickleback into ponds. We found a greater number of taxa at North, which was reflected in the diets of fish, and 2 taxa (Chydoridae and Baetidae) appeared consistently at North but not at South. Fish consumed both of these taxa—Baetidae early on and Chydoridae later. However, when we excluded these items, diets of fish at North and South appeared similar. Fish consumed 6 primary taxa: Daphniidae, cyclopoid copepods, harpacticoid copepods, ostracods, copepod nauplii, and assorted Diptera. In North ponds, replacement of larger invertebrates by smaller ones (e.g., Daph-

niidae for copepods) damped losses in overall abundance but resulted in a loss of biomass. However, at South, the presence of Ninespine Stickleback led to dramatic losses of invertebrate abundance in fish-addition ponds, whereas invertebrate abundance nearly doubled in control ponds. Continued invertebrate population growth in control ponds would lead to greater abundance, but in all ponds at South, the water level fell by up to 0.25 m in the last week of July (SML, unpublished data) because of dry conditions in 2012 (Koch et al. 2014). This loss of volume concentrated invertebrates in open water, away from grassy pond margins, enhanced our ability to capture most taxa, and increased the availability of invertebrates to fish in fish-addition ponds (Gilinsky 1984, Hornung and Foote 2006), which could have increased the difference between addition treatments at South ponds.

Predation pressure on specific taxa led to shifts in invertebrate community structure (similar to findings by Bendell and McNicol 1987, Herbst et al. 2009, Winkelmann et al. 2011). Fish diet breadth is hypothesized to be narrower and selection of larger prey to be stronger when prey exist at high densities (Werner and Hall 1974, Maszczyk and Gliwicz 2014). Ninespine Stickleback exhibited this type of prey selectivity early in the experiment, when 50 to 70% of their diet consisted of 1 or 2 relatively abundant taxa, Daphniidae and Baetidae. Selective feeding exerted top-down control on invertebrate communities (Herbst et al. 2009, Helenius et al. 2015), so Ninespine Stickleback predation shaped the community over time as they sequentially consumed prey in accordance with availability (Delbeek and Williams 1988).

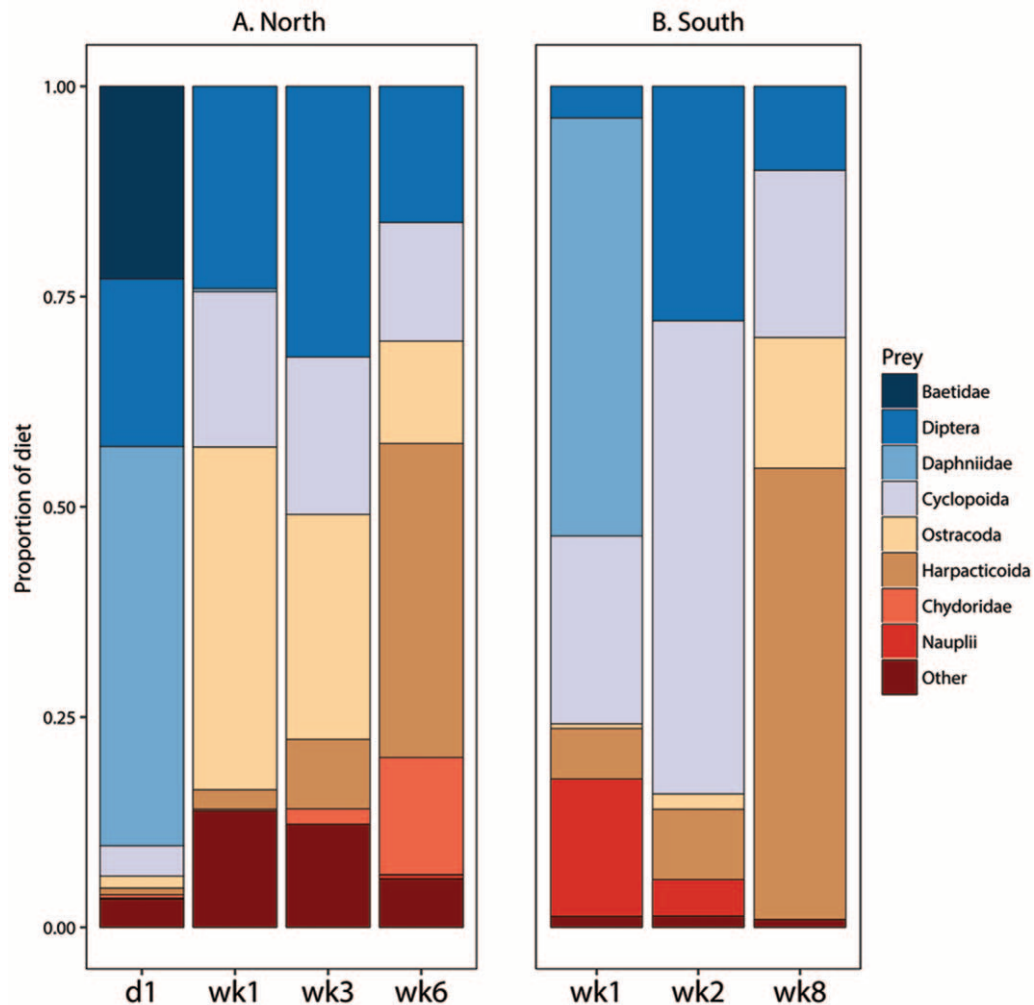


Figure 4. Diet proportions, by number, of common prey items found in Ninespine Stickleback stomach contents at each sampling time. At North (A), we collected contents 1 day (d1), 1 wk (wk1), 3 wk (wk3), and 6 wk (wk6) post-addition, and at South (B) we collected contents 1 wk (wk1), 2 wk (wk2), and 8 wk (wk8) post-addition. Diptera includes larvae and pupae of Chironomidae, Chaoboridae, Ceratopogonidae, Dixidae, Empididae, Tipulidae, and digested (unknown) Diptera.

The shift to smaller taxa was more prominent in ponds at North than South. At North, abundance of small-bodied cyclopoid and harpacticoid copepods increased in fish-addition ponds relative to control ponds, but we did not see this pattern at South. At North, these 2 taxa became so abundant relative to other taxa that they made up nearly the total invertebrate composition in fish-addition ponds in contrast to the declines in abundance of all taxa observed at South. Increased abundance of small taxa is common in the presence of selective foragers like Ninespine Stickleback (Helenius et al. 2015). Increase in small-bodied taxa could result if Ninespine Stickleback reduced the abundance of large-bodied insectivorous or planktivorous taxa that feed upon smaller individuals without consuming the small-bodied pond residents themselves (Batzer et al. 2000). Another explanation is that, under intense predation, size selection for Daphniidae by Ninespine Stickle-

back could ease competition between Daphniidae and small copepods, thereby allowing small-bodied zooplankton to dominate (Brooks and Dodson 1965). Furthermore, small taxa, like Harpacticoida and Ostracoda, generally are associated with the bottom, whereas cladocerans are in the water column. The cover of benthic sediments may allow these taxa to avoid predators, especially when other large-bodied prey are available (Bendell and McNicol 1987).

However, no significant reduction of invertebrate size was evident over time. Size selection by Ninespine Stickleback might have been less apparent because overall variation in the sizes of invertebrates present in the ponds was small. In other words, size selection might have been less apparent than taxonomic selection (i.e., Daphniidae consumed first). However, Ninespine Stickleback have gape limitations (largest reported taxa from diets studied by Cameron et al. 1973 was 10 mm). Some resident pond taxa

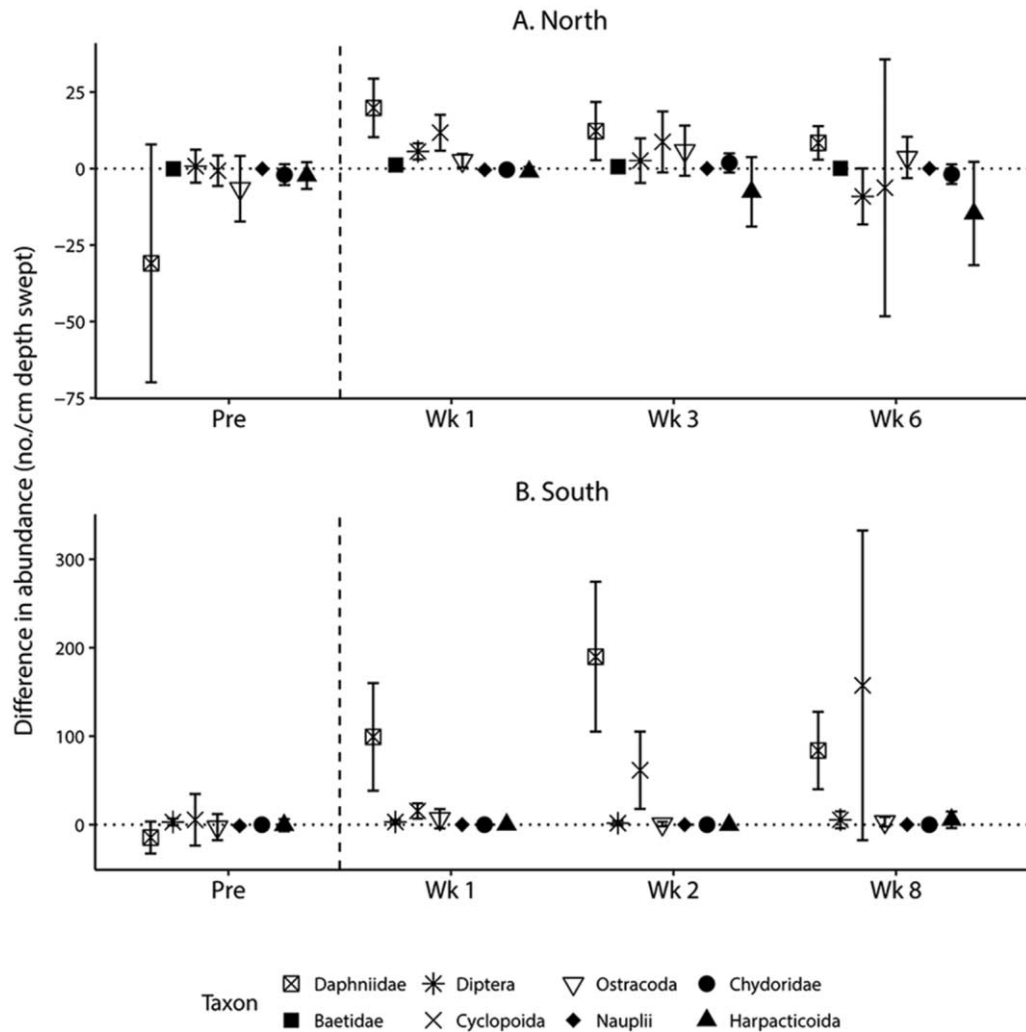


Figure 5. Mean (95% CI) difference in abundance between control and fish-addition ponds of invertebrate taxa common in the stomach contents of Ninespine Stickleback at North (A) and South (B). Points represent the mean control-pond abundance minus the mean fish-addition-pond abundance. Values > 0 indicate control ponds had greater abundance than fish-addition ponds. Values < 0 indicate fish-addition ponds had greater abundance than control ponds. The vertical dashed line separates pre-addition and post-addition sampling dates. Diptera includes larvae and pupae of Chironomidae, Chaoboridae, Ceratopogonidae, Dixidae, Empididae, Tipulidae, and digested (unknown) Diptera. No. = number, Wk = week, pre = pre-addition.

(e.g., Gastropoda or Trichoptera) that were physically too large to be consumed (SML, personal observation) persisted over time and could have maintained the average size of invertebrates during the experiment. Our inability to capture all large-bodied taxa (e.g., Dytiscidae) efficiently prevented us from including them in our analyses and reduced our ability to discern size-based trends.

Data collected prior to introduction of Ninespine Stickleback provided important baseline information for understanding the shift in invertebrate community taxonomic richness, abundance, biomass, and invertebrate size in the presence of fish. For example, pre-addition communities were more similar to those in control than in fish-addition ponds at all sampling times. Some taxa, like Culicidae and

Chaoboridae, underwent metamorphosis to their adult stages early in the experiment (week 1). This emergence probably led to a drop in abundance of these taxa in control and fish-addition ponds. Sampling for emergent adults could provide more detail for understanding predation effects in the aquatic and terrestrial environment and would be an excellent future step in assessing Ninespine Stickleback effects on community structure. How many of these emergent taxa were lost from fish-addition ponds because of ingestion by Ninespine Stickleback vs natural phenology is unknown because losses occurred over the same time period. Examination of the diets of Ninespine Stickleback at North on day 1 suggested that they consumed some of these invertebrates (Chaoboridae and Baetidae), but these items were not found

in stomach contents 1 wk post-addition. Rapid consumption of these taxa probably reduced their numbers, but Baetidae abundance did not differ between fish-addition and control ponds by week 3 despite combined losses from both ingestion and emergence from fish-addition ponds and only emergence from control ponds.

The potential of Ninespine Stickleback to influence the structure of simple aquatic communities must be understood before results can be scaled to larger, more complex systems where effects could be obscured (Gilinsky 1984, Zimmer et al. 2001). The trough ponds to which we introduced Ninespine Stickleback would not have naturally occurring populations of these fish because of their isolated locations. However, other troughs that connect and form a hydrologic network (similar to a stream) or that are in proximity to larger thermokarst ponds may occasionally support Ninespine Stickleback. By examining the effects of Ninespine Stickleback introduction on invertebrate communities at small, fish-naïve ponds with simple morphometry, we tried to control for bottom-up factors that may confound top-down effects so that we could isolate potential effects on the invertebrate community.

Changes in nutrient, light, and thermal regimes that occur as water bodies increase in size cause the emergence of different physical habitats, which support different invertebrate communities (Hobbie 1984, Rautio et al. 2011, Koch et al. 2014). Relatively complex ponds with diverse substrates may contain a heterogeneous assemblage of invertebrates (Power 1994, Zimmer et al. 2001) that respond differently to fish predators. The effect of fish on invertebrate communities can vary with spatial complexity, habitat heterogeneity, or connectivity (Gilinsky 1984, Power 1994, Shurin 2001). For example, submerged vegetation in larger, thermokarst ponds adds complexity to habitats and supplies cover for invertebrate taxa (Zimmer et al. 2000, Hornung and Foote 2006). In lakes and ponds with complex shorelines, terrestrial invertebrates may be more available as prey items, thereby potentially releasing pressure on aquatic invertebrates (Nakano et al. 1999, Mehner et al. 2005). Connection to adjacent habitats or regional surface-water networks provides dispersal pathways for certain colonizing invertebrates (Shurin 2001). Together these factors, along with indirect effects, confound trophic relationships or mitigate the role of predators (Winkelman et al. 2011), leading to premature conclusions on the effects of fish, especially in larger systems (Batzer et al. 2000).

The heterogeneous landscape of ponds, lakes, and streams of the central Arctic Coastal Plain in Alaska presents a variety of potential habitats for occupancy of Ninespine Stickleback. Local- and regional-scale differences in water-body characteristics, such as surface area, depth, watershed connectivity, location, and habitat complexity, affect presence and abundance of Ninespine Stickleback, but also influence the presence and abundance of sympatric fishes and the in-

vertebrate prey base (Cameron et al. 1973, Shurin 2001, Haynes et al. 2014, Laske et al. 2016). We were able to demonstrate consistent top-down effects resulting from the presence of Ninespine Stickleback on invertebrate community structure because our study design accounted for potential variation caused by physiographic locations and pond phenology. By first studying these simplistic food webs, we gain knowledge on trophic effects of ubiquitous Ninespine Stickleback. This study provides needed baseline information on a regionally common fish species, and is a first step in discerning foodweb patterns in the central Arctic Coastal Plain.

Ninespine Stickleback have a wide-ranging, global distribution that includes Asia, Siberia, Europe, Greenland, and North America (Morrow 1980). Thus, they probably exert top-down pressures in other biomes. The Arctic Coastal Plain of Alaska is a unique ecosystem where this species is an extremely successful opportunist (Haynes et al. 2014). However, its adaptability and tolerance suit it well for any number of habitats with a range of physical characteristics and associated biota (e.g., high Arctic: Gallagher and Dick 2011, brackish waters: Arai and Goto 2005, deep temperate lakes: Nelson 1968). In these settings, this relatively small species might play an important role in the transfer of energy via an array of aquatic food webs.

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