

Trophic ecology of introduced populations of Alaska blackfish (*Dallia pectoralis*) in the Cook Inlet Basin, Alaska

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Abstract Introduced non-native fishes have the potential to substantially alter aquatic ecology in the introduced range through competition and predation. The Alaska blackfish (*Dallia pectoralis*) is a freshwater fish endemic to Chukotka and Alaska north of the Alaska Range (Beringia); the species was introduced outside of its native range to the Cook Inlet Basin of Alaska in the 1950s, where it has since become widespread. Here we

characterize the diet of Alaska blackfish at three Cook Inlet Basin sites, including a lake, a stream, and a wetland. We analyze stomach plus esophageal contents to assess potential impacts on native species via competition or predation. Alaska blackfish in the Cook Inlet Basin consume a wide range of prey, with major prey consisting of epiphytic/benthic dipteran larvae, gastropods, and ostracods. Diets of the introduced populations of Alaska blackfish are similar in composition to those of native juvenile salmonids and stickleback. Thus, Alaska blackfish may affect native fish populations via competition. Fish ranked third in prey importance for both lake and stream blackfish diets but were of minor importance for wetland blackfish.

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Introduction

Invasive species are second only to habitat loss as a cause of extinction of native species in the United States, and pose a similar threat worldwide (Lassuy 1995; Wilcove et al. 1998; Strong and Pemberton 2000; Mooney and Cleland 2001). Biological invasions may result in alterations of natural ecosystems, including nutrient cycling, disturbance regimes, habitat structure, and community composition (Drake et al. 1989). The establishment of non-native fish populations is of particular concern because fish introductions often correlate

with reduction or extinction of native fishes due to predation (Brown 1989). Additionally, invasive fish establishment can result in dramatic changes in invertebrate communities, including reductions in potential prey resources for native fishes (Macan 1966, 1977; Brown 1989; Gerking 1994; Knapp et al. 2001; Byström et al. 2007). The success of invasive fishes is often attributed to low dietary specialization and the ability to capitalize on diverse prey resources (Moyle and Marchetti 2006). In the United States, many native fish species are listed as threatened, endangered, or negatively impacted by introduced fishes (Wilcove and Bean 1994) and resulting human economic losses are conservatively estimated at more than one billion U.S. dollars annually (Pimentel 2007).

Alaska lists 14 introduced fishes within its boundaries (McClory and Gotthardt 2008), including two species that are native to some regions of the state but introduced to others: northern pike (*Esox lucius*) and Alaska blackfish (*Dallia pectoralis*; hereafter blackfish; Fig. 1). The blackfish is endemic to fresh waters of Beringia, the subcontinent of eastern Siberia to western Yukon that remained ice-free during the Pleistocene (Fig. 2). The native range of blackfish extends from 55° to 72° N latitude on the Chukchi Peninsula of eastern Siberia, across western Alaska from the Arctic Coastal Plain to the Alaska Peninsula, and inland through the Yukon-Tanana drainage (Mecklenburg and Mecklenburg 2002). Introduced blackfish populations are found on St. Paul Island in the Bering Sea and in numerous lakes, ponds, and streams of the Kenai Peninsula and Matanuska-Susitna Valley within the Cook Inlet Basin of southcentral Alaska (Fig. 2; Morrow 1980; Stratton and Cyr 1997; Mecklenburg and Mecklenburg 2002; Eidam 2015).

Blackfish are well known for their adaptations to life in arctic and subarctic waters, adaptations that have facilitated their spread in the Cook Inlet Basin. They can tolerate living in high densities in small tundra pools (Morrow 1980). They exhibit extreme cold tolerance (Scholander et al. 1953; Scholander et al. 1957). A vascularized esophagus functions as an air-breathing organ and is known in only two other teleosts, the shanny (*Lipophrys pholis*) of northern European marine waters (Laming et al. 1982) and the Asian swamp eel (*Monopterus albus*), which is invasive in freshwater habitats of the southeastern United States (Liem 1967; Liem 1987; Fuller et al. 1999). Facultative air breathing enables blackfish to survive under hypoxic conditions

by gulping air at the surface, such as in warm shallow wetlands in summer when oxygen levels drop below 2.3 mg/L, and also via surface holes in iced-over waters during winter (Ostdiek and Nardone 1959; Crawford 1974; Morrow 1980).

Fisheries managers in Alaska have expressed concern over possible competition and predation by blackfish impacting native and stocked salmonids (Trent and Kubik 1974; Hepler and Bowden 1986). A previous study in their introduced range reported substantial numbers of salmonids in blackfish gut contents (Chlupach 1975).

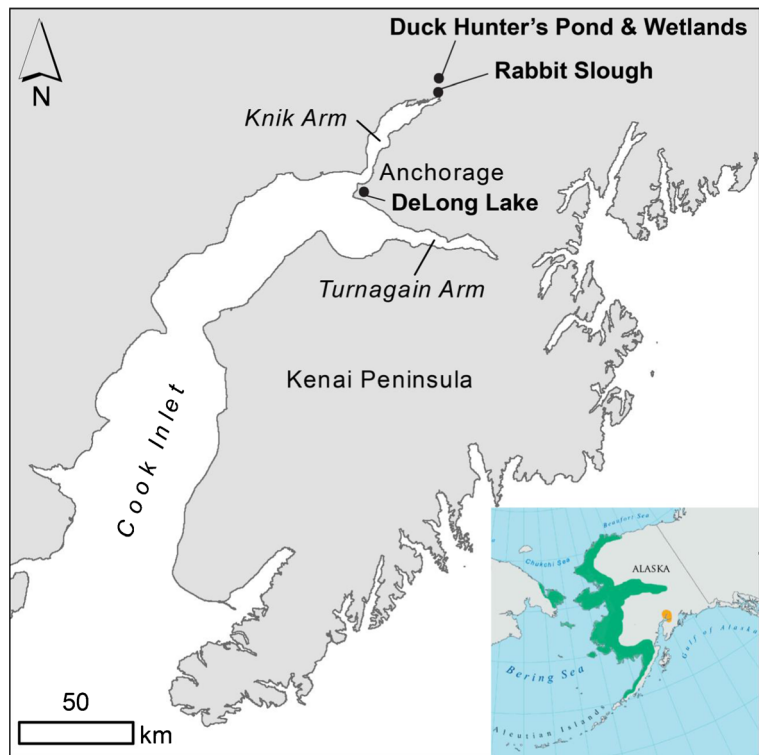
Fish diet analysis is an effective tool for understanding the potential impacts of introduced fishes on aquatic ecosystems and native fishes (Garvey et al. 1998; Vander Zanden et al. 2000; Chipps and Garvey 2007). Diet composition reveals the trophic position of a species within the food web as well as the prevalence of predation on other fish species (Pauly et al. 1998; Stergiou and Karpouzi 2002). Dietary overlap can indicate potential resource competition between introduced and native species. Prey type diversity helps to define specialist versus generalist feeders, while spatial and temporal diet shifts highlight opportunistic, flexible feeding strategies. Trophic interactions including feeding habits can help to reveal the extent of ecosystem alteration by introduced fishes, thereby providing useful information for ecosystem-based management (Pauly et al. 1998; Bachok et al. 2004; Stobberup et al. 2009).

Management actions have been taken to reduce or eliminate non-native blackfish populations in southcentral Alaska based on the assumption that these introduced populations represent a significant risk to the native and stocked fishes and natural resources. In this study we explore the implicit hypothesis that introduced



Fig. 1 Adult blackfish in laboratory aquarium at the University of Alaska Anchorage. Fish is feeding on previously frozen *Chironomid* larvae. Photograph by Dr. Thomas C. Kline, Jr., salmonography.com, copyrighted and used with permission

Fig. 2 Map of study sites in the Cook Inlet Basin, Alaska. The map of Alaska (lower right) shows the native range of the Alaska blackfish (green) and the introduced range within the Cook Inlet Basin (orange)



blackfish populations pose a measureable risk to the ecology of the invaded waterbodies and native and stocked fishes of southcentral Alaska. Specifically, we examine the predictions that fish constitute a major prey component in blackfish diets, and that blackfish diets overlap greatly with those of native fishes and stocked sportfish. Additionally, because most successful fish invaders show low dietary specialization and a high capacity to use available resources (Moyle and Light 1996a, 1996b; Marchetti et al. 2004; Gido and Franssen 2007), we predict that blackfish stomach contents vary significantly by waterbody, season, sex, and body size.

Materials and methods

Study sites

Three freshwater habitats—a wetland, stream, and lake—were selected within the Cook Inlet Basin of southcentral Alaska, based on year-round presence of blackfish (Fig. 2). Duck Hunter's Pond and surrounding wetland (61.53920° N, 149.25460° W) within the Matanuska-Susitna Valley lowlands consist of a marsh, constructed rectangular pool, and narrow drainage ditch

containing a large blackfish population (Eidam 2015). Blackfish and the occasional threespine stickleback (*Gasterosteus aculeatus*) and ninespine stickleback (*Pungitius pungitius*) are the only fish species we documented from the site. The water in this site is shallow and heavily vegetated.

Rabbit Slough (61.53750° N, 149.25460° W) is a stream within the Palmer Hayflats State Game Refuge located 0.15 km south of Duck Hunter's Pond, separated from it by a road. The stream drains into the Knik Arm of upper Cook Inlet and is characterized by slow-flowing, tannic-colored water with abundant overhanging forb, graminoid, and willow and alder shrub vegetation. Soft silty benthos support rooted macrophytes with some floating macrophytes as well. Rabbit Slough serves as a coho salmon (*Oncorhynchus kisutch*) nursery and a popular coho fishery, and is home to other native fishes including Dolly Varden char (*Salvelinus malma*), threespine stickleback, ninespine stickleback, slimy sculpin (*Cottus cognatus*), sockeye salmon (*Oncorhynchus nerka*), and chinook salmon (*Oncorhynchus tshawytscha*).

DeLong Lake (61.16390°N, 149.95550°W) in Anchorage is an 8 ha lake with a mean depth of 4 m and maximum depth of 7 m. Invasive waterweed (*Elodea*

canadensis and likely hybrids with *E. nuttallii*) forms dense stands of long-stemmed, rooted macrophytes. The urban lake is a popular sport fishery stocked annually with hatchery rainbow trout (*Oncorhynchus mykiss*) and chinook salmon. Catchable fish usually average 18 cm total length or longer; in 2010, 15,000 fingerling rainbow trout (mean total length 6.6 cm) were stocked (ADF&G 2011).

Sampling methodology

Blackfish were captured once a month over a 12-month period at each location using 0.32 cm and 0.64 cm wire mesh unbaited minnow traps. Optimal trap-soaking times were three hours or less to avoid digestion of stomach contents while fish were in the traps; however, soaking times were increased when trapping yielded low numbers of fish. Blackfish were euthanized with an overdose of pH-neutral MS-222 anesthetic and then blotted and wet-weighed to the nearest 0.1 g. Fish were measured with digital calipers to the nearest 1.0 mm for total length and standard length (SL) and then injected through the mouth with buffered 37 % formaldehyde solution to halt digestion. Whole specimens were placed into labeled teabags and fixed in buffered 10 % formalin for three weeks prior to rinsing with water; they were then transferred to 70 % ethanol.

Gastrointestinal tracts were dissected and esophageal and stomach contents of each fish washed with 70 % ethanol into a Petri dish. Prey items protruding into the mouth were included in the analyses. Prey organisms were viewed under a dissecting microscope, sorted, identified to major taxonomic category (McCafferty 1998; Thorp and Covich 2001; Merritt et al. 2008), and counted. Mean dry mass for each prey type was obtained by drying and weighing a representative number of organisms. Prey were loaded into 3.5 × 5 mm or 4 × 6 mm pre-weighed pressed tin capsules, dried at 60 °C in a drying oven, and weighed to the nearest 0.001 mg on a Sartorius microscale. Larger prey were placed in Petri dishes, dried, and weighed to the nearest 0.001 g on an analytical balance. Weights were computed from a subsample (80 % to 100 % for rare prey and 10 % to 50 % for other prey) of the total prey items for each prey category. Diptera, Coleoptera, Trichoptera, and Gastropoda were divided into subgroups for weighing in order to account for variable sizes and morphologies. Digested prey without identifiable parts were excluded.

Stomach content analysis

To obtain a measure of overall importance of each prey category, we used the index of relative importance (*IRI*): $IRI = (\%N + \%M) * (\%F)$, where *N* equals the actual count of individual prey items and highlights the importance of small prey such as zooplankton; *M* is the dry mass of prey items and emphasizes large, bulky prey; and *F* is the number of stomachs containing a specific food organism (Pinkas et al. 1971; Cailliet et al. 1986). *IRI* values were computed for the following eight sample groupings: combined sites and seasons, combined sites by season, combined seasons by site, each site by season, males and females by combined sites and seasons, and size classes by combined sites and seasons.

Statistical analysis

All statistical analyses were performed using SPSS v.22. A General Linear Model MANCOVA was used to test for differences in diet among waterbodies, among seasons, and by sex. For grouping of seasons, winter (November–March) corresponded to the period when waterbodies were covered in ice and snow; spring (April–May) was during ice and snow thaw; summer (June–August) was the warmest period free of ice and snow; and fall (September–October) was when snow and ice began forming again. Diet response variables consisted of prey masses of nine prey categories equal to or greater than 1 % *IRI* for combined sites and seasons (thus seven prey categories were omitted). Covariates were SL and trapping hours. Additional MANCOVAs were performed to test for seasonal differences in diet within each site. A binary logistic regression was also performed to analyze presence of fish in diet, using sex and size class as predictor variables. Size differences among sites were analyzed with ANOVA and between sexes were analyzed with a two-sample Student's *t*-test assuming equal variances using a pooled estimate of the variance.

We used non-metric multidimensional scaling (NMS) ordination to visualize patterns of diet among the 277 captured blackfish in the three waterbodies and seasons. We used raw prey mass from ten taxonomic diet categories (Ostracoda, Copepoda, Cladocera, Diptera, Trichoptera, Odonata, Gastropoda, Bivalvia, Teleostei, and Angiospermae) and included a categorical variable for fish with an empty gut, because it is not possible to generate *IRI* scores for individual fish. NMS

is a standard free ordination technique in ecology to explore patterns in multivariate data (Peck 2010). NMS has the advantages over linear ordination techniques (e.g., PCA) of not requiring linear relationships among variables or normal distributions of response variables to ordination axes; its use of ranked distances aids in linearizing the relationship between distances measured in species space and distances in environmental space; and it can be used with any distance measure (Fasham 1977; Peck 2010). The original data were used to generate a Bray-Curtis dissimilarity matrix. NMS was first run using the “Autopilot” mode, with six starting dimensions twice to determine dimensionality in PC-Ord (McCune and Mefford 2006). Once the dimensionality of the solution was determined, NMS was run in manual settings with two axes, 250 runs, and instability criterion of 10^{-6} . This analysis was conducted three times and results compared to ensure consistency (Peck 2010).

Results

Trapping times and body size comparisons

Trapping times ranged from 2.5–13.5 h with a mean of 5.7 h; processing times ranged from 0.5–5.5 h with a mean of 1.9 h. Total trapping plus processing times (time from trap placed in water to specimen placed into formalin) ranged from 3.5–14.5 h with a mean of 7.6 h. Trapping times in excess of 10 h occurred overnight during summer in the lake and stream. Overall prey consumption and trapping hours were not significantly related ($F(9, 244) = 1.779$, $p = 0.073$; Table 1), indicating a representative sampling.

From a total of 470 blackfish collected and fixed in formalin, 302 fish were dissected for stomach content analysis: 84 from the lake, 104 from the stream, and 114 from the wetland (Suppl. Table 1). In spring, only wetland fish were captured and analyzed due to unsafe ice conditions at the other sites. Seventy-eight percent of dissected blackfish were trapped during daytime compared to 22 % trapped overnight, in summer, from the lake and stream. Among specimens examined, males (SL mean = 98.90 mm, $SD = 15.51$, $n = 145$) were larger ($t(297) = 7.23$, $p < 0.001$) than females (SL mean = 91.67 mm, $SD = 15.44$, $n = 154$), though sizes broadly overlapped (Suppl. Fig. 1). Seventy-five percent of all fish were in 75–115 mm SL size range. The three

sites varied significantly (ANOVA, $F = 7.14$, $p < 0.001$) in SL (lake mean SL = 90.96 mm, stream mean SL = 97.61 mm, wetland mean SL = 94.61 mm). Blackfish did not vary significantly in SL by season.

Prey categories and dietary diversity

Blackfish gut contents from the three study sites contained prey from 20 taxonomic groups distributed among five animal phyla (mollusks, annelids, arthropods, bryozoans, and chordates) and one plant division (Suppl. Table 2). In the stomach content analysis, insects were classified as Insecta adults (Order unknown), Diptera larvae, Trichoptera larvae, Odonata larvae, and Ephemeroptera larvae. Order Coleoptera included both larvae and adults. Bryozoa/Plumatellida from DeLong Lake consisted of over-wintering cysts (statoblasts). Angiosperms in blackfish gut contents were represented by seeds of unknown plants. Occasional plant stem and leaf tissue found in the guts of blackfish were excluded from analysis because of their rarity.

Consistent with the prediction of high diet diversity, blackfish in these populations typically had many prey types in their guts. The number of different prey types, based on 20 broad prey categories (Suppl. Table 2) found in each nonempty gut (esophagus + stomach + intestines) ranged from 1 to 10 (Fig. 3). The mode for number of prey categories per examined gut was three in the lake and stream samples, and four in the wetland samples. Waterbody and season were significant predictors of the nine response variables (nine prey categories whose % $IRI \geq 1$), as was the interaction between them (Table 1). Blackfish size and sex were not significant predictors of prey types across all nine prey categories, although the frequency of fish in diet was related to blackfish size and sex (Chi-square = 9.487, $df = 2$, $p = 0.009$).

Stomach contents by combined sites and seasons

Figure 4 provides a graphic representation of the IRI from all samples combined for prey categories with ≥ 3 % IRI . For combined waterbodies and seasons, gastropods were by far the dominant prey group (51 % IRI). Ostracods contributed 28 % of the percent IRI , while all other prey taxa recorded 7 % IRI or less. Twelve other categories made minor contributions to blackfish diets at these sites (% $IRI < 0.5$ %; Table 2). Ostracods were the primary prey in terms of total number, while gastropods

Table 1 Multivariate effects on diet of blackfish. The MANCOVA is based on three factors (waterbody, season, and sex), two covariates (SL, trapping hours), and nine response variables (nine prey categories whose % *IRI* ≥ 1). SL = standard length, *ns* = not significant

Variable	Pillai's Trace	<i>F</i>	Hypothesis <i>df</i>	Error <i>df</i>	<i>p</i>
SL	0.063	1.82	9	244	<i>ns</i>
Trapping hrs.	0.062	1.78	9	244	<i>ns</i>
Site	0.287	4.56	18	490	< 0.001
Season	0.231	3.56	18	490	< 0.001
Sex	0.061	1.76	9	244	<i>ns</i>
Site \times season	0.413	3.16	36	988	< 0.001

and teleosts were the two most important prey in terms of biomass. Fish as prey ranked fourth in importance by percent *IRI*, while frequency of fish consumption was less than 10 %. Dipterans were found most frequently in guts (62 % frequency), followed by gastropods (46 % frequency). Overall, six prey types were consumed by at least 25 % of all blackfish: dipteran larvae, gastropods, copepods, trichopteran larvae, ostracods, and bivalves. Plant seeds were found in 14 % of all guts.

Stomach contents by site

Prey consumption differed by waterbody for seasons pooled ($F(18, 490) = 4.56, p < 0.001$; Table 1). A different prey taxon dominated gut contents for each site: dipterans (66 % *IRI*) in lake fish, gastropods (78 % *IRI*) in stream fish, and ostracods (59 % *IRI*) in wetland fish (Suppl. Fig. 2, Suppl. Tables 3, 4, 5). All other prey values at each site were less than 20 % *IRI*. Teleosts contributed at least 60 % of the percent biomass in gut contents from lake fish, while gastropods contributed 70 % of overall biomass in gut contents for stream fish. No single taxon dominated by percent biomass for wetland fish. Dipteran larvae were the most frequently

consumed prey of lake fish, compared to gastropods and dipteran larvae for stream fish. Wetland blackfish had the greatest variety of prey in their guts, consuming three prey categories at 50 % or greater frequency and three additional taxa at frequencies of 24 %–35 %. Fish ranked third in prey importance for both lake and stream blackfish but were of minor importance for wetland blackfish.

Stomach contents by season

Prey consumption differed by season (spring excluded) for waterbodies pooled ($F(18, 490) = 3.56, p < 0.001$; Table 1). During summer, gastropods were the single major prey (69 % *IRI*), while all other groups contributed less than 10 % *IRI* (Suppl. Tables 6). Gastropods also dominated in summer by biomass (79 % mass), followed by teleosts (10 % mass). More than half of all guts in summer contained gastropods and dipterans. Small ostracods and cladocerans outnumbered larger prey.

Dominant prey groups in autumn consisted of gastropods and ostracods, which contributed 48 % and 24 % of the percent *IRI* values, respectively (Suppl. Table 7). Gastropods were the most important prey in terms of biomass (61 % mass). At least 45 % of all guts in autumn contained dipterans, gastropods, trichopterans, and ostracods.

Prey in winter switched to Ostracoda (39 % *IRI*) followed by Diptera (24 % *IRI*) and Teleostei (19 % *IRI*; Suppl. Table 8). Fish were the most dominant winter prey by biomass (72 % mass), although their total count (13) was small compared to ostracods (4452). The most frequently consumed winter prey were dipteran larvae and copepods.

We chose to interpret a significant (randomization test $p = 0.004$) two-dimensional NMS solution with mean stress of 12 after verifying consistency of

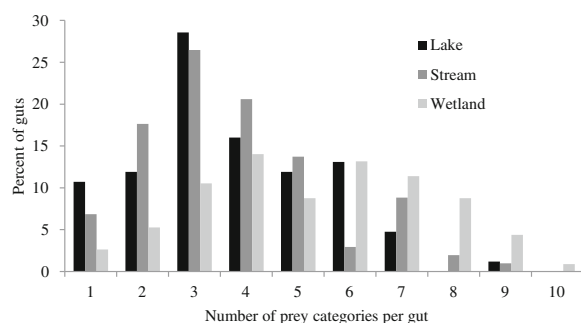


Fig. 3 Diet diversity histogram. For each site, the percentage of esophagus + stomach + intestines containing 1–10 prey categories is given. This is the only analysis that included intestine contents

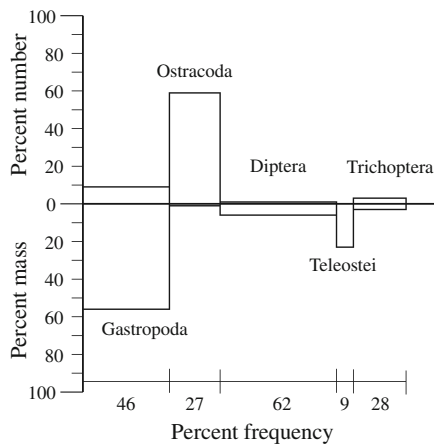


Fig. 4 Prey IRI diagram for combined sites and seasons. Only major prey categories $\geq 3\%$ IRI are shown. The IRI for each prey category is represented by a rectangle with area proportional to the values used in calculating the $IRI = (\%N + \%M) * \%F$, where N equals the number of individual prey items; M is the dry mass of prey items; and F is the number of stomachs containing a specific food organism. Frequency of occurrence axis begins at zero for each prey category

interpretation among the three NMS solutions. Blackfish with a greater mass of gastropods in their gut are associated with greater positive Axis 1 values; blackfish with a greater mass of teleosts in their gut are associated with greater positive Axis 2 values; blackfish with a greater mass of dipterans in their gut are associated with lower Axis 2 values (Fig. 5). Blackfish with more mixed diets and low mass of the six arthropod categories (including ostracods, copepods, dipterans, and trichopterans) are located in the center of the biplots, while blackfish with an empty gut are represented by the lowest Axis 1 value.

The biplots of waterbodies across the three seasons (summer, autumn, winter) show overlap in diet for many blackfish (Fig. 5). However, lake blackfish are concentrated on the upper-left side (greater mass of teleosts, and mixed arthropods); stream blackfish extend to the right side (greater mass of gastropods and teleosts, lower mixed arthropods), and wetland blackfish occupy the center portion of the biplots (greater mass of mixed arthropods, low mass of gastropods and teleosts). In general, diets varied considerably within each waterbody, though wetland blackfish had a less variable diet, especially in summer. Little difference was evident among the summer and fall biplots. In winter, however, diets for the stream and wetland blackfish constricted along Axis 1 and expanded along Axis 2. This is associated with a reduction in gastropods and increase in

teleosts and copepods in their diets. Diets among fish in the three waterbodies converged more in winter. Lake blackfish showed little change in diet composition across seasons in the ordination.

Fish in diet

Gut contents from pooled waterbodies and seasons showed that 9 % of all blackfish had recently consumed a total of 35 fish (Table 2, Suppl. Table 9). Seven percent of the lake blackfish had fish in their guts—four threespine stickleback, one juvenile blackfish, and two unidentifiable fish (Suppl. Table 3). Stream blackfish were the most piscivorous (17.3 % frequency; Suppl. Table 4); fish prey included 10 threespine stickleback, four ninespine stickleback, one coho, and three unidentified fish. Piscivory among blackfish in the wetland was lowest at 3.5 % frequency across the year (2.2 % when spring samples are excluded; Suppl. Table 5), with threespine stickleback, juvenile blackfish, and one unidentified fish. Overall, the frequency of cannibalism for all waterbodies and seasons was 1.3 %, excluding unidentifiable prey fish. Less than 1 % of blackfish had salmonids in their guts.

The likelihood of fish in blackfish diet was related to both sex and blackfish size (Chi-square = 9.487, $df = 2$, $p = 0.009$). The Wald statistic showed that both sex ($p = 0.043$) and size ($p = 0.045$) made significant contributions to the model. Fish consumption first appeared in blackfish with a SL of at least 78 mm, although few blackfish this small had fish in their guts (Suppl. Table 9). Fish were more important in the diets of blackfish greater than 105 mm SL. Males tended to consume more fish than did females. Approximately 13 % of males consumed fish, while 6 % of females consumed fish.

Discussion

Dietary diversity

Introduced populations of blackfish in the Cook Inlet Basin displayed an opportunistic, generalist diet consisting primarily of benthic epiphytic invertebrates—gastropods, ostracods, and dipteran larvae (Table 2). While their diets were diverse, we did not detect surface feeding in these populations, and consumption of adult insects was rare.

Table 2 Prey values for combined sites and seasons ($n = 302$). Major and minor prey categories are given in descending order by percent *IRI*. Grey-colored rows are prey categories shown in *IRI*

Prey	Total no.	% no.	Total mass (mg)	% mass	% freq	IRI	% IRI
Gastropoda	1307	8.7	6697.817	56.2	46.4	3009	50.5
Ostracoda	8921	59.1	142.214	1.2	27.5	1658	27.8
Diptera	187	1.2	657.617	5.5	61.9	419	7.0
Teleostei	35	0.2	2729.331	22.9	9.3	216	3.6
Trichoptera	512	3.4	354.070	3.0	28.1	179	3.0
Bivalvia	262	1.7	495.639	4.2	25.2	148	2.5
Copepoda	643	4.3	10.288	0.1	30.5	132	2.2
Cladocera	1123	7.4	23.583	0.2	13.2	101	1.7
Angiospermae	172	1.1	172.860	1.5	14.2	37	0.6
Odonata	95	0.6	207.100	1.7	10.6	25	0.4
Coleoptera	37	0.2	237.826	2.0	7.6	17	0.0
Plumatellida	429	2.8	38.610	0.3	3.6	12	0.0
Corixidae	30	0.2	108.330	0.9	4.0	4	0.0
Gammaridae	28	0.2	12.852	0.1	5.3	2	0.0
Insecta adult	6	0.0	11.005	0.1	1.7	0	0.0
Araneae	6	0.0	7.533	0.1	2.0	0	0.0
Hydracarina	10	0.1	0.560	0.0	2.3	0	0.0
Ephemeroptera	6	0.0	1.304	0.0	1.7	0	0.0
Hirudinea	2	0.0	0.998	0.0	0.7	0	0.0
Unknowns	2	0.0	0.337	0.0	0.7	0	0.0
Collembola	1	0.0	0.052	0.0	0.3	0	0.0

Blackfish diets varied by site and by season (Fig. 5). Lake blackfish consumed mainly dipterans, stream blackfish consumed mainly gastropods, while ostracods were the major prey of wetland blackfish. Important prey based on biomass included teleosts among lake fish and gastropods among stream and wetland fish. Such spatial variation in the food habits of blackfish supports the trophic model of a generalist feeder, whose diet consists mostly of a diversity of benthic invertebrates selected in part based on availability. The occasional consumption of fish by this species is also indicative of an opportunistic strategy (Gerking 1994), and the seasonal importance of fish prey in terms of biomass indicates that piscivory may be important energetically for some larger blackfish.

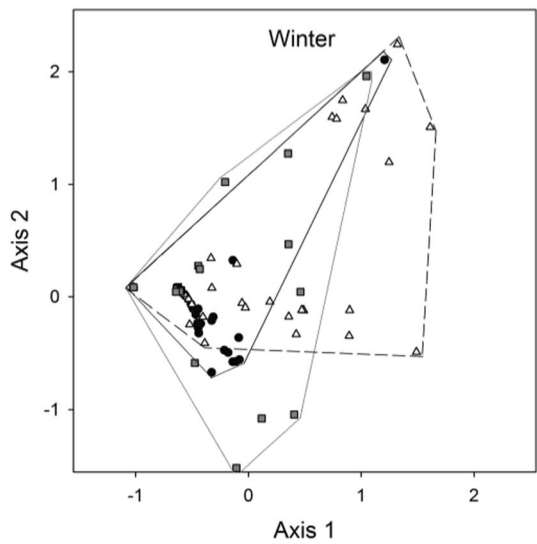
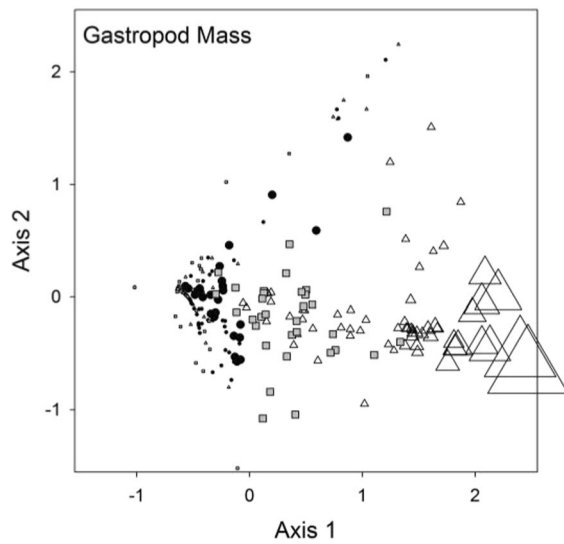
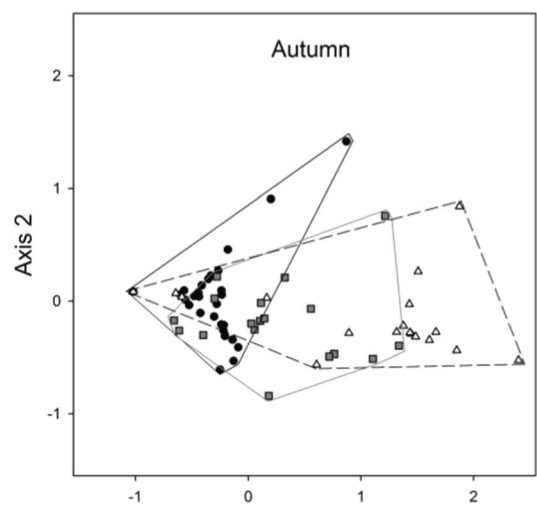
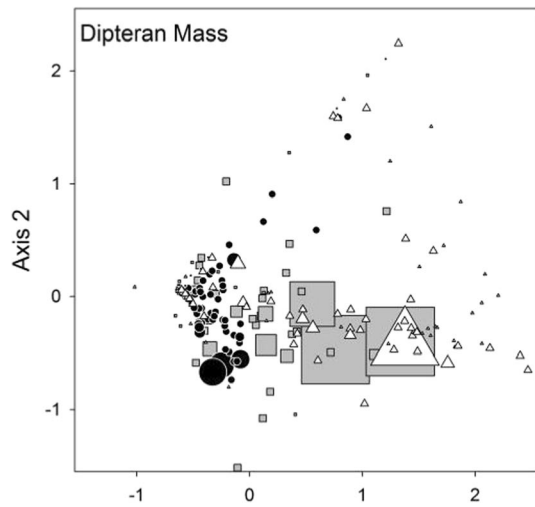
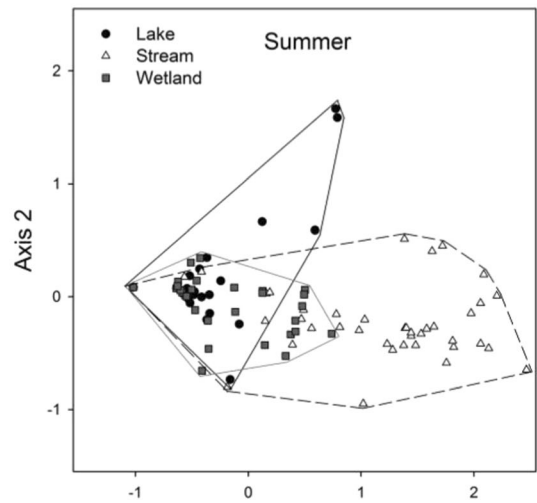
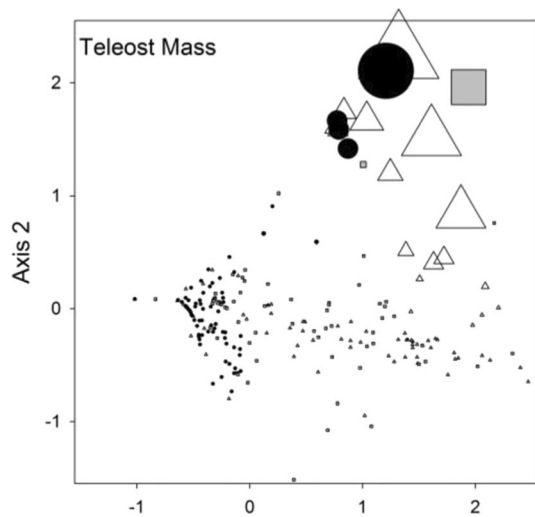
Diets varied significantly across seasons for combined sites, as expected (Suppl. Tables 6–8). Temporal prey shifts support a trophic model of adaptability based on seasonal prey availability. The high trophic flexibility of these blackfish

diagram (Fig. 4). Diptera, Odonata, Trichoptera, and Ephemeroptera represent larvae

may be partially responsible for their successful colonization of multiple freshwater habitats.

Gut contents of 77 blackfish collected during summer in its native range on the Arctic Coastal Plain of Alaska contained 17 prey categories including nematodes and algae (Ostdiek and Nardone 1959). In the current study, Cook Inlet Basin blackfish guts from summer contained 16 prey categories, with no evidence of nematodes or algae. Most frequently consumed prey of the Arctic Coastal Plain blackfish were cladocerans (91 %), dipteran larvae (90 %), and ostracods (88 %); fish consumption occurred at less than 3 % frequency. By comparison,

Fig. 5 Non-metric multidimensional scaling ordination biplots of blackfish diets by waterbody. Lake blackfish are shown as *black circles*, stream blackfish are shown as *triangles*, wetland blackfish are shown as *gray squares*. The three panels on the left show diets for all three seasons combined with symbol size scaled to mass of three prey categories (top = teleosts, middle = dipterans, bottom = gastropods). The three panels on the right show diets in the three waterbodies for summer (*top*), fall (*middle*), and winter (*bottom*). Minimum convex polygons are drawn around each waterbody



Cook Inlet Basin blackfish during summer most frequently ate gastropods (57 %) and dipteran larvae (54 %), while fish consumption occurred at a frequency of 11 %.

A study of 320 Meadow Lakes (Anchorage) blackfish harvested during September reported gut contents as follows: major prey by relative frequency, Cladocera (59 %) and Copepoda (32 %), and six minor prey valued at less than 5 % frequency (Hemiptera, Diptera, Odonata, Teleostei, Mollusca, and Ephemeroptera; Chlupach 1975). By comparison, 67 Cook Inlet blackfish collected in autumn in the current study ate Diptera (79 %), Gastropoda (69 %), and Trichoptera (63 %) as well as six other prey types valued between 10 and 40 %. These results support the model of the blackfish as a generalist opportunist that feeds on a wide range of prey species, with variable sizes and morphologies, from more than one trophic level. Such low dietary specialization is often characteristic of successful fish invaders (Moyle and Marchetti 2006).

Management implications

Fish consumption

Fish consumption was infrequent among these three introduced blackfish populations (Table 2), indicating that blackfish are unlikely to impact native or stocked fish populations in the studied sites. In contrast, other studies reported dominance of fishes in blackfish diet. Stomachs of adult blackfish from native populations in Western Alaska contained mostly small blackfish and northern pike (Baxter 1973; unpublished, cited in Chlupach 1975). Stomach contents of 320 introduced blackfish from Meadow Lake (Anchorage) contained 132 fish identified as Salmoniformes (Chlupach 1975). Such spatial heterogeneity in blackfish diet suggests that although blackfish may not pose a major threat to native fishes or sportfishes in the three populations investigated in this study, they may impact fishes through predation in other Cook Inlet Basin sites and may have seasonal impacts that vary by site.

This study found a significant relationship between blackfish size and fish consumption. As expected, ontogenetic diet shifts were observed in that prey size increased with predator size; smaller

juvenile blackfish consumed small invertebrates and no fish (Eidam 2015), while adult blackfish fed on a greater variety of both small and large prey including fish (Suppl. Table 9). Therefore, in habitats containing abundant small fishes and blackfish that grow to large sizes, the impact on fishes is predicted to be greater.

Fish consumption was also based on the sex of the blackfish. In these populations, males were more than twice as likely as females to consume fish (Suppl. Table 9). Blackfish males are slightly larger than females (Suppl. Fig. 1). Such sexual size dimorphism is frequently documented in vertebrates and can result in niche divergence (Shine 1989) in which diets of males and females differ (Holtby and Healey 1990; Houston and Shine 1993; Laufer et al. 2009; Keppeler et al. 2013).

Dietary overlap

Diets of introduced blackfish in Cook Inlet Basin fresh waters overlap with those of native fishes and stocked sportfish. Threespine stickleback feed on small benthic invertebrates including dipteran larvae, ostracods, mollusks, copepods, cladocerans, and amphipods (Hynes 1950; Greenbank and Nelson 1959), while slimy sculpin typically feed on slightly larger organisms on or just below the sediment—amphipods and larvae of dipterans, trichopterans, and odonates (Morrow 1980; Flecker 1984; Hershey 1985).

Juvenile Dolly Varden char forage on small crustaceans, insect larvae, snails, clams, spiders, and fish (Morrow 1980). Coho salmon fry consume microzooplankton, mites, Collembola, and spiders, while larger juveniles also eat adult beetles (Morrow 1980). Similarly, blackfish consume diverse epiphytic benthic prey across a wide size range. In contrast to blackfish, coho salmon fry feed heavily on surface insects including winged dipterans and trichopterans, and large adults can also become primarily piscivorous (Morrow 1980). Blackfish swim to the surface to breathe atmospheric air but are not known to eat surface insects.

Rainbow trout feeding habits also overlap to some extent with those of blackfish. Rainbow trout diet shifts ontogenetically from cladocerans for small juveniles to dipteran larvae and winged adults, leeches, amphipods, gastropods, water beetles, and fishes for large adults

(Scott and Crossman 1973; Morrow 1980; Beauchamp 1990). Rainbow trout feed at the surface, in mid current, and sometimes at the bottom. Blackfish feed demersally by picking organisms off of benthic macrophytes or by probing sediment in search of buried clams and large dipteran larvae, using their protruding lower jaw like a scoop (Eidam 2015). In contrast, rainbow trout do not burrow for prey (Frost and Brown 1967; Knapp et al. 2001).

These comparisons indicate that the potential for resource competition between blackfish and some native fish species warrants further research, including quantitative analysis of dietary overlap on a species by species basis. The dietary breadth of blackfish detected in the current study could also be quantitatively compared to dietary breadth of both native and non-native species to test the hypothesis that a generalist feeding strategy facilitates invasion.

Blackfish as an invasive species

Alterations of aquatic invertebrate communities associated with the introduction of non-native fishes are a common occurrence (e.g., Goldschmidt et al. 1993; Gerking 1994; Knapp et al. 2001; Byström et al. 2007). Introduced brown trout (*Salmo trutta*) significantly decreased overall benthic biomass including larvae of dipterans and trichopterans (Macan 1966, 1977). Brook trout (*Salvelinus fontinalis*) stocked in a fishless lake in New York immediately impacted the benthic fauna, including eliminating *Chaoborus* dipteran larvae (Gloss et al. 1989). Selective feeding by introduced yellow perch (*Perca flavescens*) in a lake in Quebec changed the overall community structure, resulting in reduced populations of larger invertebrates and more abundant populations of smaller invertebrates (Berglund 1968; Crowder and Cooper 1982; Post and Cucin 1984). Removal of a fish predator in some cases caused measurable increases in benthic organisms (Gerking 1994). The magnitude of the alterations to the aquatic community by invasive fishes, however, is likely to be reflected in the abundance of the invaders.

Introduced blackfish are documented in large numbers in many Cook Inlet Basin lakes (K. Dunker, ADF&G, personal communication; Eidam 2015). However, to our knowledge no systematic studies of blackfish population sizes exist from either native or introduced locations. Although direct predation of salmonids was infrequent in this study, the substantial dietary

overlap with native fishes and sportfishes indicates that blackfish may impact the ecology of invaded freshwater systems. We suggest that introduced populations of blackfish likely reduce prey availability to other fishes, as well as affect broader ecological interactions, notably competitive interactions, among aquatic invertebrate guilds, and potentially alter community composition (e.g., Chase and Knight 2003). To establish the scale of that impact, however, it will be necessary to produce robust estimates of the size of introduced blackfish populations, increase our understanding of competitive and facilitative relationships among aquatic invertebrates in these systems, and conduct manipulative experiments to estimate the effect of blackfish on growth rates of native fishes.

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