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Diets of invasive channel catfish are subsidized by invasive riparian trees

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Funding information

Alfred P. Sloan Foundation; American Philosophical Society; Intertribal Timber Council; National Science Foundation; Purdue University

Abstract

Russian olive (*Elaeagnus angustifolia*) is an invasive, fruit-bearing riparian tree that dominates riparian zones of the San Juan River in the southwestern United States. Previous research in this river suggests olive fruit is common in diets of invasive channel catfish (*Ictalurus punctatus*), but its energetic importance is unknown (i.e. critical for catfish fitness vs. incidental consumption). We assessed Russian olive consumption in channel catfish diets bimonthly for 1 year, hypothesizing that olive consumption would be greatest during periods of high olive availability and low benthic aquatic invertebrate availability. We found that catfish consumed olive fruit throughout the year and that olive comprised up to 44% of total stomach contents by mass, with peaks in spring and fall. Regression models revealed the presence and mass of olive fruit in catfish stomachs were positively associated with catfish total length, with a significant interaction between water temperature and river discharge. Catfish were more likely to consume olive fruit during higher flows, regardless of temperature and at low discharge with higher temperature. Contrary to our hypothesis, neither olive nor benthic invertebrate availability were associated with olive presence in channel catfish diets. Nutrition analysis indicated that olive alone was a low-quality diet item but has the potential to provide a reliable energy source. We used seasonal data to estimate the energetic contribution of olive fruit to catfish populations using a bioenergetic model, which estimated that olive fruit accounted for 35.6% of energy (Joules) consumed by catfish populations and satisfied 38% of their metabolic demand. Our results suggest that Russian olive fruit is a significant subsidy to channel catfish in the San Juan River. However, more research is needed to determine the indirect effects of this interaction on native fishes and ecosystem function.

KEYWORDS

bioenergetic model, channel catfish, diet analysis, *Elaeagnus angustifolia*, facilitation, *Ictalurus punctatus*, invasive species, resource subsidy, Russian olive

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1 | INTRODUCTION

Freshwater ecosystems are under continuous threat from many anthropogenic stressors, including habitat alteration and invasive species (Dudgeon et al., 2006). While these two stressors are of great concern individually, multiple stressors can interact to yield non-additive effects that increase the rate and magnitude of ecological change (Bruder et al., 2017; Darling & Côté, 2008; MacDougall & Turkington, 2005). Invasive species can act synergistically to increase the rate and success of additional species introductions (Simberloff, 2006; Simberloff & Von Holle, 1999). For example, monocultures of invasive riparian trees can have particularly acute effects on both habitat and nonnative species introductions in riverine ecosystems (Heinrich et al., 2021; Katz & Shafroth, 2003; Mahoney et al., 2019; Mineau et al., 2012). Specifically, riparian invasion can alter sediment transport and retention, causing changes in channel morphology (West et al., 2020). In addition, invasive riparian trees can affect riverine food webs by altering the quality, timing and magnitude of leaf litter inputs (Going & Dudley, 2008; Mineau et al., 2012; Swan et al., 2008), as well as influencing terrestrial prey inputs (Roon et al., 2016). Therefore, understanding the role of invasive riparian trees in aquatic ecosystem function will enhance conservation and management of riverine ecosystems.

Rivers across the southwestern United States are at risk due to increasing human water demand, numerous nonnative species introductions and a depauperate but unique and vulnerable fish fauna (Gido & Propst, 2012; Olden et al., 2006; Propst & Gido, 2004; Tyus & Saunders, 2000). The San Juan River is a major Colorado River tributary and is highly impacted by flow alteration that has facilitated the spread of many nonnative riparian plant species, including invasive Russian olive (*Elaeagnus angustifolia*; hereafter, olive). These changes in the riparian community have increased bank vegetation cover from 10% in the 1930s to more than 90% in 2010s, contributing to channel restriction and incision (Bassett, 2015). In addition to changing channel morphology, olive has the potential to restructure riverine food webs by contributing large seasonal pulses of its fruit and litter (Mineau et al., 2012).

Nonnative channel catfish (*Ictalurus punctatus*; hereafter, catfish) were introduced to the San Juan River basin in the late 1800s and are now abundant invaders that threaten imperilled native fishes through competition and predation (Franssen et al., 2014). Hedden et al. (2021) estimated that catfish populations consumed 820 and 320 native fish/ha in 2018 and 2019, respectively, and documented only two incidences of catfish predation on endangered Colorado pikeminnow (*Ptychocheilus lucius*). The San Juan River Recovery Implementation Program has attempted to control catfish population since 1991, but there is no evidence of positive effects on native fishes (Franssen et al., 2014). Pennock et al. (2018) illustrated that control efforts are unlikely to yield adequate exploitation rates needed for population collapse but have reduced size structure. The removal program may thus benefit native fish populations by reducing the abundance of large catfish that are more likely to consume fish prey (Hedden et al., 2021, 2022).

Catfish are omnivorous and adapted to take advantage of a wide range of prey items including aquatic arthropods, terrestrial insects, terrestrial arthropods, isopods, terrestrial vertebrates (mammals, reptiles, amphibians), crayfish, fish and fruits (mulberry, olive) (Chick et al., 2003; Evelyn et al., 2022; Tyus & Nikirk, 1990). In the San Juan River, olive fruit is a common diet item found in catfish stomach contents (Brooks et al., 2000; Evelyn et al., 2022; Hedden et al., 2021, 2022). Some of the first diet studies based on San Juan River catfish in the early 1990s revealed that most individuals consumed olive, with the fruit comprising up to 40% of diet items for some catfish size classes (Brooks et al., 2000). Recent San Juan River catfish diet studies detected terrestrial plant material, which included but was not limited to olive fruit, in 86% of stomachs with identifiable food items and found that olive comprised 55%–58% of stomach content dry weight (Hedden et al., 2021). Moreover, Hedden et al. (2022) reported the probability of terrestrial plant material in catfish stomachs was best described by a regression model with an interaction effect of water temperature and discharge, whereby terrestrial plant material occurred in diets more frequently during periods of higher discharge with cool temperatures and during periods of lower discharge with warmer temperatures. However, Hedden et al. (2022) did not measure the availability of olive fruits or alternative prey for catfish and, therefore, could not consider how prey availability influenced consumption of olive fruit.

Consumption of olive fruit by catfish is not surprising given that they are omnivorous and known to exhibit frugivory in their native range (Chick et al., 2003). However, little is known about the importance of olive for sustaining catfish (i.e. whether the olive fruit are energetically important for catfish, or if they are simply consumed opportunistically). Olive fruit may provide an important energetic subsidy for catfish in the San Juan River similar to that reported for common carp (*Cyprinus carpio*) elsewhere. Specifically, Heinrich et al. (2021) found that ~58% of common carp tissues were derived from olive fruit in a small Idaho stream. Using bioenergetic modeling, Heinrich et al. (2021) also reported that olive fruit provided a trophic subsidy that facilitated the invasion of nonnative common carp and that the subsidy resulted in higher carp biomass after the invasion. A similar relationship may exist between olive and catfish, but catfish are less adapted for consuming seeds (e.g. they lack pharyngeal teeth necessary for crushing seeds) and digesting plant material (i.e. short intestinal tract) compared to carp. Therefore, research is needed to determine the energetic and nutritional value of olive fruit and its relevance to catfish production in the San Juan River.

In this study, we examined the spatial and seasonal patterns of olive consumption by catfish in the San Juan River and quantified the energetic contribution of olives to catfish energy demands over a 13-month period. To explore spatial and seasonal consumption, we quantified catfish diet, olive fruit availability and invertebrate prey availability in four 8 river km sections of the San Juan River in New Mexico and Utah. We hypothesized that catfish would rely on olive fruit during periods of high olive availability (fall and spring) and low benthic invertebrate abundance. In addition, we hypothesized that

although olive fruit is a low-quality energy source, it substantially contributes to catfish production in the San Juan River. Our objectives were to: (1) Quantify the effects of prey abundance, olive fruit availability, temperature and discharge on consumption of olive fruit by catfish and (2) Estimate the contribution of olive fruit to catfish production in the San Juan River using a bioenergetic model.

2 | MATERIALS AND METHODS

2.1 | Field methods

The study area included four 8 river km study sites along the San Juan River mainstem, with ≥ 40 river km between sequential study sites (Figure 1). Sections were dispersed along a longitudinal gradient of increasing water temperature, turbidity and discharge from upstream to downstream. Olive trees were present in all sections but were most abundant in the middle sections (2 and 3). We randomly selected three 1.6 km reaches within each study site that were ≥ 1.6 river km apart. We sampled fish diets and food item availability bimonthly from September 2016 to September 2017. To capture catfish, we used a non-motorized, raft-based electrofishing unit (Smith Root GPP 9.0) operated as a single pass from upstream to downstream, with emphasis on shallow habitats near riverbanks. Electrofishing passes began along the left or right bank (randomly determined) and effort alternated between banks at the mid-point of the reach. Catfish were netted, placed in a live well, and later euthanized using MS-222 (Tricaine-S, Western Chemical). Field personnel measured total length (TL, mm) and weight (g) and then determined sex and removed stomachs for all captured catfish. Stomachs were placed in individually labelled Whirl-Pak® bags and stored on wet ice until they were later transferred to a freezer (-20°C) for later processing.

We quantified benthic macroinvertebrate biomass as a proxy for alternative prey availability based on samples collected from six randomly selected transects within each study reach (18 transects/section). We collected 10 kick samples along each transect in shallow, wadable habitats using a D-ring kick net (500 μm mesh; Wildco®, Yulee, FL). Each kick encompassed $\approx 0.1\text{m}^2$ and the total sample along each transect was $\approx 1\text{m}^2$. When water depth or velocity prohibited sampling along a single transect, we sampled multiple transects separated by $\geq 10\text{m}$. The combined 10 kicks along a transect were preserved as a single sample using 70% ethanol for later processing.

We measured olive fruit availability along the study reaches using litter traps placed under the canopy of randomly selected olive trees that were within 2.6 m of the river channel (Figure 2). The traps consisted of a 25 cm diameter funnel attached to a 13 cm section of 6 cm diameter PVC pipe capped with a wire screen on the bottom to catch the fruit to minimize predation by small mammals and to limit moisture pooling in the trap. Traps were attached to a metal post 1 m from the base of a randomly selected olive tree. Traps were placed under the canopy of three randomly selected olive trees within each reach (nine per section; 36 total seed traps). We emptied the litter traps during each sampling event, stored the contents in a plastic bag, and placed the bagged samples in a freezer (-20°C) for processing in the laboratory. We separated litter and olive fruit, counted the number of fruits collected, dried the sampled fruit at 60°C for 72 h and weighed ($\pm 0.01\text{g}$) the dried fruit samples. We quantified olive availability as the dry weight of fruit per day ($\text{g}/\text{m}^2/\text{day}$).

2.2 | Laboratory methods

Frozen stomach content samples were thawed 1–2 h prior to laboratory processing. Once thawed, we separated the stomachs and

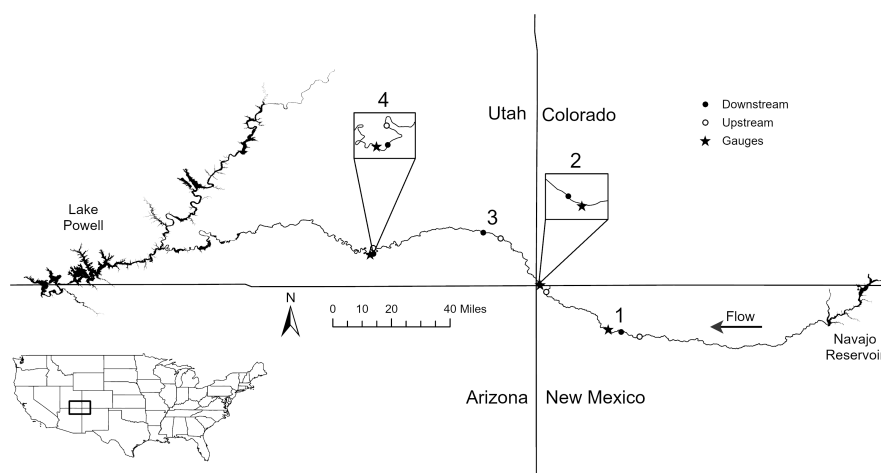


FIGURE 1 Map of the study area on the San Juan River where channel catfish (*Ictalurus punctatus*) stomach content and prey availability data were collected. Hollow circles represent the upstream boundaries and filled circles represent the downstream boundaries of the study sections. Stars represent the locations of USGS gauge stations where discharge and temperature were collected. Section numbers on the map correspond to Figure 3. The flow arrow indicates the direction of flow from Navajo Reservoir west to the confluence with the Colorado River at Lake Powell.



FIGURE 2 From the top left to bottom right: Russian olive (*Elaeagnus angustifolia*) fruit and litter washed onto a sandbar on the banks of the San Juan River near Montezuma Creek, UT. Channel catfish (*Ictalurus punctatus*) stomach contents from the San Juan River showing the prevalence of olive fruits in September 2017. Technician (Matthew Vorhees) collecting benthic invertebrate availability samples using a D-ring kick net. Funnel trap attached to a t-post used to sample availability of Russian olive fruits to catfish.

intestines at the pyloric sphincter. We then dissected the stomachs and rinsed the contents into a 250- μm sieve. Large items such as olive seeds, fishes and crayfish were removed and set aside. The remaining contents were placed in a Petri dish and sorted under a dissecting stereoscope (Nikon Model SMZ1275) or lighted bench magnifying glass. We identified invertebrates to order and fishes to species when possible. When identification was not possible, we grouped items in broader categories (e.g. aquatic insects, terrestrial insect, fishes and crayfish). Once the stomach contents were sorted and identified, we counted the number of individuals within each prey category. We measured the wet weight (± 0.01 g) of the stomach contents after removing surface water with a dry paper towel. After processing the samples, we grouped the prey items in broader categories for analysis, including olive, aquatic invertebrates, terrestrial arthropods, terrestrial vertebrates, fish, crayfish, plant debris and unknown or other.

We sorted benthic macroinvertebrate samples into two habitat categories: riffle and run. All samples of each habitat type were combined for each reach, typically three riffles and three runs, resulting in one aggregate riffle sample and one aggregate run sample per reach. We subsampled the aggregate samples to estimate invertebrate biomass by picking and rinsing coarse debris from the sample and then evenly spreading the remaining sample across a sorting tray with 15.7-cm² cells. Three cells within the tray were randomly selected and the contents, both debris and invertebrates, were removed from the cells and placed in a Petri dish. The contents of the

Petri dish were sorted under a lighted bench magnifying glass and then checked for smaller invertebrates using the dissecting microscope. We stored the sorted invertebrates in 70% ethanol and later counted the number of individuals in each order. Most aquatic insect taxa were in the orders Ephemeroptera, Trichoptera, Odonata, Plecoptera and Diptera. Invertebrates from all subsamples for each reach were then combined and placed in a drying oven at 60°C for 72 h to measure the total dry weight of all invertebrate subsamples for each site (± 0.01 g). The resulting dry weights were used as proxies of overall aquatic insect prey availability within a study reach (i.e. dry invertebrate biomass/m²).

2.3 | Analytical methods

We downloaded mean daily water temperature (°C) and discharge (m³/s) data for the field sampling dates from United States Geological Survey (USGS) monitoring stations located at Shiprock (USGS 09368000), Four Corners (USGS 09371010) and Mexican Hat (USGS 09379500). Gages at Shiprock and Four Corners were within the study segments, and the Mexican Hat gage was ≈ 1.6 km downstream of the last study segment. Study segment 3 had no gaging station sufficiently close to provide direct temperature and discharge measures. Temperature and discharge for this segment were averaged using data from the closest upstream and downstream stations.

We summarized stomach content sample data as percent weight, percent count and percent frequency of occurrence for each diet item category (Garvey & Chipps, 2012). Each of these diet composition measures is biased. To account for bias, we used the index of relative importance (IRI) to calculate the importance of each diet item category. IRI was calculated as the percent frequency multiplied by the sum of percent number and percent weight. IRI is presented as percent IRI, as suggested by Cortés (1997) and was calculated as the IRI score divided by the sum of the IRI scores for all diet categories and multiplied by 100.

To understand seasonal differences, we used linear mixed effects regressions (LMERs) to estimate differences in olive and benthic invertebrate availability between months or seasons. These models contained a single fixed effect of month or season, with a random intercept of reaches nested within sections; these random effects accounted for nonindependence due to subsampling within sections and reaches. We also used linear mixed effects models with the same random effect structure as those above to evaluate differences in mass of stomach contents for single diet categories (e.g. olive fruit, aquatic invertebrates) between seasons and sections. These models were implemented using *lme4* package in R version 4.2.1 (Bates et al., 2015; R Core Team, 2021). We used estimated marginal means to estimate pairwise differences for categorical predictors in the *emmeans* package (Lenth et al., 2019) using a Kenward-Roger method to calculate degrees-of-freedom.

To determine seasonal and spatial (sections) variation in diet composition, we used a permutational multivariate analysis of variance to estimate differences in diet composition between seasons and sections using the *adonis* procedure in package *vegan* (Oksanen et al., 2013). We included season and section as main fixed effects and included an interaction between season and section. We assessed pairwise differences in diet composition (mass) between seasons and sections using multilevel pairwise comparisons with Bray–Curtis dissimilarity and a Bonferroni correction. Multilevel pairwise comparisons were implemented using the '*pairwiseAdonis*' package in R (Martinez, 2017). We used similarity percentage (*simper* function), to estimate contribution of diet categories to the dissimilarities between seasons and sections (Clarke, 1993).

To evaluate the effects of olive availability and alternative prey availability, we used mixed effects models to predict the presence and mass of olive fruits in catfish stomachs based on binomial and Gaussian distributions, respectively. We selected five environmental variables that we predicted would affect olive consumption: catfish TL (mm), combined mass of all non-olive diet items in gut (g), olive fruit availability ($\text{g m}^{-2} \text{day}^{-1}$), invertebrate availability (g m^{-2}), water temperature (C) and daily mean discharge ($\text{m}^{-3} \text{day}^{-1}$). We checked for collinearity among explanatory variables using Pearson correlation coefficients ($r \leq 0.60$) and variance inflation factor ($\text{VIF} \leq 2$) and found that all explanatory variables had acceptably low collinearity. Due to the varying scales of the continuous explanatory variables, we scaled and centred explanatory variables to mean=0 and standard deviation=1 for both models. Both models included a random

intercept of reaches nested within sections to account for spatial nonindependence. We did not include season categorically in models because all explanatory variables were correlated seasonally. Following Hedden et al. (2022), we also included temperature, discharge and their interaction effect. Explanatory variables were identified as statistically significant if the 95% confidence intervals of their regression coefficients did not bound zero. Models were implemented with the *glmmTMB* package (Magnusson et al., 2017) in R. To explore the interaction effect of discharge on temperature, we used the *interactions* package (Long, 2021) in R to plot the effect of temperature on olive mass or presence in the stomachs at low discharge (-1SD), mean discharge and high discharge ($+1 \text{SD}$). To evaluate the discharge values for which the slope of the effect of temperature on olive consumption were significant, we used Johnson-Neyman intervals with a correction for Type I and Type II errors (Esarey & Sumner, 2018).

2.4 | Bioenergetic modelling

We used the Wisconsin bioenergetic model (Fish Bioenergetics 4.0 (version v1.1.5)) (Deslauriers et al., 2017) to predict energy consumption (Joules) and estimate the proportion of energy intake that olive fruit provided to catfish in the San Juan River. The model was implemented through a shiny application (v1.4.0) in R-Studio (R-Studio Inc, v3.5.3). Model runs encompassed 394 days, from September 1, 2016 to September 28, 2017. We used the equation presented by Kitchell et al. (1977) in the Hewett and Johnson (1992) model of fish growth to predict energy and biomass consumption for each prey category. Each model run represented the daily energy consumption of a cohort and all estimates were fit to annual growth (g). The von Bertalanffy growth curve for the San Juan River ($L_{\infty} = 810 \text{mm}$; $K = 0.089$; $t_0 = -2.378 \text{years}$), presented by Pennock et al. (2018), was used to estimate the starting and ending total length for each cohort. Eight size classes were designated to represent estimated annual growth in model runs using the following initial catfish total lengths: 300, 350, 390, 425, 458, 488, 516 and 540mm. The length-weight formula ($\text{Log}_{10}(\text{weight}) = [\text{Log}_{10}(\text{length}) \times 3.349] - 5.959$) from Pennock et al. (2018) was then used to convert starting and ending weight for the cohort over 394 day of the sampling period. We used inputs of temperature, prey energy density, predator energy density, diet proportion, a set of physiological parameters and the indigestible proportion of prey items to estimate catfish energy demands. The model inputs included a combination of field data presented in this paper and values from the literature (Table S1). We summarized diet proportion for each prey category or fish between 300 and 400mm and fish >400mm from the field observations. Diet proportions varied daily to incrementally shift between field sampling events.

We used physiological parameters from Blanc and Margraf (2002) developed for catfish populations in West Virginia Lakes (Table S1) and modified this model to adjust for varying digestibility of each prey category. Because catfish diets are diverse, we used a temperature and consumption-dependent model. We

used published literature to model the indigestible proportion of each diet category and prey energy density values (Table S1). We found no studies that reported digestibility, nutritional content or energy density of olive fruits. We calculated the indigestible proportion of olive fruit by first estimating the ratio of fruit weight to seed weight. Seeds were not digested by catfish and, therefore, were included as part of the indigestible portion of fruit consumed. To calculate the indigestible component of olive fruits, we measured the fruit weight to seed weight ratio of whole olive fruit. The indigestible portion of the fruit pulp was assessed through nutritional analysis.

Olive energy density was calculated from proximate analyses of nutritional content. Samples (100g each; $N=3$) of olive fruit tissue (seeds removed) were submitted to the University of Missouri Agricultural Experiment Station Chemical Laboratory for analyses of crude protein (Kjeldahl; Total $N \times 6.25$), crude fat, moisture and crude fibre. The crude 'by difference' method was used to estimate the percent carbohydrate ($100\% - (\% \text{ protein} + \% \text{ fat} + \% \text{ fibre} + \% \text{ ash} + \% \text{ moisture})$) (FAO, 2003). Energy density was calculated as gross calories by multiplying content by average energy content for each category (protein = 4 cal g^{-1} ; carbohydrate = 4 cal g^{-1} ; fat = 9 cal g^{-1} ; fibre = 2 cal g^{-1}) (Merrill & Watt, 1973) and converted to Joules g^{-1} . We included plant (mostly olive leaves), algae and other material (e.g. sand, woody debris, rocks) in the diet proportions because they were often found in fish stomachs at considerable volume and were given an indigestible proportion value of 0.99, providing little to energy consumed. We used seasonal predator energy densities from Blanc and Margraf (2002) and interpolated predator energy density between sampling periods.

To estimate the total consumption for catfish populations in the San Juan River, we used Lincoln-Peterson mark-recapture abundance estimates of catfish >300mm reported by Pennock et al. (2018) and Hedden et al. (2021) of 42,056 fish (95% CI = 33,973–52,253 fish) mostly composed of catfish between 350 and 450mm (67%). Length-frequency estimates from Pennock et al. (2018) were used to estimate the proportion of the population within each cohort. To

calculate the number of catfish within each cohort, we multiplied the proportion of catfish in each size class by the abundance estimate for catfish >300mm.

The Fish Bioenergetics 4.0 model allows users to specify population size and annual mortality. We used a natural mortality rate of 0.20 from Raibley and Jahn (1991), which was constant for all age classes. Size-specific estimates of fishing (in this case removal) mortality rates caused by SJRIP nonnative fish control efforts were added to conditional mortality to provide size-specific mortality for each cohort (Pennock et al., 2018). Fishing mortality ranged from 0.15 at 300mm to 0.37 at 540mm. The model interpolates annual mortality to daily mortality to reflect the loss of individuals from the population and the resulting reduction in consumption. The estimated per-capita daily consumption (Joules) for each prey item was multiplied by the cohort abundance at each time step. The sum of daily consumption for each cohort was used to estimate the total annual consumption (g and J) for each age class. The sum of total consumption for all cohorts was used to calculate the total population consumption for catfish in the San Juan River during our study period.

3 | RESULTS

Olive fruit was available to catfish during all sampling events, but olive availability varied seasonally (LMER: $F_{3,70} = 5.55$; $p = .0078$) and was abundant in the winter and spring (Table 1; Figure 3a). Olive availability also varied spatially (LMER: $F_{3,70} = 6.36$; $p = .0007$) and was highest in the middle reaches (2 and 3) and lowest in the upstream and downstream reaches (1 and 4). Availability of benthic invertebrates varied between seasons (LMER: $F_{3,73} = 3.72$; $p < .034$) but not between sections (LMER: $F_{3,73} = 3.72$; $p < .22$). Benthic availability was highest in the summer, but all other seasons were not significantly different (Figure 3b).

A total of 749 catfish stomachs were processed to estimate diet composition. The number of catfish captured during each sampling

TABLE 1 Descriptive statistics for all sampling periods including number of fish sampled with stomach contents present, percent of empty stomachs, mean Russian olive mass in stomachs (g) and mean catfish total length (mm).

Month	Season	Year	Fish	Empty (%)	Olive mass	TL	Wt	Temp	Discharge	Olive avail	Benthic avail	Other mass
Sep	Fall	2016	166	29.0	1.64	329	408	18.9	246	0.93	0.3	0.62
Nov	Fall	2016	134	10.5	0.29	336	385	10.6	295	1.02	0.01	0.99
Jan	Winter	2017	45	60.5	0.19	374	531	2.1	263	1.85	0.01	2.50
Mar	Spring	2017	72	25.5	3.94	398	711	13.0	386	1.68	0.01	5.88
May	Spring	2017	41	6.8	1.77	318	330	12.4	1937	1.38	-	5.69
Jul	Summer	2017	93	17.2	0.73	323	396	27.8	329	1.67	0.09	2.24
Sep	Fall	2017	56	28.2	3.2	378	539	19.5	240	2.13	0.05	0.96
Total			607	27.2	1.52	345	450	14.9	528	1.52	0.03	2.70

Note: Means of the predictor variables for the regression analysis are included as means of water temperature (C), discharge ($\text{m}^3 \text{ second}^{-1}$), Russian olive availability ($\text{g dry mass m}^{-2} \text{ day}^{-1}$), benthic invertebrate availability (g dry mass m^{-2}) and mass (g wet weight) of non-olive diet items in the stomach contents. May data was not used for regression models due to missing benthic availability data.

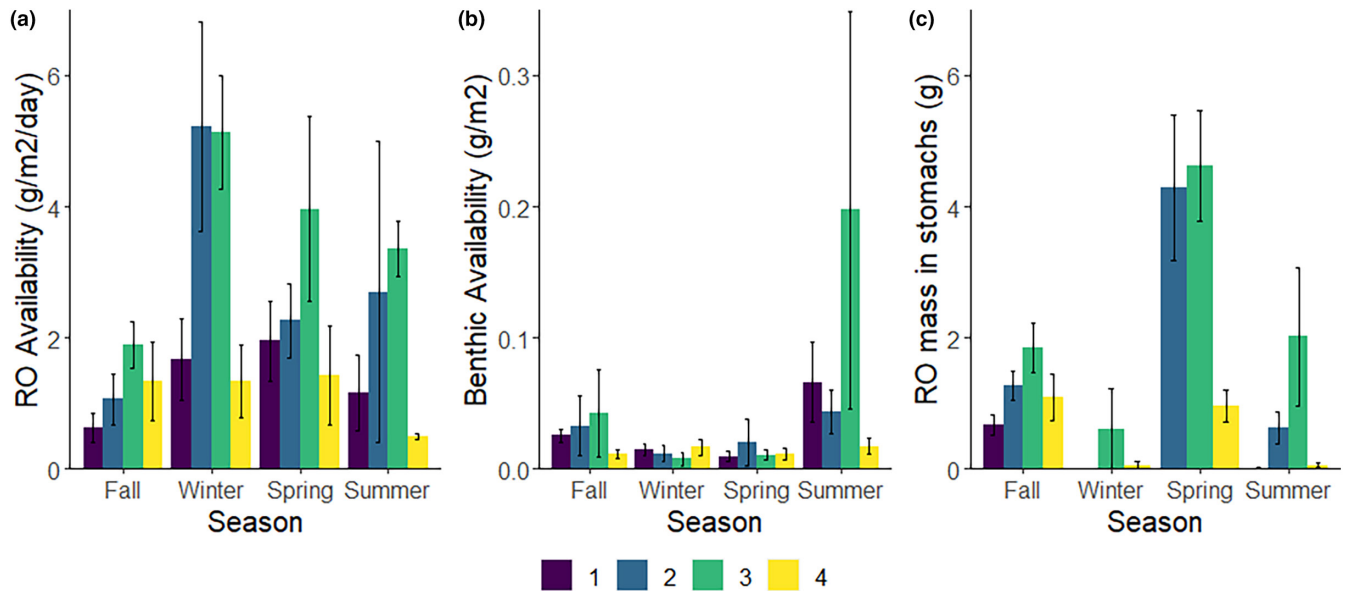
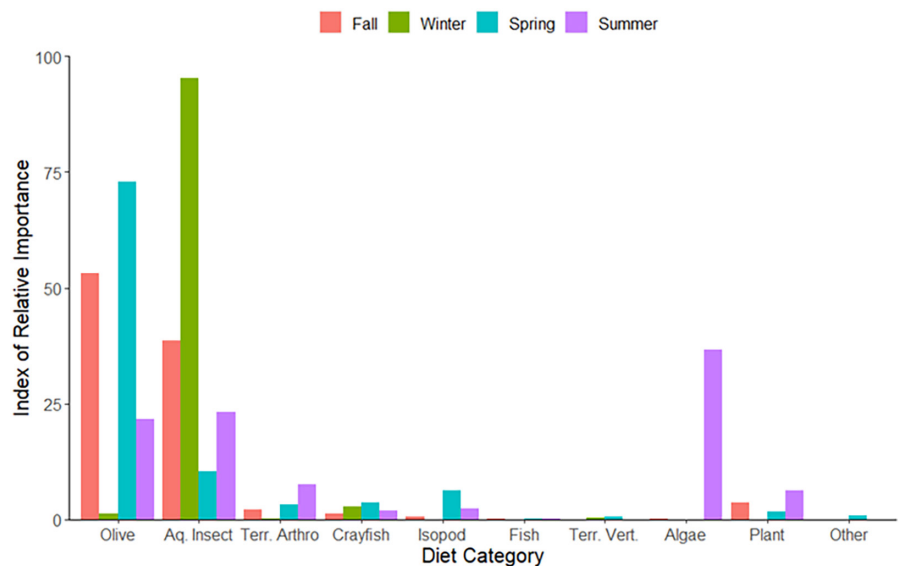


FIGURE 3 Means (\pm SE) summarized by season and section (bar colour; 1 most upstream and 4 is the most downstream section) for: (a) Russian olive (RO; *Elaeagnus angustifolia*) from seed traps ($\text{g m}^{-2} \text{ day}^{-1}$), (b) benthic aquatic invertebrate availability from kick-net sampling ($\text{g dry weight g m}^{-2}$) and (c) mass (g wet weight) channel catfish (*Ictalurus punctatus*) stomach contents composed of olive fruit. Samples classified by season as: September and November=fall, January=winter, March and May=spring and July=summer. No catfish were collected with olive in their stomach in reach 1 in the winter or spring seasons. Benthic availability was not collected in May 2017 due to high discharge at the time of sampling.

FIGURE 4 Index of Relative Importance (IRI) scores for San Juan River channel catfish (*Ictalurus punctatus*) diet categories by season from September 2016 through September 2017. IRI scores for each diet category were calculated as the percent frequency multiplied by the sum of percent number and percent weight. IRI values are presented here as percent IRI, which was calculated as the IRI score divided by the sum of the IRI scores for all diet categories and multiplied by 100 (Cortés, 1997).



period varied, with most stomachs collected during the fall ($N=356$). The IRI revealed that olives were an important food source in the fall and spring (Figure 4). Aquatic invertebrates were also important food sources, especially during the winter sampling events. Contrary to our hypotheses, olive fruit was consumed across all time periods and was not limited to short pulses of olive availability (Figure 3c). The mass of olive fruits in stomach contents varied seasonally (LMER: $F_{3,603}=12.53$; $p<.001$) and was greatest in the spring. However, the other seasons were not significantly different. The mass of olive in the gut varied between sections (LMER: $F_{3,603}=8.72$; $p<.001$), with the highest masses in the middle sections (2 and 3) and significantly

lower masses of olive fruit in the upstream and downstream sections (1 and 4).

In addition to olive fruits, we observed a variety of aquatic invertebrates (*Odonata*, *Trichoptera*, *Ephemeroptera*, *Diptera*), terrestrial insects (primarily *Coleoptera* and *Hemiptera*), terrestrial isopods (primary woodlice family *Armadillidiidae*), terrestrial vertebrates (mice, lizards, snakes and birds), Nonnative virile crayfish (*Faxonius virilis*), fish (primarily catfish and speckled dace, *Rhinichthys osculus*), algae, plant material excluding olive fruit (leaves and other seeds) and other (including unknown, gravel and sand). Mean mass and percent of stomach contents for each diet category are presented in Table 2 and Figure 5.

TABLE 2 Numbers of channel catfish (*Ictalurus punctatus*) collected with contents in their stomachs (N) during bimonthly sampling events conducted between September 2016 and September 2017 in the San Juan River.

Month	N	Olive		Aq. Ins		Isopod		Terr. Invert		Terr. Vert		Cray		Fish		Algae		Plant		Other	
		g	%	g	%	g	%	g	%	g	%	g	%	g	%	g	%	g	%	g	%
Sep	166	1.64	22.1	0.11	53.0	0.01	3.7	0.03	4.8	0.03	1.5	0.10	5.1	0.00	5.2	0.21	0.7	0.09	3.2	0.01	0.7
Nov	134	0.29	54.1	0.07	13.5	0.02	2.3	0.02	5.4	0.20	0.6	0.39	1.9	0.26	0.8	0.01	4.9	0.00	15.6	0.03	0.9
Jan	45	0.19	4.1	0.05	86.1	0.00	0.0	0.02	1.3	1.95	5.0	0.48	2.5	0.01	1.0	0.00	0.0	0.00	0.0	0.00	0.0
Mar	72	3.94	21.7	0.10	14.1	0.44	5.0	0.02	11.7	0.44	1.0	1.06	2.4	0.59	1.9	0.00	38.4	0.08	3.1	3.07	0.5
May	41	1.77	56.0	0.40	9.2	0.11	9.8	0.02	4.8	1.06	2.3	0.20	4.8	0.00	1.9	0.00	1.0	0.65	3.9	0.04	6.2
Jul	93	0.73	51.8	0.15	8.4	0.18	3.8	0.02	14.0	0.01	5.2	0.23	0.7	0.09	0.1	1.00	0.0	0.03	14.2	0.07	1.9
Sep	56	3.17	75.8	0.01	10.5	0.28	5.4	0.02	0.9	0.00	0.0	0.58	3.2	0.02	2.6	0.00	0.0	0.02	1.1	0.01	0.6
Total	607	11.74	40.4	0.88	26.6	1.04	4.1	0.13	6.0	3.68	1.6	3.03	3.1	0.98	2.2	1.22	7.5	0.86	7.0	3.24	1.4

Note: Mean mass (g wet weight) and percent by weight for diet categories observed in the catfish stomach samples are also provided.

The mass of stomach contents comprised of terrestrial invertebrates (LMER: $F_{3, 601} = 10.07, p < .001$), terrestrial vertebrates (LMER: $F_{3, 568} = 6.01, p < .001$), and total stomach content mass (LMER: $F_{3, 582} = 18.36, p < .001$) varied seasonally. Terrestrial invertebrates made up the most mass of stomach contents in the spring, and terrestrial vertebrates comprised more mass in the winter. Total stomach content mass was highest in the spring and all other seasons were not significantly different. The masses of aquatic invertebrates, crayfish and fish in stomach contents were not significantly different between seasons. We detected significant differences in the masses of aquatic invertebrates ($F_{3, 600} = 3.68, p < .012$), algae ($F_{3, 601} = 4.47, p < .004$) and total stomach contents ($F_{3, 601} = 7.51, p < .001$) among sections. The total mass of stomach contents was greatest in sections 2 and 3, which is likely associated with higher consumption of olive fruit in those reaches. Mass of aquatic invertebrates in the stomachs was highest in section 1, and all other pairwise comparisons between sections were not significantly different. Catfish in section 4 had significantly more algae in stomach contents compared to other sections. The mass of terrestrial invertebrates, terrestrial vertebrates, crayfish and fish were not significantly different between sections.

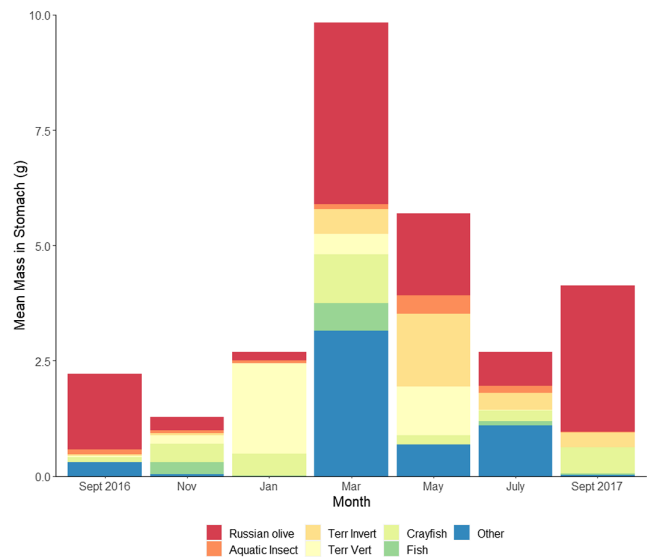
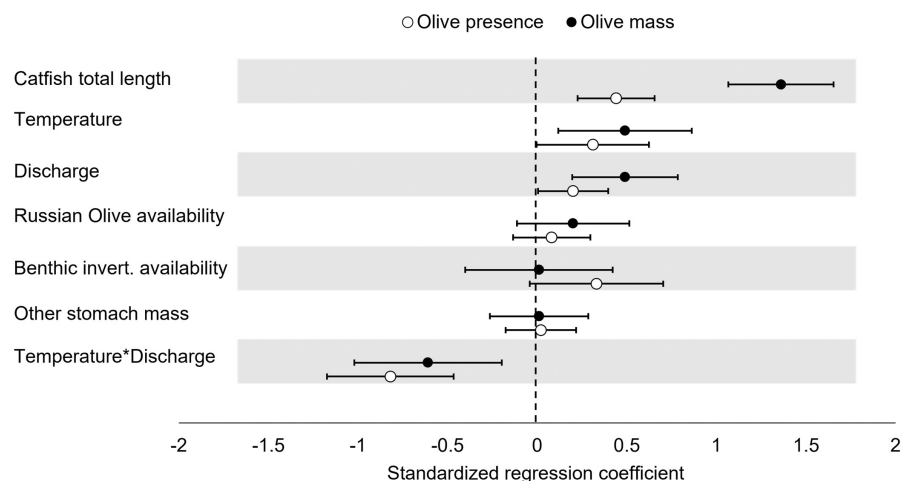


FIGURE 5 Bimonthly mass of channel catfish (*Ictalurus punctatus*) stomach contents by wet weight (g) for seven prey categories collected in the San Juan River (NM/UT) from September 2016 to September 2017. The proportion of diet for each category is displayed as fill. Russian olive (red) category consisted of fruit and seeds found in the gut. Aquatic insects (orange) were primarily composed of insects in the orders Diptera, Trichoptera, Ephemeroptera and Odonata. Terrestrial invertebrates (dark yellow) were largely composed of Isopods (pill bugs), with terrestrial insects in the orders Coleoptera and Hemiptera also common. Terrestrial vertebrates (light yellow) include mice, snakes, frogs and lizards. Crayfish (dark green) found in the stomachs were nonnative *Faxonius virilis*. Fish (dark green) was primarily composed of juvenile and young-of-year channel catfish with speckled dace (*Rhinichthys osculus*) and juvenile flannelmouth sucker (*Catostomus latipinnis*) present but rare. The other category (blue) was composed of algae, leaves, sand, sticks and unidentifiable material.

Diet composition varied among seasons (PERMANOVA: Pseudo- $F_{3, 606} = 15.98, p < .01, R^2 = .07$) and sections (PERMANOVA: Pseudo- $F_{3, 606} = 3.70, p < .01, R^2 = .02$) and all pairwise comparisons were significantly different for both (Figure S2). The interaction effect of season and section was also significant (PERMANOVA: Pseudo- $F_{3, 606} = 4.03, p < .01, R^2 = .04$). The mass of algae, aquatic invertebrates, terrestrial invertebrates and olive fruit in catfish stomachs contributed significantly to differences in diet composition between seasons. Olive fruit was the most influential diet category in all seasonal contrasts but was only significant in the winter–spring and fall–spring contrasts. Consumption of terrestrial arthropods and algae contributed significantly to differences in diet composition between summer and all other seasons. Aquatic invertebrate consumption contributed appreciably to seasonal diet composition differences in winter–fall and winter–summer contrasts.

Mixed effects models revealed that the presence of olive in catfish stomach contents increased with catfish total length and water temperature (Figure 6). There was also a significant interaction between temperature and discharge. The effect of benthic invertebrate availability was positive and marginally significant in this model. The olive fruit mass in catfish stomach contents was positively associated with catfish total length, water temperature and discharge. There was also a significant interaction between discharge and temperature. Olive availability, benthic invertebrate availability and total mass of stomach contents were not significantly associated with olive mass in catfish stomachs (Figure 6). In both models, the effect of temperature on olive consumption was contextualized by discharge. At high discharge (+1 SD), there was no effect of temperature on olive mass (Est: $-0.08 \pm 0.31, SE: p = .79$), but temperature had a marginally negative relationship with olive presence in the diet (Est: $-0.51 \pm 0.27, p = .06$). At mean and low flows, there was a positive relationship between temperature and olive consumption in both presence (mean flow: Est: $0.31 \pm 0.16, p = .05$; low flow: Est: $1.13 \pm 0.19, p < .00$) and mass models (mean flow: Est: $0.51 \pm 0.18, p = .01$; low flow: Est: $1.10 \pm 0.25, p < .01$; Figure S3).

FIGURE 6 Standardized regression coefficients from mixed effects models estimating effects of six independent variables and one interaction on the presence (hollow) and mass (filled) of Russian olive (*Elaeagnus angustifolia*) fruit in the guts of channel catfish (*Ictalurus punctatus*) in the San Juan River from September 2016 through September 2017. The 'Other stomach mass' category is the sum of all non-olive items in catfish stomachs.



3.1 | Nutritional analysis

We estimated that indigestible seeds make up 48.6 (± 2.8)% of total fruit weight. The indigestible portion of fruit tissue was estimated as 9.1% calculated from proximate nutritional analysis (Table 3) for a total indigestible portion of 52.3% of fruit by wet weight. This yielded a considerably higher proportion of indigestible material compared to other prey items of the diet (Table S1). Nutritional analysis also revealed that carbohydrates comprised the majority (73.6%) of olive fruit pulp, with low levels of protein (5.6%) and fat (1.7%). From the proximate analyses, we calculated energy density of olive fruit (no seeds) to be 1605 J/g, which was considerably lower than other diet items in the study and less than half that of aquatic insects (4300 J/g) or fish (4200 J/g).

3.2 | Bioenergetic model

All model runs were balanced, and the proportion of maximum consumption ranged from 0.86 to 0.98. Total per-capita consumption

TABLE 3 Mean ($N=3$) nutrient content (grams per 100 g of olive fruit) and energy density (Joules/gram RO) of Russian olive fruit (seeds removed).

Nutrient	Content
Crude protein (%)	5.6
Crude fat (%)	1.7
Crude fibre (%)	5.8
Ash (%)	3.3
Moisture (%)	10.0
Carbohydrate (%)	73.6
Energy (Joules/g)	1605

Note: Proximate analyses were used for crude protein (Kjeldahl), crude fat, moisture and crude fibre. The crude 'by difference' method was used to determine percent carbohydrate. Energy density was calculated as gross calories by multiplying content by average energy content for each category (Merrill & Watt, 1973).

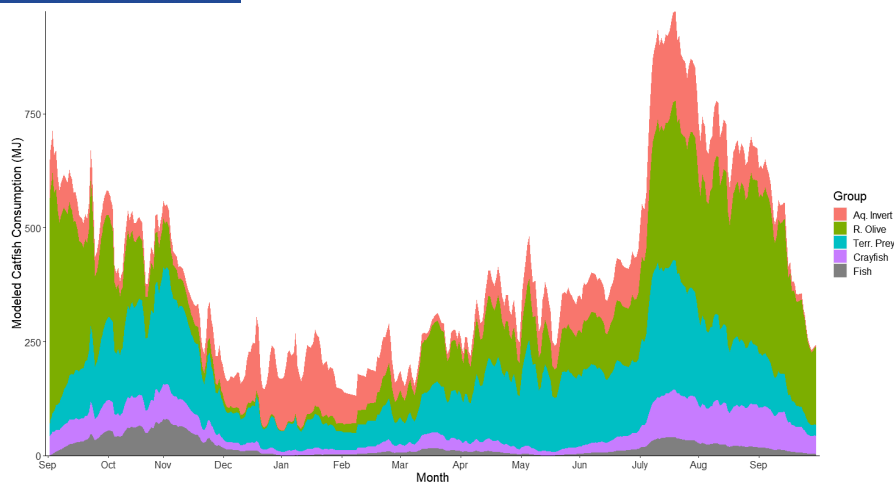


FIGURE 7 Modelled energy consumption (millions of joules) for adult catfish (*Ictalurus punctatus*) populations in the San Juan River for each diet category from September 2016 to September 2017. Consumption was estimated using the diet composition estimated bimonthly during this period, water temperature, bioenergetic parameters from published literature (Table S1), and growth and population estimates from Pennock et al. (2018). Models interpolated diet composition between sampling events and assumed a 0.20 annual natural mortality and size-specific exploitation mortality.

was greatest in summer months when the temperature was highest (Figure 7). Total energy consumed from olive fruit was greatest in the fall and spring. Terrestrial prey were also important sources of energy throughout the sampling. Nonnative crayfish were an important energy source for catfish >400mm and provided up to 30% of energetic demand for catfish >500mm. Annual cohort consumption was greatest for catfish between 350 and 450mm because they were the most abundant. These age classes also derived the greatest proportion of their diet from olive fruit. After summing annual consumption across all cohorts, we estimated that energy consumed from olive fruit made up 35.6% of energy (J) consumed by catfish >300mm in 153km of the San Juan River during our study period. Terrestrial prey (invertebrate+vertebrate) composed 31.4% of population energy demands. Allochthonous inputs of terrestrial prey and olive fruit comprised 67% of energy consumed by catfish populations in our simulation. Our model predicted that aquatic invertebrates, fish and crayfish made up 18.3%, 10% and 4.6%, respectively, of annual population energy consumption during our sampling period. Energy consumed from olive accounted for 38.7% of metabolic demand (respiration, egestion, excretion and specific dynamic action) for catfish during this period (Figure S4).

4 | DISCUSSION

We estimated that olive fruit comprised 44% of catfish diets during our study. Our diet composition results agree with those presented by Hedden et al. (2022) and provide additional perspective on the effects of prey availability on consumption of olive fruit by nonnative catfish. Contrary to our hypotheses, catfish consumed olives regardless of their availability and the availability of benthic invertebrate prey. Olives were most abundant in spring but were

available year-round and were never sufficiently scarce to cease their consumption by catfish. We expected olive fruit consumption would also correspond with low availability of alternative prey, but our results did not support this hypothesis. In fact, the marginally significant effect of invertebrate prey availability was positively associated with olive fruit mass and presence in stomach contents. When both olives and alternative prey were abundant, catfish consumed both prey categories. Our results suggest that catfish rely on olive routinely as a reliable energy source and do not switch to alternative prey items based on availability of benthic invertebrates.

Both the presence and mass of olive fruits in catfish stomach contents were associated with water temperature, but the effect was modified by river discharge. Olive consumption was highest during periods of high discharge. Inundation of riparian habitats during high flows and transport of olive during rain events likely increased the availability of fruit to catfish. Catfish consumed more olives during periods of high temperature-related metabolic demand, supporting our hypothesis that olives are an energetic subsidy for catfish. We also found a positive effect of catfish total length on presence and mass of olive fruit in stomach contents, which agreed with the results of Evelyn et al. (2022) and revealed a difference in diet between juvenile and adult catfish. Olive fruit is relatively large, and olive consumption by small catfish (<200mm) is likely gape-limited (Evelyn et al., 2022).

Frugivory by catfish has been observed in their native habitats (Chick et al., 2003). However, prior to this study the energetics of catfish consuming olive fruit were not well understood. Olive fruit is not an ideal diet item for catfish because it is high in carbohydrates, low in protein and low in fats (Table 3). Commercial aquaculture diets provide a benchmark for catfish nutrition to optimize growth, with commercial feeds typically having between 26%–32% protein, 4%–6% lipids and 25%–35% carbohydrate (Robinson

& Li, 2015; Simco & Cross, 1966). Interestingly, our diet estimates indicated that carbohydrates contributed approximately 27.4% of catfish diet during our study, an amount within acceptable limits for catfish growth. Catfish inefficiently assimilate complex carbohydrates into growth in aquaculture settings (Wilson & Poe, 1987), but they can utilize carbohydrates for metabolic energy (Garling Jr & Wilson, 1977). In our study, olive was often consumed alongside other prey items and was supplemental to other prey. To fully understand the interaction between olive and catfish, future research should address how catfish are able to utilize the energy from olive fruit. Three hypotheses may describe why catfish feed on such a relatively poor diet item: (1) olive fruit supplies metabolic energy to catfish but does not provide the dietary content required for growth or development of reproductive tissue, (2) olive fruit is a low-quality diet item but either availability or access to superior prey items is limited, forcing the use of sub-optimal energy sources and/or (3) olive fruit is an ecological trap for catfish, providing no benefit to catfish fitness.

Bioenergetic estimates of consumption indicated that olive contributed 35.6% of energy (J) required for catfish growth rates in the San Juan River during our study period. Olive fruits subsidized all age classes modelled (>300mm) and were most valuable to catfish between 350 and 450mm, the most abundant size class in this population (Pennock et al., 2018). The results suggest that olive fruit provided an energetically valuable resource subsidy for catfish. Energy from olive fruit accounted for 38% of the metabolic costs for catfish, supporting our hypothesis that energy from olive subsidizes energy demands and allows other food items with necessary protein and lipids to contribute to growth. Energy subsidies may be particularly important during periods of high metabolic demand and allow consumers to maintain weight. Terrestrial prey items also provided a significant subsidy to catfish populations, comprising 34.1% of population energy consumption. It is likely that olive tree production also plays a significant role in riparian food webs, and production of terrestrial prey may represent an indirect subsidy from olive trees to catfish (Katz & Shafroth, 2003; Pendleton et al., 2011). Future research should incorporate the use of isotope analysis to quantify the contribution of olives to aquatic and terrestrial food webs to better understand the importance of the resource.

Optimal foraging theory assumes that animals select forage items that minimize the time or energy allocated to foraging to acquire the most energy, and natural selection should favour easily acquired diets that maximize net energy intake (Pyke, 1984; Stephens & Krebs, 1986). Olive consumption could have negative consequences if it results in lower net energy gained. However, given the frequency of olives in catfish stomachs in multiple studies in the San Juan River, we do not expect this interaction to represent an ecological trap or sub-optimal foraging. Olive fruit is a 'costly' diet item in that it is difficult to handle or digest without specialized adaptations (Langerhans et al., 2021) due to its high indigestibility and unbalanced nutrition. The consumption of costly prey items is common in many fish species and is often driven

by low alternative prey abundance. Consuming costly diet items can maximize energy intake and increase compensatory growth when higher-quality food sources become available (Langerhans et al., 2021). In fact, channel catfish fed diets with high energy to protein ratios exhibited faster compensatory growth in feed trials (Gaylord & Gatlin III, 2001). Despite quantifying seasonal changes in the relative availability of alternative prey, we were unable to assess whether alternative prey limited catfish growth or if the catfish selected olive fruit over other prey items. Based on this evidence, we do not expect olive consumption to reflect sub-optimal foraging. We suggest that olive fruit provides an additional resource for catfish populations because it is abundant and requires low foraging effort and time.

We were unable to assess the full spectrum of prey available to catfish (e.g. terrestrial prey), which limited our ability to detect variation in olive consumption. Because of their generalist omnivore feeding strategy, assessing prey availability for channel catfish is difficult. This study improves upon previous diet studies by quantifying two common prey items. Long-term diet studies on catfishes or other generalist consumers should consider quantifying the availability of multiple prey items to better understand prey switching in these species (Schmitt et al., 2019). We also acknowledge that our measure of olive availability only accounted for fruit falling from the trees directly into the water and did not account for fruit that dropped in terrestrial habitats and was carried by wind or water to the river where it would be available to catfish. The influx of fruit during rain events can be substantial (C. Cheek, pers. obs.), and buoyant fruit can be transported long distances by water (Brock, 1998; Pearce & Smith, 2001). Olive fruits ripen in late summer and early fall, but fruit can remain on the trees throughout the winter (Katz & Shafroth, 2003). This is a common adaptation of fruit trees with seeds dispersed by birds (Stiles, 1980). The largest influxes of fruit occurred in January and March samples. Our estimates indicate that olives were both temporally and spatially available to catfish throughout the year, but the effect of olive availability may be observed with better field methodologies that account for olive transport in water.

Our study is also limited by evaluating catfish diet composition and prey availability during a 1-year period; thus, it only observed the interaction between olive and catfish under a narrow range of environmental conditions. It is, therefore, possible that higher-quality diet item availability was especially low during our study year and our results overestimated the importance of olive in San Juan River catfish diets. However, our olive consumption results were comparable with the rates reported by Hedden et al. (2022). Our bioenergetic model could also be improved by incorporating individual variation in diet composition and growth. In addition, better estimates and variability of seasonal growth would improve model estimates of consumption. Bioenergetic models are sensitive to energy density estimates for both the prey and predator, and all prey energy density values, except olive, were from peer-reviewed publications. Better estimates of energy density for both consumers and food items would increase model accuracy. Even with these caveats,

we believe our estimates provide additional and robust evidence that olive plays an important role in supporting catfish energetic demands in this system.

Catfish have the potential to act as seed dispersal agents for olives, thereby providing a reproductive fitness benefit. Many catfishes act as dispersal agents for terrestrial plants (Correa et al., 2007), and catfish can transport viable seeds and increase germination potential of other riparian plants such as red mulberry (*Morus rubra*) and swamp privet (*Forestiera acuminata*) (Chick et al., 2003). Olive receives seed dispersal and germination benefits through interactions with frugivorous mammals and birds (Campbell & West, 2022; Edwards et al., 2014) but more research is needed to determine if catfish can provide this benefit. If catfish promote reproductive success of olives, the interaction could represent a mutualism in which food and dispersal are exchanged to the benefit of both participants (sensu Silknetter et al., 2020). If the interaction is mutually facilitative, it may represent a case of invasion meltdown, in which positive interactions among invaders facilitate one another, thereby increasing their biomass, establishment success or persistence on the landscape (Simberloff & Von Holle, 1999). The presence of a facilitating invader is not required for invasion success in most cases (Simberloff, 2006), and there are certainly habitats where catfish and olive have successfully invaded without the facilitation of the other. However, the interaction between olive and catfish may be beneficial for native species by decreasing predation on native fishes and/or decreasing competition for other prey items (Hedden et al., 2022). Including the results of this study, catfish consuming olive fruit is well documented (e.g. Brooks et al., 2000; Evelyn et al., 2022; Hedden et al., 2021, 2022), yet all known examples are from the San Juan River. Rivers across the western US have considerable populations of both olive and catfish, but the extent of their interaction across these basins remains unknown. To understand the strength of this interaction, researchers should evaluate the frequency of this interaction in other locations where the species co-occur.

Researchers must focus more on the impact of olives because it threatens rivers in grasslands and arid environments that are already imperilled by river regulation, fragmentation, water withdrawals and aquatic nonnative species. Because these ecosystems did not evolve with a large abundance of fruit-bearing trees in the riparian corridor, olive can alter aquatic food webs. Olive fruit is known to be an important food resource for many birds and mammals (Campbell & West, 2022; Edwards et al., 2014), and we observed many terrestrial vertebrates utilizing olive fruits in their diet, including bears, raccoons, squirrels, mice, coyotes, horses and turkeys and many other bird species (Cheek, pers. observation). The availability of olive fruits in riparian environments may benefit some native consumers, especially terrestrial vertebrates. However, the traits of most native fishes in this system are not adapted to take advantage of this resource (e.g. the subterminal mouths of suckers are inefficient for surface feeding) because they did not evolve with fruiting riparian trees. Olive availability may provide a disproportionate advantage to nonnative catfish and carp, which have evolutionary histories of frugivory (Chick et al., 2003; Heinrich et al., 2021). However, the net

effects of olive subsidies likely depend on consumer traits in the recipient community. Given the prevalence of Russian olive trees and their potential to alter channel geomorphology, biochemical processes and trophic dynamics, it is important to determine whether nonnative fishes are facilitating their spread and how this novel resource subsidy affects native species and ecosystem function.

AUTHOR CONTRIBUTIONS

Christopher A. Cheek, Brandon K. Peoples and Reuben R. Goforth conceived and designed the investigation. Christopher A. Cheek performed field and laboratory work. Christopher A. Cheek and Brandon K. Peoples analysed the data. Christopher A. Cheek, Brandon K. Peoples and Reuben R. Goforth wrote the paper.

ACKNOWLEDGEMENTS

Funding for this project was supported by grants from the Intertribal Timber Council, American Philosophical Society, National Science Foundation, Purdue University and the Sloan Foundation. We would like to thank Matthew Voorhees, Grace Carter, Josey Cline, Megan Gunn and Samantha Weiss for assisting with field work and sampling processing. This work would not have been possible without assistance from Navajo Nation Department of Fish and Wildlife, US Bureau of Reclamation, US Fish and Wildlife Service, Utah Division of Wildlife Resources and New Mexico Department of Fish and Wildlife. We thank Dr. Mark McKinstry and Dr. Tim Patton for their field observations and assistance with conceptual development of the project. We also thank Dr. Mark Pyron and the anonymous reviewers who provided valuable feedback to improve the manuscript. Dr. Reuben R. Goforth and his laboratory were partially supported by funding provided by the U.S. Department of Agriculture's National Institute of Food and Agriculture. This material is also based upon work supported by the NIFA/USDA, under project number SC-1700599 and represents Technical Contribution Number 7211 of the Clemson Experiment Station.

CONFLICT OF INTEREST STATEMENT

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

The data for this project is not currently available; however, the authors will consider sharing the data upon request.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

How to cite this article: Cheek, C. A., Peoples, B. K., & Goforth, R. R. (2023). Diets of invasive channel catfish are subsidized by invasive riparian trees. *Ecology of Freshwater Fish*, 00, 1–14. <https://doi.org/10.1111/eff.12753>