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Invasive pike establishment in Cook Inlet Basin lakes, Alaska: diet, native fish abundance and lake environment

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Abstract Northern pike (*Esox lucius*) were introduced to the northern Susitna Basin of south-central Alaska in the 1950's, and have since spread throughout the upper Cook Inlet Basin. Extirpations of several native fish populations have been documented in this area. It is hypothesized here that invasive pike remodel the ecology of lakes by removing vulnerable prey types and that these changes are reflected in the diet of invasive pike. Trends in pike diet suggest that pike switch to less desirable but more abundant macroinvertebrate prey as preferred fish prey are eliminated. The impacts of pike introduction were studied in detail for one species of resident fish, the threespine stickleback (*Gasterosteus aculeatus*). Stickleback abundance decreases as pike invasion progresses. Conductivity is a significant environmental predictor of stickleback abundance, with higher conductivity apparently mitigating population reduction. Higher conductivity water may lessen the physiological costs of developing more robust armor, which reduces vulnerability to predation. Maximum lake depth also appears to predict stickleback abundance, though this trend was only marginally significant. Deeper lakes may provide an open-water refuge from pike predation by allowing stickleback to exist outside of the pike inhabited littoral zone. These findings indicate the importance of diverse habitat types and certain chemical and physical characteristics to the outcome of invasion by fish predators.

Keywords Trophic cascade · Invasive fish · Stomach contents · Northern pike · Threespine stickleback

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Introduction

Invasive species are a considerable force of change globally, altering ecological systems and evolutionary trajectories in their introduced ranges. In the United States, invasive species are the number two cause of extinction of native species after habitat loss (Wilcove et al. 1998; Pimm and Raven 2000). In fresh water, legal and illegal stocking of sportfish species has resulted in the loss of native species and unique regional phenotypes (e.g., Patankar et al. 2006; Rahel 2007). Top-down, cascading effects initiated by predation of resident fish by non-native piscivores have been well documented (Carpenter and Kitchell 1993; Byström et al. 2007). In south-central Alaska, the introduction and spread of northern pike (*Esox lucius*) is altering the ecology of lakes and streams in the Cook Inlet Basin (Rutz 1996, 1999; Patankar et al. 2006). This paper examines shifts in diet as pike become established in lakes and focuses on impacts of pike introduction on the abundance of a model species of resident freshwater fish, the threespine stickleback (*Gasterosteus aculeatus*).

The northern pike is native to Alaska north and west of the Alaska Range (Morrow 1980), and was illegally introduced to the Susitna Watershed of the Cook Inlet Basin during the 1950's (Fay 2002; Alaska Department of Fish and Game [ADF&G] 2007). Pike have since spread to the Matanuska Valley, Anchorage Bowl, and Kenai Peninsula naturally and through further anthropogenic introductions (Fig. 1). Since their introduction, pike have spread to more than one hundred lakes and over a dozen tributaries in the Susitna Basin alone (Rutz 1996; Begich unpublished data).

Pike are sit-and-wait predators that rely on aquatic vegetation for cover. Therefore, pike densities are highest in the littoral zones of shallow vegetated lakes and streams. Shallow lakes and sloughs are common in south-central Alaska, serving as critical

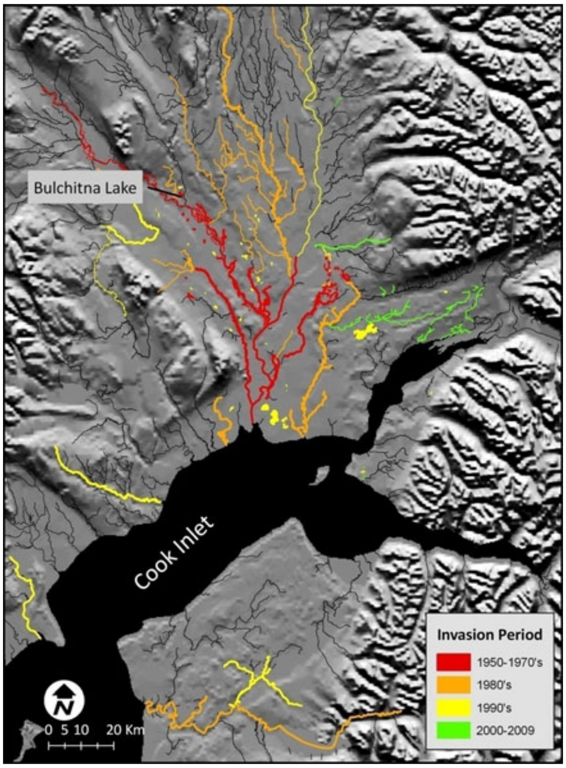


Fig. 1 Invasion pattern of northern pike into rivers and lakes in the Cook Inlet Basin from the 1950's to 2009. Original introduction occurred at Bulchitna Lake

rearing habitats for numerous species of salmonids, including coho salmon (*Oncorhynchus kisutch*), rainbow trout (*O. mykiss*) and Dolly Varden (*Salvelinus malma*). Pike prefer to eat soft-rayed fish over spiny-rayed fish (Hoogland et al. 1957; Eklov and Hamrin 1989) and in south-central Alaska, juvenile salmon and trout are the preferred prey of pike (Rutz 1996, 1999). Many once healthy lake populations of native rainbow trout have been extirpated and in some Cook Inlet lakes pike are the sole remaining fish species (Rutz 1996; Patankar et al. 2006).

Despite prey preferences, pike are known to be trophically adaptable and can be sustained by a wide variety of prey types (Beaudoin et al. 1999). This adaptability allows them to make rapid changes in prey selection in response to changes in abundance or vulnerability of potential prey (Mann 1985). Changes in prey selection are likely to be non-linear functions of prey density (Holling 1965). In the vegetated lakes and slow moving sloughs of south-central Alaska's boreal wetlands, potential non-salmonid fish prey species include threespine stickleback, ninespine stickleback (*Pungitius pungitius*), whitefish (*Coregonus* spp.), burbot (*Lota lota*), slimy sculpin (*Cottus cognatus*) and longnose sucker (*Catostomus catostomus*).

Threespine stickleback of the Cook Inlet Basin are exceptional in that they exhibit tremendous morphological diversity, ranging from fully armored marine, anadromous and resident freshwater populations with robust pelvic and dorsal spines and a full row of bony lateral plates to low armored resident freshwater populations lacking pelvic spines and most lateral plates (Bell et al. 1993). Pike introduction has been implicated in the extinction of at least one unusual population of weakly armored stickleback in this region (Prator Lake, Patankar et al. 2006).

The magnitude and trajectory of pike induced perturbations in stickleback abundance are likely to be at least partially determined by the environmental context in which they occur. For example, habitat segregation may allow for coexistence in lakes where alternative habitats are present (Gjelland et al. 2007). Deep areas in lakes may provide stickleback with predation-free refugia outside of the pike inhabited littoral zone. Consequently, in invaded lakes where deep pelagic areas exist, stickleback may be at less risk of extinction than those in uniformly shallow lakes. Additionally, high ionic conductivity and the presence of native fish predators may play a role in the outcome of pike introduction as both factors favor more robustly armored stickleback, better able to cope with fish predators (Bell et al. 1993).

Pike invasion to Cook Inlet Basin lakes is likely to result in the extirpation of naïve native fish species, beginning with the most preferred and vulnerable prey (juvenile salmonids). With time, pike may exclude other native fish prey, including threespine stickleback, resulting in a remodeled trophic ecology. We expect pike diet to shift from a regime dominated by piscivory in newly-invaded lakes to a diet composed largely of non-fish prey in lakes where pike have become established. We predict that stickleback abundance declines with time since pike introduction, while stickleback frequency as a prey species for pike initially increases as preferred salmonids are eliminated and then decreases as stickleback abundance declines. We expect stickleback abundance to be less impacted in large deep lakes as well as in lakes with high ionic strength water and with native fish piscivores. These predictions are explored by sampling northern pike diet and stickleback abundance across a set of lakes exhibiting a spectrum of pike introduction years.

Methods

Lake variables

Year of pike invasion, maximum depth, lake area, number of hydrologic connections and conductivity were determined for all lakes ($n = 32$) in order to understand the temporal and environmental context of pike diet and stickleback abundance. Pike invasion year was estimated for each lake using ADF&G test fishing data (9 lakes) and angler reports to the ADF&G statewide harvest survey (7 lakes). Year of first reported pike observation was used as the estimated pike invasion year (EPIY). For 11 lakes in the upper Fish Creek drainage lacking first report data, pike introduction year was estimated using an average annual rate of spread for the drainage. Annual rate of spread was calculated by using GIS to measure stream distance between lakes of known introduction years and then dividing the distance by the difference in introduction years ($n = 3$, mean $= 559$ m/year, SD $= 107$). Upstream colonization was assumed and invasion dates were estimated by dividing the stream distance to the nearest downstream neighbor of known invasion date by the average annual rate of spread. A minimum of $+1$ year was applied between lakes. Years of pike residence for each lake was then determined by subtracting EPIY from the sampling year. Five pike-free lakes were included in analyses. Maximum lake depth (meters) was determined from ADF&G lake maps or by completing a sounding transect where no bathymetric survey data were available. Lake surface area (hectares) was determined from ADF&G lake maps or calculated using ArcGIS. Lake connectivity, the total number of permanent hydrological connections, was determined from United States Geological Survey (USGS) quadrangle maps, ADF&G lake maps and GIS datasets. Conductivity (μS/cm) was determined using a YSI-80 conductivity meter during June–August 2008; within-lake seasonal and annual variation in conductivity appears to be minor in this area (e.g., Lescak 2010).

Fish collection and analysis

Northern pike and threespine stickleback were collected between May 1 and September 30, 2007–2008. Northern pike were collected using rod and reel, dip net, fyke net, and angler creel surveys. For non-sportfish caught samples, pike were killed with an overdose of ms-222 fish anesthetic. Fork length, wet weight, and sex were recorded for each fish. Stomach contents were either immediately determined by dissection in the field, or subsequently in the lab. Stomachs not immediately dissected were removed and preserved in 10% buffered formalin in the field to stop digestion for later enumeration. Contents were identified to at least the Order level when digestion state allowed. In cases where digestion made quantification of contents difficult, the most abundant remain (usually the head capsule for macroinvertebrates) was used to enumerate the minimum number of individuals. Items digested beyond identification were not recorded. Sample size adequacy was evaluated a posteriori using additive prey-diversity curves for each lake by plotting the number of pooled stomachs against the cumulative number of prey types. The sample size at which the number of prey types reached a plateau was taken as an indication of adequate sample size to precisely describe diet (Ferry and Cailliet 1996). Comparisons of prey richness across lakes of different pike invasion years were not made because some lakes did not show an asymptote in number of prey types.

Percent frequency of occurrence (%O), percent by number (%N), and percent by weight (%W) were calculated for each prey type in each lake, set of related lakes, and overall (Hyslop 1980). Percent frequency of occurrence (%O) is the percent of non-empty stomachs containing a prey type and equals the total number of stomachs containing the prey type divided by the total number of non-empty stomachs. Percent by number (%N) is the percent of any one prey type by number and equals the total number of individuals per prey type divided by the total number of all prey. Percent by weight (%W) is the percent dry weight of a specific prey type and equals the dry weight of specific prey type divided by the total dry weight of all prey. Dry weight was calculated for each prey type using the average total length for each prey type and published length-weight regression coefficients (macroinvertebrates: Benke et al. 1999; Edwards et al. 2009; fish: Schneider et al. 2000; Kimmerer et al. 2005; other: Johansen 1962; Wilson and Ruff 1999; Schulte-Hostedde et al. 2001). All calculations of dry weight used the equation: aL^b, where a equals the intercept, L equals length in millimeters and b equals the slope of the regression line. Overall dietary importance of each prey type was assessed for each lake individually and for two pooled categories that combine all lakes where stickleback were present and all lakes where stickleback were absent, using the Pinkas index, or index of relative importance (IRI) in which $\%O(\%N + \%W) =$ IRI (Pinkas et al. 1971). Percent IRI (%IRI) was used to facilitate interpretation and was calculated by summing IRI values of all prey types and calculating each prey type's percent contribution to the total (Cortes 1997).

Lakes were sampled for stickleback using 10 unbaited 1/8th inch mesh minnow traps per lake, set around the perimeter of the lake, soaked for at least 10 h, for a minimum trapping effort of 100 trap hours per lake. Trap set time and pull time were recorded and stickleback catch per trap was recorded. Stickleback catch per hour (SCPH) for each lake was calculated as the mean SCPH of all traps deployed in the lake. Where no stickleback were trapped, visual surveys were performed. Because all surveyed lakes were lowland lakes in areas where stickleback are ubiquitous (Bell and Ortí 1994; von Hippel 2008), and 27 of 32 lakes were connected by permanent surface water to documented stickleback populations, it was assumed that stickleback absences were due to extirpation by pike rather than a natural absence.

Stickleback abundance in relation to years of pike residence

Curvilinear regression was used to assess the relationship between stickleback abundance (SCPH, dependent variable) and years of pike residence (independent variable). To investigate effects of environmental variables on SCPH, a multiple linear regression was performed, again with SCPH as the dependant variable, and included years of pike residence, conductivity, maximum depth, lake area and number of hydrologic connections as independent variables. Multiple models were fit using different combinations of independent variables. A best fit model was determined from competing models using Akaike's Information Criterion (AIC).

Multiple logistic regression was utilized to investigate factors predicting stickleback extirpation. Lakes were scored as either "1" (extant) or "0" (extirpated) based on SCPH and survey results. Independent variables for the logistic regression were years of pike residence, conductivity, and maximum depth. Again, a best fit model was determined using AIC.

Pike diet in relation to years of pike residence and stickleback abundance

Trends in prey type occurrence across years of pike residence and SCPH were identified using regression analyses. Best fitting curves were determined using the curve fitting function in SPSS v. 16. Percent importance (%IRI) of each taxonomic or functional prey type by lake (dependent variable) was regressed on either years of pike residence or SCPH (independent variable). Variables containing zero values were transformed by adding a constant of .001 to facilitate the fitting of logarithmic curves. In cases where multiple statistical comparisons were performed using a common dataset, P values were corrected using the Bonferroni correction. All P values displayed are corrected values unless otherwise noted. Due to non-normal distribution of data, Spearman's rank correlation was also computed for all situations employing curvilinear regression; in all cases the direction and significance of results were not affected and only the parametric results are provided here.

Results

Thirty-two lakes were sampled for stickleback abundance, year of pike invasion, maximum depth, lake area, number of hydrologic connections and conductivity (Table 1). Stickleback were absent from thirteen lakes, and mean stickleback catch per hour per trap ranged from 0 to ~7.5. Historical documentation of the presence of stickleback exists for nine of the 32 lakes sampled (Havens 1979, 1985; Kyle et al. 1994); stickleback were not detected in two of the nine (Prator, Redshirt). Pike invasion to this set of lakes is estimated to span 28 years.

A limnological survey of 108 lakes in the Matanuska-Susitna Valley (Jones et al. 2003) reported a mean conductivity of 76 µs/cm, while the mean

Table 1 Study lakes, locations and variables: maximum depth, lake area, conductivity, number of hydrologic connections, estimated pike invasion year (EPIY), and stickleback catch per hour (SCPH)

Lake	Latitude	Longitude	Max depth (m)	Lake area (ha)	Cond (µS/cm)	Connectivity	EPIY	SCPH
Ardaw*	61.6663°	−150.0698°	13.0	26.27	14.2	2	1990	0.377
Bald	61.6796°	−150.0336°	10.0	24.77	20.9	0	No pike	7.395
Big*	61.5317°	−149.9375°	27.1	1009.69	118.9	2	1996	1.432
Big No luck*	61.6517°	−150.0909°	12.2	27.52	13.7	1	1998	4.176
Charr*	61.6448°	−150.0670°	7.0	14.64	24.2	3	1989	0.000
Chicken	61.6417°	−150.1038°	12.0	57.06	12.3	1	1988	0.234
Crystal*	61.7100°	−150.1081°	7.3	53.42	8.1	1	2005	5.558
Florence	61.7197°	−150.1141°	12.5	22.26	12.9	0	No pike	4.032
Frazer*	61.6553°	−150.0524°	7.0	30.52	25.8	2	1988	0.000
Honey Bee	61.7116°	−150.0530°	10.7	23.47	85.0	1	No pike	7.181
Jackknife*	61.6633°	−150.0531°	3.5	1.81	34.0	1	1989	0.000
James*	61.6364°	−150.0908°	7.5	42.41	12.5	2	1992	0.596
Little Frazer	61.6483°	−150.0560°	20.0	9.21	33.1	2	1988	0.000
Little No Luck*	61.6550°	−150.1039°	6.5	13.82	12.8	2	1993	0.006
Long*	61.7265°	−150.0854°	7.0	111.29	122.2	3	2000	6.912
Lynne	61.7114°	−150.0383°	23.5	28.33	86.8	1	No pike	4.061
Lynx*	61.6374°	−150.0560°	12.0	143.70	68.4	3	1987	0.000
Milo*	61.6682°	−150.0819°	5.0	24.17	16.1	2	1989	0.562
Milo pond	61.6598°	−150.0986°	2.5	1.82	14.2	2	1999	0.000
Nancy*	61.6900°	−150.0142°	19.8	307.97	81.9	3	1987	7.062
Owl*	61.6392°	−150.0785°	6.5	23.43	12.6	2	1991	0.047
Prator	61.6198°	−149.7345°	7.0	39.66	26.7	0	1996	0.000
Rabbit*	61.7074°	−150.9256°	4.0	28.13	30.7	0	1985	0.000
Rainbow	61.6962°	−150.0948°	13.7	60.70	109.5	1	2008	3.624
Redshirt*	61.6385°	−150.1562°	15.3	478.74	70.3	3	1980	0.000
Rhein	61.6778°	−150.1047°	19.9	34.40	23.6	2	No pike	4.385
Scout*	60.5329°	−150.8448°	6.1	38.45	21.2	0	2005	6.045
Shem Pete*	61.6705°	−150.0553°	7.0	10.00	15.1	1	1992	0.000
Shirley*	61.7413°	−150.1038°	6.1	48.97	111.8	2	1999	7.457
South Rolly*	61.6673°	−150.1273°	19.2	43.71	30.3	1	1989	0.999
Sucker*	61.6589°	−150.9012°	5.0	105.98	35.1	1	1985	0.000
Tanaina*	61.6728°	−150.0916°	33.6	44.11	14.4	2	1988	1.751

* Indicates lake sampled for pike for stomach content analysis

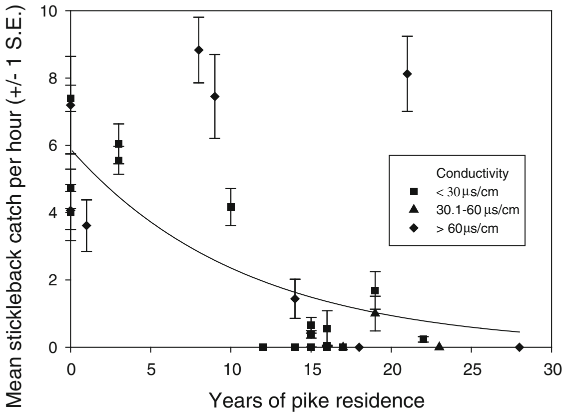


Fig. 2 Years of pike residence versus stickleback catch per hour (SCPH). $y = 5.9184e^{-.0917x}$, $R^2 = .4298$, $P < .001$, n = 32

conductivity for our 32 lakes was 41 µs/cm. Of the 11 lakes lacking stickleback in this study, nine were below the latter mean.

Relationships between years of pike residence and stickleback abundance

Curvilinear regression shows years of pike residence to be a significant predictor of SCPH with a negative exponential curve providing the best biologically plausible fit (Fig. 2). The attempt to fit a more complete model of SCPH by including four additional variables (maximum depth, lake surface area, conductivity, and number of hydrologic connections) using multiple linear regression identified conductivity as an additional significant predictor of SCPH, increasing predictive ability of the model from $R^2 = .439$, $P < .001$ to $R^2 = .534$, $P = .021$ (Table 2). Year of pike residence was a significant predictor of extirpated (n = 11) and extant (n = 21) populations in the logistic regression, while maximum depth was a marginally significant predictor (Table 3).

Pike diet: overall description and prey types

Four hundred and thirty five non-empty pike stomachs were scored from 23 lakes (6–30 per lake), containing a total of 19 prey types (Fig. 3). Additive prey-diversity curves indicate adequate sample size to precisely describe diet for 13 of the 23 lakes. Because low sample sizes tend to underestimate importance of rare prey items (Ferry and Cailliet 1996), results for rare prey types should be viewed with caution. Stickleback were a common prey type in lakes where they were present, and were present in over 43% of stomachs in those lakes (Fig. 4). Odonates were the most dominant taxonomic prey type and were found in over 60% of all pike stomachs (Fig. 3). Additionally, odonates were significantly more important in lakes where stickleback were absent ($f_{1,21} = 11.762$, $P = .002$; Fig. 4).

Taxonomic prey types were grouped into four functional categories (Fig. 3). In lakes where stickleback were absent, large macroinvertebrates were the most important prey group followed by small macroinvertebrates, other (frogs, shrews, and voles), and native fish respectively (Fig. 5). In lakes where

Table 2 Summary of linear regression models predicting SCPH

Model (R^2)	Variable	β_1	SE	P	AIC
1 (.439)	Pike years	−0.263	0.054	<0.001	151.769
2 (.534)	Pike years	−0.243	0.051	<0.001	147.862
	Conductivity	0.027	0.011	0.021	
3 (.534)	Pike years	−0.243	0.052	<0.001	149.861
	Conductivity	0.027	0.011	0.028	
	Max depth	0.002	0.057	0.971	
Full (.537)	Pike years	−0.244	0.067	0.001	153.627
	Conductivity	0.028	0.015	0.080	
	Max depth	0.003	0.065	0.954	
	Connections	0.152	0.552	0.785	
	Area	<−0.001	0.001	0.753	

R^2, variables, slope (β_1), standard error, significance (P) and Akaike's Information Criterion (AIC) are shown

Table 3 Summary of logistic regression models and variables predicting stickleback absence or presence

Model	Variable	β_1	SE	P	AIC
1	Pike years	−0.207	0.089	0.020	35.116
2	Pike years	−0.263	0.115	0.022	31.665
	Max depth	0.174	0.095	0.068	
Full	Pike years	−0.272	0.122	0.025	33.549
	Max depth	0.185	0.103	0.074	
	Conductivity	−0.006	0.016	0.731	

Variables, slope (β_1), standard error, significance (P) and Akaike's Information Criterion (AIC) are shown

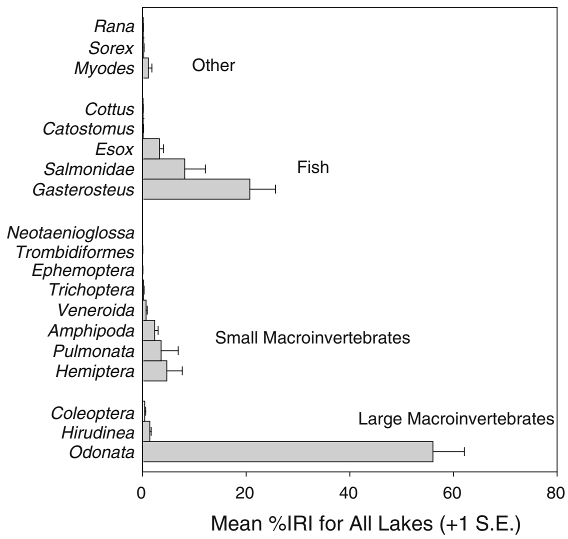


Fig. 3 Average relative importance (%IRI) and standard error of prey items in pike diet from all lakes sampled

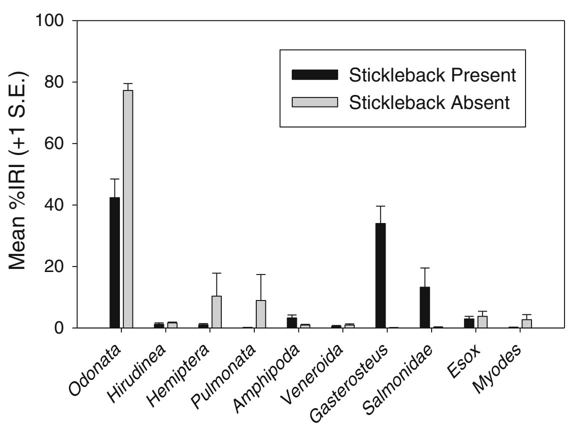


Fig. 4 Comparison of relative importance (%IRI) of prey types between lakes where stickleback were present and where stickleback were absent

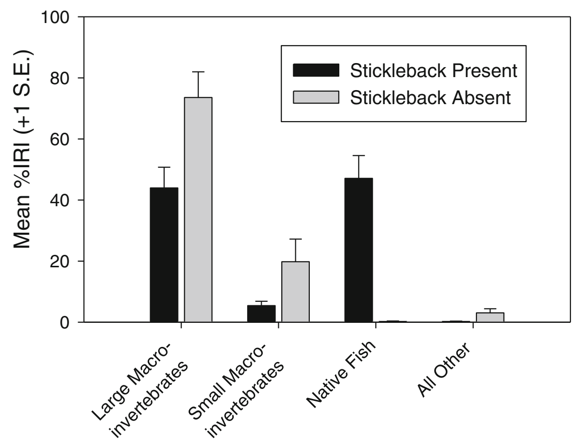


Fig. 5 Comparison of relative importance (%IRI) of functional prey type categories between lakes where stickleback were present and lakes where stickleback were absent

stickleback were present, native fish and large macroinvertebrates contributed approximately equally to pike diet followed by small macroinvertebrates and other (Fig. 5). Large macroinvertebrates were significantly more important ($f_{1,21} = 7.495$, $P = .012$) and native fish less important ($f_{1,21} = 24.889$, $P < .001$) to pike from lakes lacking stickleback as compared to lakes where stickleback were present.

Pike diet in relation to years of pike residence and stickleback abundance

Regressions identified significant relationships between years of pike residence and %IRI of prey types in pike stomachs. Macroinvertebrate %IRI increases and native fish %IRI decreases as years of pike residence increases (Fig. 6). Significant trends in %IRI were also found across SCPH. Prey types significantly related to SCPH included four

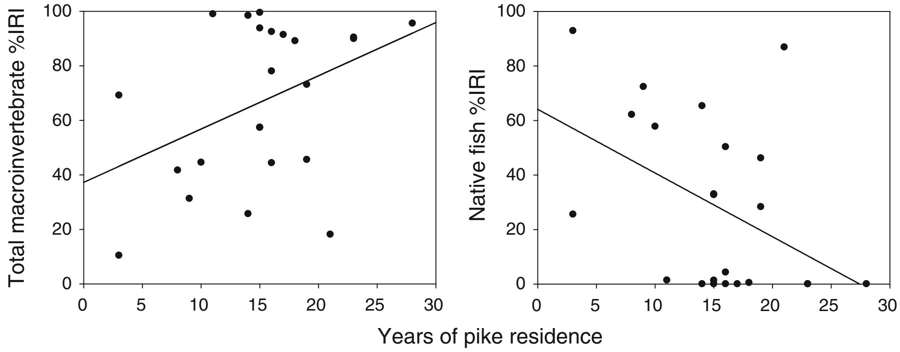


Fig. 6 Trends in %IRI of macroinvertebrate and native fish prey in pike diet over years of pike residence. Total macroinvertebrates: $y = 2.439x + 32.77$, $R^2 = .283$, $P = .022$, n = 23. Native fish: $y = -2.917x + 69.45$, $R^2 = .347$, $P = .004$, n = 23

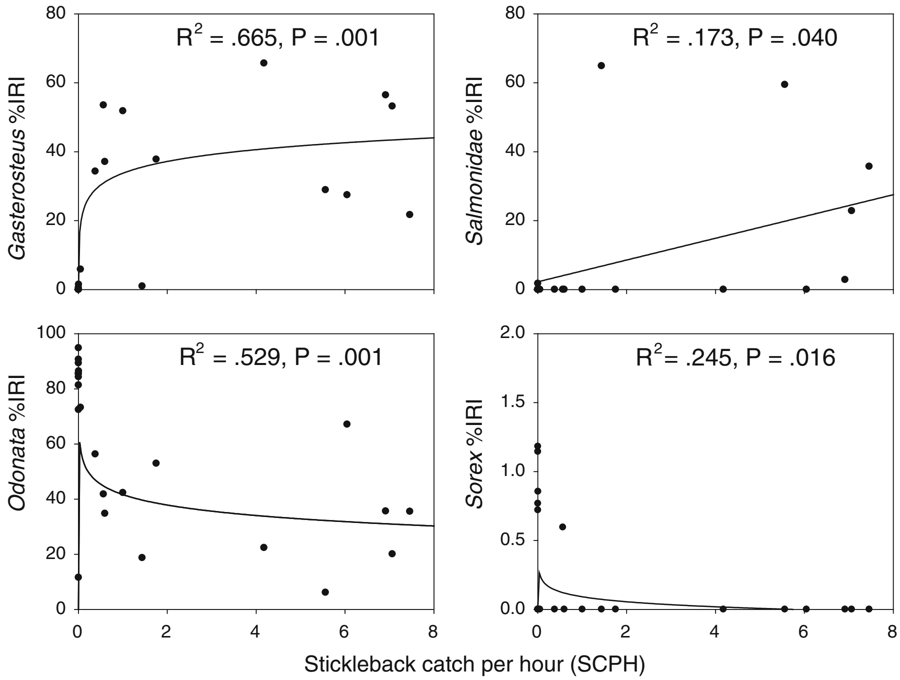


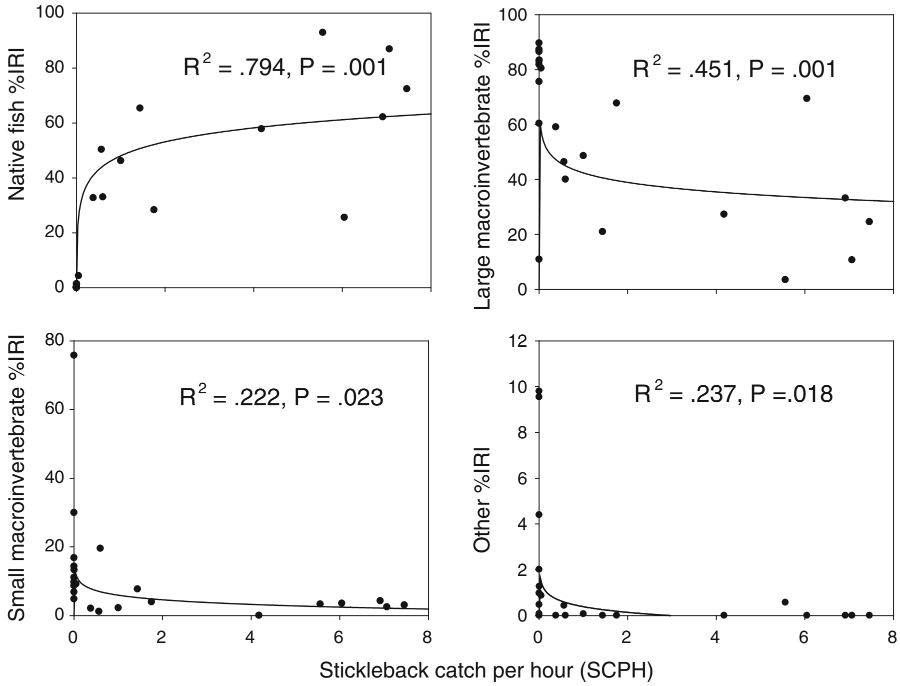
Fig. 7 Relationships between %IRI of taxonomic prey type and stickleback abundance (SCPH). *Gasterosteus*: $y = 4.923\ln(x) + 33.633$, *Salmonidae*: $y = 2.641x + 2.877$, *Odonata*: $y = -5.452\ln(x) + 41.734$, *Sorex*: $y = -0.052\ln(x) + .093$, n = 23 in all cases. *P* values for *Salmonidae* and *Sorex* are uncorrected

taxonomic groups (*Gasterosteus* (stickleback), *Salmonidae*, *Odonata*, and *Sorex*; Fig. 7) and all four prey categories (native fish, large macroinvertebrates, small macroinvertebrates and other; Fig. 8). The majority of the significant relationships between %IRI and SCPH were best described by logarithmic functions (Figs. 6, 7, 8).

Discussion

This study supports the hypothesis that predation by invasive pike impacts the abundance and existence of native fish species, including three-spine stickleback (Fig. 2), in the Cook Inlet Basin. Native fish become less important and macroinvertebrates become more important in the diet of pike as years of pike residence increases (Fig. 6). Salmonids were a rare prey item in this study (Fig. 3), likely because they are reduced in abundance or extirpated from lakes more rapidly than armored fish, such as stickleback, following pike invasion. Pike are unlikely to coexist with self-sustaining populations of salmonids (Spens and Ball 2008). Salmonids are preferred as prey over stickleback by pike in the Susitna Basin (Rutz 1996, 1999) and many lakes sampled for this study are known to have contained abundant native and stocked resident and rearing anadromous salmonid populations.

Fig. 8 Relationships between %IRI of prey type categories and stickleback abundance (SCPH). Native fish: $y = 7.296\ln(x) + 47.887$, Large macroinvertebrates: $y = -4.989\ln(x) + 42.44$, Small macroinvertebrates: $y = -1.917\ln(x) + 6.004$, Other: $y = -0.354\ln(x) + .399$, n = 23 in all cases. *P* values for small macroinvertebrates and other are uncorrected



Wood frogs (*Rana sylvatica*) were also a rare prey item in this study, despite being abundant in the region. Amphibian distribution is affected by the presence of fish predators (Hecnar and M'Closkey 1997) and frogs are likely highly susceptible to pike predation. As with salmonids, the scarcity of frogs in pike stomachs may result from frog populations being quickly reduced or eliminated upon pike invasion.

Reduction of preferred salmonid prey likely shifts predation pressure to stickleback. In lakes where stickleback were present, they were a major component of pike diet (Fig. 4). Stickleback abundance, as estimated by catch per unit effort, is reduced as pike residence time progresses (Fig. 2). Furthermore, years of pike residence is a significant predictor of stickleback extirpation (Table 3). As fish prey are eliminated, macroinvertebrate prey types become increasingly important, with odonates in particular composing a larger portion of pike diet (Figs. 4, 5, 6, 7, 8).

Piscivorous fish are able to eat preferred fish prey disproportionally more than other available prey species even when preferred prey types are at low densities (Juanes et al. 1999). The logarithmic function of the relative importance (%IRI) of stickleback in pike diet as stickleback abundance declines (Fig. 7) shows stickleback maintaining a high %IRI across a wide range of stickleback abundance (SCPH), with stickleback %IRI decreasing only as SCPH nears or reaches zero. In addition, the logarithmic function of increasing %IRI of macroinvertebrate prey as SCPH decreases shows pike switching to increased levels of macroinvertebrate consumption (Fig. 8) only at very low SCPH. These results suggest a strong preference for stickleback prey over macroinvertebrate prey, because pike continue to prey heavily on stickleback despite low stickleback abundance and only increase reliance on macroinvertebrate prey types once stickleback become severely reduced in abundance.

Prey switching in predators may have a stabilizing effect on prey populations if predation pressure is reduced as prey density decreases and ceases once some threshold density is reached, as in a sigmoidal functional response (Murdoch and Oaten 1975; Rindorf and Gislason 2005). The logarithmic functional response to decreasing stickleback abundance shown here suggests that such stabilizing relationships are unlikely between invasive pike and native fish species in Cook Inlet Basin lakes. This relationship, where stickleback continue to compose a large portion of pike diet even as stickleback abundance is depleted, is a likely explanation for the correlation between years of pike residence and extirpation (Table 3). More generally, these data suggest that stabilizing relationships between predators and prey may be unlikely when the predator is an invasive species.

Results presented here support the hypothesis that environmental factors are likely to play a role in determining the coexistence of native fish species, such as stickleback, and invasive pike, and likely mediate the type of adaptive response of resident fish populations. Conductivity was a significant predictor of stickleback catch per hour, with lakes of higher conductivity showing greater abundance of stickleback in the face of pike invasion (Table 2). Robustly armored stickleback are more common in lakes with higher conductivity (Bell et al. 1993), presumably due to the lower physiological costs of calcium importation. Fish with longer spines and more robust lateral plates are less vulnerable to being swallowed by gape-limited young pike and less likely to be fatally injured during unsuccessful predation attempts (Hoogland et al. 1957; Reimchen 1991a, b, 1992).

Native fish outcompeted by invaders may respond by altering habitat use, resulting in habitat segregation that allows coexistence (Gjelland et al. 2007) and similar habitat use alterations may occur when the invader is a predator. Deeper areas may present pike-free refugia for native fishes. Maximum depth was a marginally significant predictor of stickleback extirpation in this set of lakes, with deeper lakes less likely to be absent of stickleback (Table 3). Many lakes in this area are too uniformly shallow to provide such protective habitats. Future research with a larger sample size that includes more deep lakes and higher resolution bathymetric profiles would indicate if this trend is real. Supporting evidence for a relationship between depth and stickleback habitat use in pike-invaded lakes is found in a study of stickleback trophic morphology and its relationship to environmental variables (Willacker et al. 2010). Willacker et al. (2010) found that pike-invaded lakes in the Cook Inlet Basin were significantly more likely to contain stickleback that are morphologically adapted to limnetic habitat than benthic habitat, indicating a selection-based habitat shift to deeper areas of lakes.

The results of this study suggest that invasive northern pike have a detrimental effect on the continued existence of native fish populations because of their trophic adaptability. The ability of pike to be sustained by a variety of prey sources allows them to supplement their diet with less desirable prey (macroinvertebrates) as preferred prey (native fishes) are reduced in abundance. This allows pike to continue to thrive and exert predation pressure on native fish regardless of native fish abundance, resulting in native fish population declines and extirpations. The degree to which populations of native fishes are reduced likely depends on characteristics of the habitat in which the invasion occurs. In the case investigated here, conductivity played a significant role, and lake depth a marginally-significant role, in the likelihood of continued existence of native stickleback populations. However, despite the significance of these factors in the severity of reduction or probability of extirpation, introduction of pike had a negative effect on stickleback abundance regardless of lake type.

The introduction of non-native top predators and the subsequent reduction and loss of native fishes likely have cascading effects on the composition, structure and functioning of aquatic communities. This is due to the radically altered predation regime (gain of new top predator and loss of native fish predators) and altered competitive regime (release of some macroinvertebrates, consumption of others, and altered feeding regime on plankton). The loss of native anadromous fishes is also likely to have far reaching consequences as the delivery of marine derived nutrients to oligotrophic systems is halted. The Cook Inlet Basin, which contains numerous lakes and streams at various stages of pike invasion, is an ideal study system in which to investigate such complications of invasion ecology.

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