

Iowa State University

---

From the Selected Works of Michael J Weber Dr

---

July, 2014

# Evaluation of Trophic Niche Overlap between Native Fishes and Young-of-the-Year Common Carp

Michael J Weber, *South Dakota State University*

Jessica M. Howell, *South Dakota State University*

Michael L. rown, *South Dakota State University*



Available at: [https://works.bepress.com/michael\\_weber/2/](https://works.bepress.com/michael_weber/2/)

## **Evaluation of Trophic Niche Overlap between Native Fishes and Young-of-the-Year Common Carp**

Author(s): Jessica M. Howell, Michael J. Weber and Michael L. Brown

Source: The American Midland Naturalist, 172(1):91-106.

Published By: University of Notre Dame

DOI: <http://dx.doi.org/10.1674/0003-0031-172.1.91>

URL: <http://www.bioone.org/doi/full/10.1674/0003-0031-172.1.91>

---

BioOne ([www.bioone.org](http://www.bioone.org)) is a nonprofit, online aggregation of core research in the biological, ecological, and environmental sciences. BioOne provides a sustainable online platform for over 170 journals and books published by nonprofit societies, associations, museums, institutions, and presses.

Your use of this PDF, the BioOne Web site, and all posted and associated content indicates your acceptance of BioOne's Terms of Use, available at [www.bioone.org/page/terms\\_of\\_use](http://www.bioone.org/page/terms_of_use).

Usage of BioOne content is strictly limited to personal, educational, and non-commercial use. Commercial inquiries or rights and permissions requests should be directed to the individual publisher as copyright holder.

---

# Evaluation of Trophic Niche Overlap between Native Fishes and Young-of-the-Year Common Carp

JESSICA M. HOWELL,<sup>1</sup> MICHAEL J. WEBER<sup>2</sup> AND MICHAEL L. BROWN

South Dakota State University, Department of Natural Resource Management, Box 2140B, Brookings 57007

**ABSTRACT.**—Common carp *Cyprinus carpio* is a ubiquitous invasive species that commonly imposes negative effects on aquatic ecosystems. However, research evaluating the effects of carp on native fishes is limited. Carp are highly fecund and larvae and juveniles can be abundant. If age-0 carp use similar prey resources as native fishes, they may compete if food becomes limited. We used traditional diet analysis for samples during Jul. and Aug. 2008 in Brant Lake. Stable isotopes were used for samples collected during Aug. and Sep. 2009 in Brant Lake and Lake Sinai to examine prey resource use by age-0 carp and four native fishes: bluegill *Lepomis macrochirus*, black crappie *Pomoxis nigromaculatus*, yellow perch *Perca flavescens*, and orangespotted sunfish *Lepomis humilis*. Age-0 carp were generally as or more abundant than native fishes. In Jul. Daphnia dominated the diets of all fishes sampled, resulting in high (>60%) dietary overlap ranging from 87–98%. In Aug. Daphnia density in Brant Lake declined and dominant diet prey types shifted for carp (to Trichoptera and Daphnia), yellow perch (to Amphipoda), and the three Centrarchids (to Cyclops and Diaptomus). This diet shift resulted in lower diet overlap between Centrarchids and either carp (<40%) or yellow perch (3–16%) but high diet overlap within Centrarchids (67–97%). Stable isotope analysis further indicated greater resource overlap when most fishes relied on zooplankton and lesser overlap as fishes shifted to benthic prey. Our results suggest that resource competition between age-0 carp and native fishes is most likely to occur during early summer if Daphnia availability becomes limited but becomes less likely as dominant prey in diets increasingly diverge among fish species over time.

## INTRODUCTION

Translocation of species outside of their native range often occurs without an adequate understanding of the implications of such introductions on native fauna. Introductions and invasions of nonnative species can have unintended consequences on invaded ecosystems and native species through the transformation of basic ecosystem structure and function (Parker *et al.*, 1999). One of the most detrimental and widespread invasive species is common carp *Cyprinus carpio* (Lowe *et al.*, 1994). Carp were widely distributed across much of the United States during the 1800s for recreational and food purposes (Panek, 1987). Historically, such introductions were perceived as beneficial but have since resulted in numerous negative effects within invaded ecosystems (Weber and Brown, 2009). Carp populations often shift shallow aquatic ecosystems from the clear- to turbid-water stable state by increasing turbidity, nutrient availability, and noxious algal blooms and reducing aquatic macrophytes and benthic invertebrates (Parkos *et al.*, 2003; Koehn, 2004; Weber and Brown, 2009). Perturbations induced by carp on physicochemical variables and lower trophic levels may extend to higher trophic levels, resulting in reduced growth, survival, and abundance of native fishes (Wolfe *et al.*, 2009; Jackson *et al.*, 2010; Weber and Brown, 2011). Adult carp

<sup>1</sup>Corresponding author present address: Kansas Department of Wildlife, Parks, and Tourism, Emporia Research and Survey Office, PO Box 1525, Emporia, KS 66801; Telephone: (620) 342-0658; FAX: (620) 342-6248; e-mail: jessica.howell@ksoutdoors.com

<sup>2</sup>Present address: Iowa State University, Department of Natural Resource Ecology and Management, 339 Science Hall II, Ames, Iowa 50011

have been associated with declines in abundances of native fish populations under various abiotic conditions (Weber and Brown, 2011) but little is known about interactions with age-0 carp.

Invasive fishes often occupy ecological niches similar to native fishes, with the possibility for resource overlap and competitive interactions that may result in native fish population declines. Prey resource overlap may be particularly important during early life stages where prey availability can regulate foraging success, growth, and survival (Graeb *et al.*, 2004). Early life stages of many native fishes initially rely on zooplankton prey (Mittelbach, 1984; Pope and Willis, 1998) before undergoing ontogenetic diet shifts to feed on larger invertebrates or fishes (Fisher and Willis, 1997; Graeb *et al.*, 2004). High densities of some larval and juvenile omnivorous fish can greatly reduce prey resources, affecting growth and survival of co-occurring species (Stein *et al.*, 1995). Carp are highly fecund (Sivakumaran *et al.*, 2003; Weber and Brown, 2012b) with protracted spawning that can translate into a high juvenile abundance (Phelps *et al.*, 2008; Weber and Brown, 2013b). Similar to native fishes, early life stages of carp are zooplanktivorous and later undergo an ontogenetic diet shift to benthic invertebrates (Britton *et al.*, 2007; Rahman *et al.*, 2009; Weber and Brown, 2013a). High densities of zooplanktivorous carp can reduce zooplankton densities (Meijer *et al.*, 1990; Kahn *et al.*, 2003) and thus may limit prey availability for other fishes, potentially resulting in intraspecific competition (Tonkin *et al.*, 2006).

Comparing how invasive and native species use resources can help predict the extent and potential consequences of their interactions. Biologists need a better understanding of carp resource utilization and niche overlap with native fishes (Carey and Wahl, 2010), specifically during early life stages, a critical period when fishes are most abundant and overlap is likely to occur. Our objectives were to evaluate fish abundance, prey resource use, and diet overlap between age-0 carp and native fish during mid to late summer. We first compared relative abundances of age-0 carp and four common native fishes: age-0 bluegill *Lepomis macrochirus*, black crappie *Pomoxis nigromaculatus*, and yellow perch *Perca flavescens* and adult orangespotted sunfish *Lepomis humilis*. These species were chosen because they are the most abundant species regionally that co-occur with carp populations (St. Sauver *et al.*, 2009), they represent ecologically and economically important fishes for the region, and their populations may be negatively affected by carp (Weber and Brown, 2011). We then investigate prey resource overlap among these species in two lakes by quantifying fish diets using traditional diet analyses and stable isotopes.

## METHODS

### STUDY AREAS

Brant Lake is a 420 ha (3 m mean depth, 4.3 m maximum depth) glacial lake located in Lake County, South Dakota, U.S.A. (43.9215°N, 96.9489°W). Lake Sinai is a 696 ha (5 m mean depth, 10 m maximum depth) glacial lake located approximately 53 km north of Brant Lake in Brookings County, South Dakota, U.S.A. (44.2678°N, 97.0693°W). Sparse beds of sago pondweed *Potamogeton pectinatus* exist throughout parts of both lakes and cattails *Typha spp.* are present in shallow marginal areas of embayments (St. Sauver *et al.*, 2009). Fish communities in both lakes are composed of carp, black crappie, yellow perch, bluegill, orangespotted sunfish, smallmouth bass *Micropterus dolomieu*, walleye *Sander vitreus*, bigmouth buffalo *Ictiobus cyprinellus*, black bullhead *Ameiurus melas*, channel catfish *Ictalurus punctatus*, green sunfish *Lepomis cyanellus*, northern pike *Esox lucius*, spottail shiner *Notropis hudsonius*, white bass *Morone chrysops*, and white sucker *Catostomus commersonii*.

## FIELD SAMPLING

Orangespotted sunfish and age-0 carp, black crappie, yellow perch, and bluegill were sampled on Jul. 14 and Aug. 19, 2008 in Brant Lake to estimate relative abundance and a subsample of collected fish were subsequently used for diet analysis (Table 1). Additional fish were collected on Aug. 26–27 and Sep. 19–20, 2009 from lakes Brant and Sinai for stable isotope analyses, providing additional spatiotemporal insights into juvenile feeding patterns. All fish collections were done using daytime, pulsed direct-current electrofishing (5–8 A, 180–220 V) at four transects with 15 min of effort each in a single embayment that was sampled each year. Because our goal was to observe spatiotemporal overlap in age-0 fishes, we only used electrofishing to estimate the relative abundance of each species in shallow littoral habitats where this method was effective and where we expected our target species to cohabit for foraging and predator avoidance. Orangespotted sunfish used for relative abundance and diet analyses in Jul. 2008 were likely  $\geq$  age-1 whereas those used for relative abundance and diet analyses in Aug. 2008 were age-0. Upon collection in 2008, specimens were immediately preserved in 90% ethanol for diet analysis whereas those collected in 2009 for stable isotope analysis were sorted by species, placed on ice in the field, and frozen in the laboratory. Within each lake, month, year, and species, fish catch per unit effort (CPUE) was calculated as the mean number of fish captured per hour of electrofishing. Catch per unit effort data were transformed ( $\log_{10}$ -CPUE+1) and compared across species and months with repeated-measures analysis of variance (ANOVA), as CPUE from one date was not independent from samples collected on previous dates. When significant differences were detected ( $\alpha = 0.05$ ) for either main factor (species and months) or their interaction, LSD mean separation tests adjusted for multiple comparisons were used to compare CPUE of carp to each native fish species.

To evaluate zooplankton availability concurrent with fish sampling in Brant Lake during 2008, triplicate zooplankton subsamples were collected with an integrated tube sampler at three locations within the same embayment where fish were sampled. Water was filtered through 64  $\mu$ m mesh and preserved with Lugol's solution in the field. In the laboratory zooplankton samples were adjusted to 60 mL volumes, sub-sampled with three 1 mL aliquots, and identified to suborder or family. Counts were extrapolated to estimate density (number/L). In 2009 both zooplankton and benthic invertebrates were collected for stable isotope analysis but not invertebrate density estimates, in the same embayments where fish were collected. Zooplankton were collected using similar methods as in 2008 whereas benthic invertebrates were collected from three sites using triplicate Eckman dredge subsamples that were filtered through 500  $\mu$ m mesh. To purge digestive tracts, zooplankton and benthic invertebrate samples were placed in separate containers, soaked in distilled water for 4 h, and then frozen. Zooplankton used for stable isotope analysis were subsampled from combined samples of all zooplankton collected, whereas benthic macroinvertebrates were identified as Trichoptera, Chironomids, Chydorus, and Corixidae before being combined into a singular homogenous sample for stable isotope analysis. Separation of data into these two major invertebrate prey groups allowed us to identify fish reliance on pelagic (zooplankton) versus littoral (benthic invertebrates) energy pathways (France 1995).

## DIET COMPOSITION

No age-0 bluegills were captured in Jul., and we only included fish with prey in their stomachs in the diet analysis. The esophagus, stomach, and intestines were removed and examined under magnification using a dissecting microscope; prey items were identified to genus (zooplankton) or order (benthic invertebrates), enumerated, and when possible, total length (TL) was measured along the longest axis using a micrometer. Dry mass was

TABLE 1.—Summary describing the total number (N) and size distribution of fish sampled in lakes Brant and Sinai used to calculate relative abundance and the number used for diet analysis in 2008 and for stable isotope analyses in 2009. Orangespotted sunfish in Jul. 2008 were likely > age-1 based on sizes, whereas those in Aug. 2008 were likely age-0 (Miller 1963)

Lake	Year	Month	Species	N	Length range (mm)	Diet analysis	Stable isotopes
Brant	2008	Jul.	Common carp	23	21–50	23	0
			Bluegill	0	NA	0	0
			Black crappie	92	26–37	30	0
	2008	Aug.	Yellow perch	15	45–53	15	0
			Orangespotted sunfish	33	41–59	20	0
			Common carp	28	30–59	20	0
			Bluegill	702	30–48	30	0
			Black crappie	29	46–68	29	0
			Yellow perch	14	65–79	14	0
			Orangespotted sunfish	20	30–44	20	0
2009	Aug.	Common carp	42	61–100	0	10	
		Bluegill	655	29–46	0	20	
		Black crappie	9	44–65	0	9	
		Yellow perch	67	65–96	0	10	
		Common carp	7	60–88	0	7	
Sinai	2009	Sep.	Bluegill	498	36–49	0	10
			Black crappie	10	62–74	0	10
			Yellow perch	7	52–96	0	7
			Common carp	65	38–88	0	10
			Bluegill	297	28–34	0	10
2009	Sep.	Black crappie	57	25–46	0	10	
		Yellow perch	95	58–70	0	10	
		Common carp	28	57–89	0	10	
		Bluegill	127	27–46	0	10	
		Black crappie	2	68–102	0	2	
			Yellow perch	12	69–82	0	10

estimated for each prey type (zooplankton genus or benthic invertebrate order) based on established length-weight equations (Culver *et al.*, 1985; Benke *et al.*, 1999). Using estimated dry mass values, we calculated mean percent dry mass ( $PDM_i$ ) for each prey type by fish species and month as

$$PDM_i = \frac{1}{P} \sum_{j=1}^P \left( \frac{W_{ij}}{\sum_{i=1}^q W_{ij}} \right)$$

where  $W_{ij}$  is the dry weight of prey type  $i$  in the diet of fish  $j$ ,  $q$  is the number of prey types, and  $P$  is the number of fish for a given species and month that contained that prey item (Chipps and Garvey, 2007).

For each fish species and month, we calculated prey-specific abundance ( $PSA_i$ ), as

$$PSA_i = \left( \frac{\sum S_i}{\sum S_i} \right) \times 100$$

where  $S_i$  is the total dry mass of prey type  $i$  consumed and  $S_i$  is the dry mass of all prey consumed by those fish with prey type  $i$  in the diet (Amundsen *et al.*, 1996; Chipps and Garvey, 2007). Percent occurrence was calculated for each species by month as

$$PO_i = \left( \frac{N_i}{N} \right) \times 100$$

where  $PO_i$  is the percent occurrence of species  $i$ ,  $N_i$  is the number of fish with prey type  $i$  in their diet composition, and  $N$  is the total number of fish with stomach contents (Amundsen *et al.*, 1996).

$PSA_i$  was plotted on the y-axis and  $PO_i$  on the x-axis in a bivariate scatter plot for each species by month to interpret prey use in relation to feeding strategy, relative prey importance, and homogeneity of diets within the species (Fig. 1; Amundsen *et al.*, 1996; Chipps and Garvey, 2007). The complexity of factors affecting prey utilization by individual fish precludes assigning semiquantitative terms to values for each axis (*e.g.*, less than 40%  $PSA$  and less than 40%  $PO$  means a prey type is rare), which is likely why Amundsen *et al.* (1996) did not attempt to assign such values, rather relying on interpretation using graphical methods. A prey type was considered dominant if it was consumed in high abundance by a large percentage of the sample population (high  $PSA_i$  and high  $PO_i$ ; Fig. 1, bottom left panel; Amundsen *et al.*, 1996). Feeding strategy was represented along the vertical axis (Fig. 1, bottom left panel; Amundsen *et al.*, 1996). A population niche pattern was characterized as a large percentage of the sample population consuming low abundances of many prey types (Fig. 1, bottom left panel; Amundsen *et al.*, 1996).

#### DIET OVERLAP

Morisita's index of diet overlap was used to compare among prey items consumed by species pairs in each month in 2008 because it minimizes sample size biases (Wolda, 1981; Krebs, 1989). Morisita's index was calculated as

$$C = \frac{2 \sum_i^n P_{ij} P_{ik}}{\sum_i^n P_{ij} [(n_{ij} - 1) / (N_j - 1)] + \sum_i^n P_{ik} [(n_{ik} - 1) / (N_k - 1)]}$$

where  $C$  is Morisita's index of niche overlap between species  $j$  and  $k$ ;  $P_{ij}$  is proportion resource  $i$  of the total resources used by species  $j$ ;  $P_{ik}$  is proportion resource  $i$  of the total resources used by  $k$ ;  $n_{ij}$  is number of individuals of species  $j$  that use resource  $i$ ;  $n_{ik}$  is number of individuals of species  $k$  that use resource  $i$ ;  $N_j$  and  $N_k$  are total number of individuals of each species in sample (the sum of  $n_{ij} = N_j$ ; the sum of  $n_{ik} = N_k$ ). A value of 1 indicates

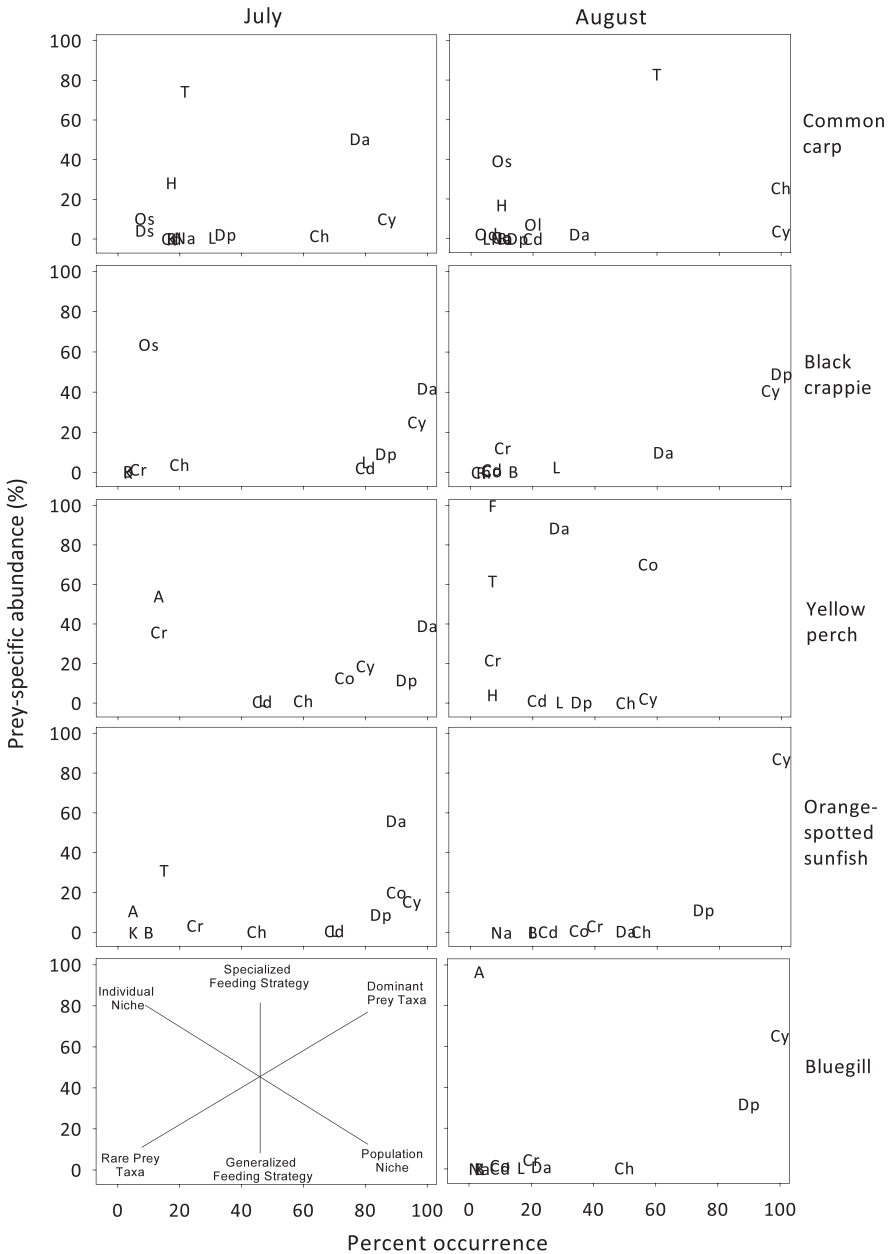


FIG. 1.—Bivariate scatter plots depicting percent occurrence and prey-specific abundance to interpret feeding strategy, relative prey importance, and niche variation during Jul. and Aug. 2008 in Brant Lake, South Dakota. For prey items: A = Amphipoda, B = Bosmina, Cd = Ceriodaphnia, Ch = Chydorus, Co = Corixidae, Cr = Chironomidae, Cy = Cyclops, Da = Daphnia, Dp = Diaptomus, Ds = Diaphanosoma, F = Fish (unidentified), H = Hydracarina, K = Keratella, L = Leptodora, Na = Nauplii, Od = Odonata, Os = Ostracod, R = Rotifer, and T = Trichoptera. Approach is adapted (lower left panel) from Chipps and Garvey (2007) and Amundsen *et al.* (1996) as first described by Costello (1990)



complete overlap, a value of 0 indicates no overlap, and a value of 0.6 or greater is considered biologically significant, suggesting a potential for prey resource competition (Morisita, 1959). Percent diet overlap was calculated by multiplying Morisita's value ( $C$ ) by 100.

#### STABLE ISOTOPES

In the laboratory fish samples were thawed, heads and digestive tracts were removed, and bodies were rinsed in distilled water. Zooplankton samples were thawed, centrifuged to separate zooplankton from phytoplankton, and rinsed with distilled water. Benthic invertebrate samples were rinsed with distilled water. Samples were dried at 60 C for 72 h, ground into a fine powder using a mortar and pestle, and weighed out into 2.5 mg samples ( $\pm 0.1$  mg). Samples were sent to the South Dakota State University Mass Spectrometry Laboratory to determine  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  ratios using a continuous flow, stable isotope mass spectrometer coupled to an elemental analyzer. Stable isotope units were expressed in delta ( $\delta$ ) notation, as parts per thousand (‰) relative to the international standard for that isotope,

$$\delta^{15}\text{N} \text{ or } \delta^{13}\text{C}(\text{‰}) = \left( \frac{R_{\text{sample}} - R_{\text{standard}}}{R_{\text{standard}}} \right) \times 1000$$

where  $R$  is the ratio of the heavier isotope to the lighter isotope, or for this experiment,  $R = \text{N}^{15}/\text{N}^{14}$  and  $R = \text{C}^{13}/\text{C}^{12}$  for  $\delta^{15}\text{N}$  (‰) and  $\delta^{13}\text{C}$  (‰), respectively (Peterson and Fry, 1987). Nitrogen was standardized against atmospheric nitrogen gas and carbon was standardized against the Pee Dee limestone deposit (Peterson and Fry, 1987). Precision for nitrogen was  $\pm 0.3\text{‰}$  and precision for carbon was  $\pm 0.2\text{‰}$  based on laboratory flour and fish standards.

Isotope biplots allowed interpretation of the diet source ( $\delta^{13}\text{C}$  on the x-axis) and relative trophic position ( $\delta^{15}\text{N}$  on the y-axis) of fishes (*see* Table 1 for numbers of each species used in stable isotope analysis). An increase of approximately 3.4‰ in  $\delta^{15}\text{N}$  corresponds to an increase of one trophic level (Peterson and Fry, 1987). The  $\delta^{13}\text{C}$  values indicate energy pathways that distinguish between pelagic (more negative) and benthic sources (more positive) in freshwater systems (France, 1995). To test for changes through time, we used independent  $t$ -tests (assuming unequal variance) to detect shifts in  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  signatures from Aug. to Sep. for each species within each lake ( $\alpha = 0.05$ ). Independent  $t$ -tests (assuming unequal variance) were conducted within each lake and month combination to test for differences ( $\alpha = 0.05$ ) in  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  signatures between each native species and carp and tablewise Bonferonni adjustments were made for multiple comparisons.

## RESULTS

### RELATIVE ABUNDANCE

We collected between 0 (bluegill during Jul.) and 702 (bluegill in Aug.) individuals per species and month from Brant Lake during 2008 (Table 1). Differences in CPUE of juvenile fishes among species in Brant Lake during 2008 depended on month ( $F_{4,10} = 29.41$ ,  $P < 0.0001$ ). In Jul. carp were more abundant than yellow perch ( $t = 2.87$ ,  $P = 0.04$ ) and bluegill ( $t = 3.01$ ,  $P = 0.03$ ) and marginally more abundant than orangespotted sunfish ( $t = 2.20$ ,  $P = 0.08$ ; Fig. 2A). In Aug. carp were more abundant than black crappie ( $t = 4.11$ ,  $P = 0.001$ ) and orangespotted sunfish ( $t = 4.41$ ,  $P = 0.007$ ) and marginally more abundant than yellow perch ( $t = 2.08$ ,  $P = 0.09$ ; Fig. 2A).

In 2009 we collected between 2 (black crappie in Sinai during Sep.) and 655 (bluegills in Brant during Aug.) individuals per species, month, and lake. Relative abundance of juvenile fishes in Brant Lake differed among species ( $F_{4,10} = 23.59$ ,  $P < 0.0001$ ) but not between

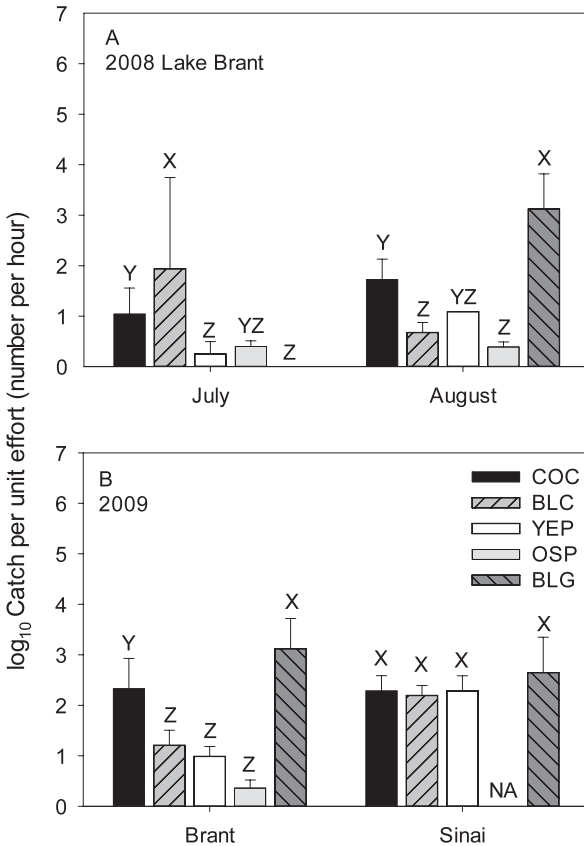


FIG. 2.—Mean catch per unit effort (number per hour  $\pm$  1SE) of common carp, black crappie, yellow perch, orangespotted sunfish, and bluegill captured in Brant Lake during 2008 (A) and lakes Brant and Sinai during 2009 (B). Different letters represent significant differences within a month or lake. Significance was determined at  $\alpha = 0.05$ . NA = not available

months ( $F_{1,10} = 0.30$ ,  $P = 0.59$ ) or among combinations of species and month ( $F_{4,10} = 0.78$ ,  $P = 0.56$ ). Carp were more abundant than black crappie ( $t = 3.32$ ,  $P = 0.008$ ), yellow perch ( $t = 4.52$ ,  $P = 0.001$ ), and orangespotted sunfish ( $t = 5.99$ ,  $P = 0.0001$ ; Fig. 2B) in Brant Lake but relative abundance was similar among species ( $F_{3,6} = 0.47$ ,  $P = 0.71$ ) and between months ( $F_{1,6} = 1.07$ ,  $P = 0.34$ ) in Lake Sinai.

DIET COMPOSITION

A total of 201 fish were processed from collections in Jul. (88) and Aug. (113) of 2008 for diet analysis (Table 1). Between 14 and 30 individuals were used per species and month. With the exception of bluegill when no individuals were collected during Jul., the mean difference in number of fish per species processed for diet analysis between months was  $1.3 \pm 0.6$  SE. Of these fish, only three had empty stomachs and were not used in diet analysis. Bluegill were not collected because larvae were likely still pelagic (Werner and Hall, 1988). Carp, bluegill, black crappie, and yellow perch (but not orangespotted sunfish) typically

exhibited a mixed feeding strategy, generalizing on a large number of prey types, whereas individuals or populations (within a lake and month) displayed specialization on particular prey. In Brant Lake during Jul. 2008, *Daphnia* was a prominent prey item for all fishes, occurring in 93% of all fish diets (78–100% by species) and representing 39–56% of prey specific abundance (Fig. 1). Total zooplankton density in Jul. samples was 419.4 ( $\pm 159.2$  SE) individuals/L and *Daphnia* density was 104.9 ( $\pm 27.4$  SE) individuals/L. In Jul. carp were generalists and *Daphnia* composed 51% of 78% of Brant Lake carp diets (Fig. 1). Most prey items were rare in carp or consumed in low abundances, but some individual carp (22%) specialized on Trichoptera (Fig. 1). Black crappie displayed a consistent feeding pattern, where *Daphnia* was the predominant prey item (41% of the diet), some individuals (10%) appeared to specialize on Ostracods, and other prey taxa were consumed in low relative abundance or were rare (Fig. 1). Yellow perch also displayed a feeding pattern where *Daphnia* were important (39% of the diets) and most other taxa were consumed in low to moderate relative abundance (Fig. 1). Orangespotted sunfish consumed a large proportion (56% of the diets of 90% of the sample population) of *Daphnia* (Fig. 1) while other prey items were consumed in low relative abundance by the Brant Lake sample population (<21% of diets) or by a few individuals (Trichoptera, 15% of the population; Fig. 1).

In Aug. *Daphnia* became a less important dietary component for many fishes, whereas Cyclops occurred in 94% of all diets (57–100% by species) and represented 2–87% of prey-specific abundance. Total zooplankton density in Aug. was 333.8 ( $\pm 47.5$  SE) individuals/L and *Daphnia* density declined nearly fourfold from Jul. densities to 24.2 ( $\pm 5.9$  SE) individuals/L. Carp specialized on Trichoptera, which was a dominant prey item, whereas Cyclops and Chydorus were consumed in lower abundances (Fig. 1). Black crappie displayed a population feeding pattern in which *Diaptomus* and Cyclops each represented nearly 50% of the prey consumed by the sample population and *Daphnia* was consumed in low abundance (Fig. 1). Yellow perch exhibited an individual feeding pattern where individuals consumed a wide variety of prey (Fig. 1). Corixidae was the dominant prey type for approximately 60% of yellow perch, while one individual (7% of perch evaluated) specialized on fish (species unknown; Fig. 1). Orangespotted sunfish specialized in Cyclops, which was the dominant prey type and accounted for 87% of the diet for the sample population (Fig. 1). Bluegills also specialized on Cyclops (65% of the diet for the population) as the dominant prey type (Fig. 1).

#### DIET OVERLAP

High diet overlap occurred in Brant Lake in Jul. when *Daphnia* was the most prevalent prey type but decreased in Aug. as carp and yellow perch progressed through ontogenetic diet shifts toward more varied diets. In Jul. a high degree of diet overlap existed among all species, ranging from 87% to 98%, with carp diet overlap with other species ranging from 87% to 95% (Table 2). In Aug. carp and native fishes tended to partition prey resources. Diet overlap between carp and native fishes decreased to 3% to 15% in Aug. (Table 2). Yellow perch diet overlap with Centrarchids also decreased in Aug., ranging from 9% to 16% (Table 2). Dietary overlap among Centrarchids remained high in Aug., ranging from 67% to 97% (Table 2).

#### STABLE ISOTOPES

During Aug. 2009 a total of 99 fish were processed for stable isotope analysis (49 from Brant Lake and 50 from Lake Sinai); during Sep., a total of 66 fish were processed (34 from Brant Lake and 32 from Lake Sinai; Table 1). In Brant Lake  $\delta^{15}\text{N}$  signatures of carp, yellow perch, and black crappie did not change from Aug. to Sep. (Table 3), indicating they were

TABLE 2.—Percent diet overlap (Morisita's C values  $\times$  100) for Brant Lake fishes collected in Jul. and Aug. 2008. COC = common carp, BLC = black crappie, BLG = bluegill, OSP = orangespotted sunfish, and YEP = yellow perch. NA = not available

Fish combination	Percent diet overlap	
	Jul.	Aug.
COC $\times$ BLC	95	9
COC $\times$ BLG	NA	15
COC $\times$ OSP	87	15
COC $\times$ YEP	93	3
BLC $\times$ BLG	NA	80
BLC $\times$ OSP	95	67
BLC $\times$ YEP	98	16
BLG $\times$ OSP	NA	97
BLG $\times$ YEP	NA	9
OSP $\times$ YEP	96	9

feeding at a similar trophic level during each month. However, bluegill  $\delta^{15}\text{N}$  signatures became more positive, though the differences were not indicative of a full trophic level shift (Fig. 3; difference  $<3.4\%$ ). In contrast  $\delta^{13}\text{C}$  signatures of all species became less negative from Aug. to Sep. (Table 3; Fig. 3). In Aug.  $\delta^{13}\text{C}$  signatures were similar between carp and bluegill and between common carp and yellow perch (Table 4), indicating all three species used similar prey resources in Brant Lake in Aug. (Fig. 3). The only significant differences in  $\delta^{15}\text{N}$  signatures in Brant Lake occurred between bluegill and carp and yellow perch and carp (Table 4), though the differences were not indicative of a full trophic level shift (difference  $<3.4\%$ ). In Sep. there were no significant differences in either  $\delta^{13}\text{C}$  or  $\delta^{15}\text{N}$  signatures between native species and carp (Table 4).

In Lake Sinai  $\delta^{13}\text{C}$  signatures were significantly higher in Sep. for bluegill and carp (Table 3; Fig. 3), indicating a higher reliance on benthic invertebrates. There were no significant changes in  $\delta^{13}\text{C}$  signatures for black crappie or yellow perch between months, but bluegill and yellow perch both exhibited decreased  $\delta^{15}\text{N}$  values in Sep. (Table 3; Fig. 3). During Aug. in Lake Sinai,  $\delta^{13}\text{C}$  signatures of black crappie and bluegill were different compared to carp, whereas yellow perch and carp  $\delta^{13}\text{C}$  signatures were similar (Table 4; Fig. 3). Carp exhibited statistically significant differences in  $\delta^{15}\text{N}$  signatures when

TABLE 3.—Two-tailed independent *t*-test results comparing  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  isotopic signatures between Aug. and Sep. of 2009 for each species within each lake. Significant P-values are indicated by an \* ( $\alpha = 0.05$ ). BLC = black crappie, BLG = bluegill, COC = common carp, and YEP = yellow perch

	Species	Brant lake		Lake sinai	
		<i>t</i> -statistic	P-value	<i>t</i> -statistic	P-value
$\delta^{13}\text{C}$ (‰)	BLC	-5.44	0.00*	-2.24	0.27
	BLG	-5.46	0.00*	-7.70	0.00*
	COC	-2.54	0.02*	-2.52	0.02*
	YEP	-5.97	0.00*	0.07	0.95
$\delta^{15}\text{N}$ (‰)	BLC	-0.54	0.60	0.22	0.86
	BLG	-2.27	0.03*	5.55	0.00*
	COC	-2.04	0.06	-1.36	0.19
	YEP	-0.72	0.48	2.58	0.02*

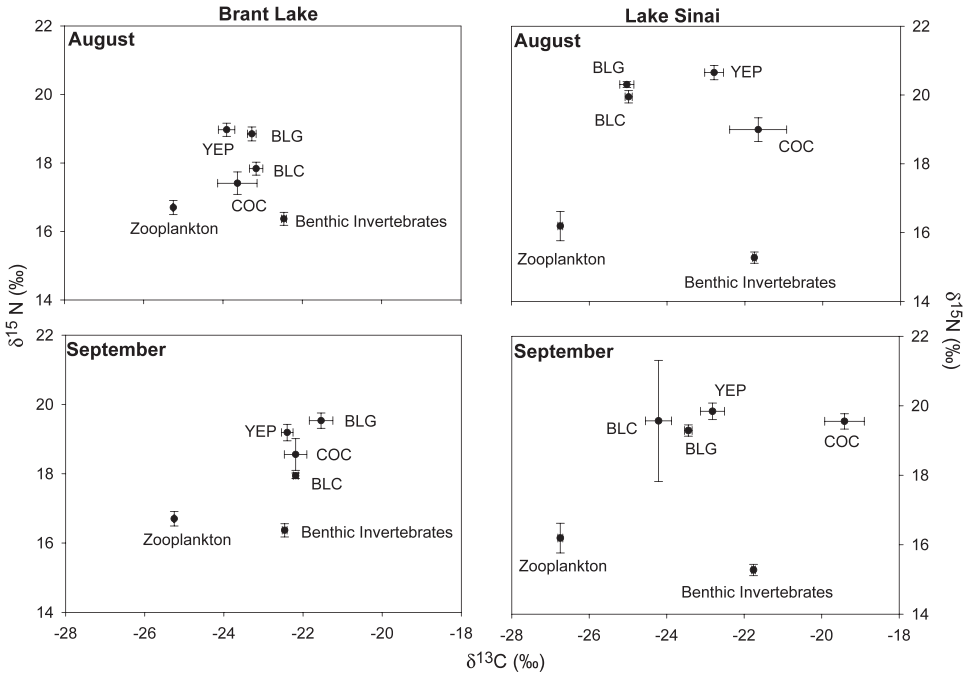


FIG. 3.—Stable isotope signatures ( $\delta^{15}\text{N}$  and  $\delta^{13}\text{C}$ ; mean  $\pm 1$  SE) for potential food sources (zooplankton and benthic invertebrates) and fishes collected in 2009 from Brant Lake (left) and Lake Sinai (right) in Aug. (top) and Sep. (bottom). BLG = bluegill, BLC = black crappie, COC = common carp, YEP = yellow perch

TABLE 4.—Two-tailed independent *t*-test results comparing  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  signatures of native species to common carp  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  signatures, respectively, in each lake each month. An \* indicates a significant difference in  $\delta^{13}\text{C}$  or  $\delta^{15}\text{N}$  signatures ( $\alpha = 0.017$ )

		Brant lake		Lake sinai		
Species		<i>t</i> -statistic	P-value	<i>t</i> -statistic	P-value	
$\delta^{13}\text{C}$ (‰)	Aug.	BLC $\times$ COC	1.12	0.28	2.45	0.03
		BLG $\times$ COC	3.73	0.00*	3.68	0.00*
		YEP $\times$ COC	4.12	0.00*	4.12	0.00*
	Sep.	BLC $\times$ COC	-1.32	0.24	0.01	1.00
		BLG $\times$ COC	1.92	0.09	-0.97	0.35
		YEP $\times$ COC	1.23	0.25	0.89	0.39
$\delta^{15}\text{N}$ (‰)	Aug.	BLC $\times$ COC	0.9	0.39	-4.52	0.00*
		BLG $\times$ COC	0.72	0.49	-4.48	0.00*
		YEP $\times$ COC	-0.5	0.62	-1.47	0.17
	Sep.	BLC $\times$ COC	0.01	1.00	-7.85	0.00*
BLG $\times$ COC		1.57	0.14	-7.73	0.00*	
YEP $\times$ COC		-0.66	0.52	-5.69	0.00*	

compared to each of black crappie, bluegill, and yellow perch (Table 4), but the changes were not large enough to indicate a difference in trophic level (Fig. 3). In Sep. there were differences in carp  $\delta^{13}\text{C}$  signatures compared to bluegill and yellow perch but not compared to black crappie (Table 4). There were no significant differences in  $\delta^{15}\text{N}$  between native species and carp (Table 4; Fig. 3).

#### DISCUSSION

Juvenile fishes (introduced and native) often occupy similar niches and consume similar prey items, which may result in interspecific competition (Matthews *et al.*, 1992; Sutton and Ney, 2002). Comparisons of resource use between native and introduced species can help predict potential interactions among species and mechanisms of biotic resistance (Carey and Wahl, 2010). However, despite their utility, food web approaches are rarely used to inform and guide efforts to understand, manage, and restore invaded aquatic ecosystems (Vander Zanden *et al.*, 2003). Here, we outline potential food web effects of juvenile carp on native fishes.

Juvenile carp were as or more abundant than native fishes in Jul. and Aug. and initially relied extensively on zooplankton. High dietary overlap (87–93%) existed between carp and native fishes during Jul. when carp and native species relied primarily on *Daphnia*. Although diet analyses were conducted on different numbers of individuals across species and months, a relatively large ( $\geq 14$ ) number of individuals per species were evaluated in both Jul. and Aug. 2008. Thus, our results are likely reflective of these fish populations at large. Age-0 individuals of carp (Tonkin *et al.*, 2006), yellow perch (Mills *et al.*, 1984), and black crappie (Pope and Willis, 1998) often prefer *Daphnia* to other zooplankton when gape size permits and, as a result, may compete for this prey resource. In addition to diet overlap, juvenile carp, yellow perch, bluegill, and black crappie use similar habitats in shallow lakes (Weber and Brown, 2012a) and in this study were collected in similar habitats, thus increasing the likelihood of competitive interactions. Prey availability is often an important determinant of growth, survival, and recruitment during early life stages (Cushing, 1990; Weber *et al.*, 2011). Fishes foraging on *Daphnia* may experience higher growth and survival during early life stages compared to those foraging on alternative, smaller zooplankton (Graeb *et al.*, 2004). However, *Daphnia* are highly vulnerable to predation and their densities may be greatly reduced by larval and juvenile fishes (Mills *et al.*, 1987; Khan *et al.*, 2003), forcing fishes to switch to alternative prey.

*Daphnia* density declined nearly fourfold from Jul. to Aug. in Brant Lake in 2008, coinciding with the time period when most age-0 fishes switched to consuming either alternative zooplankton taxa or benthic invertebrates. Carp generally exhibit an ontogenetic diet shift to benthic taxa at 100 mm fork length (Britton *et al.*, 2007) to 150 mm TL (Kahn, 2003). However, in Brant Lake, carp diets shifted from *Daphnia* in Jul. to Trichoptera in Aug., when individual fish ranged between 30 and 58 mm TL. Similarly in Aug. 70 mm TL yellow perch switched their dominant prey type from zooplankton to benthic invertebrates (Corixidae). Such ontogenetic diet shifts are typically beneficial because energy return is higher for macroinvertebrates and often increases growth rates of juvenile fishes (Graeb *et al.*, 2005). We did not evaluate benthic invertebrate densities in Brant Lake during 2008, but the timing of the ontogenetic shifts may have coincided with increases in availability of this prey type. In contrast to diet shifts by carp and yellow perch, Centrarchids (black crappies, bluegills, and orangespotted sunfish) remained primarily zooplanktivorous in Aug., consuming *Diaptomus* and *Cyclops* as their dominant prey types. Because the three Centrarchids continued to consume similar zooplankton prey during Aug., diet overlap

among these fishes remained relatively high. Other studies have indicated that juvenile sunfishes share similar prey resources and may experience competition (Werner and Hall, 1977; Collingsworth and Kohler, 2010). In contrast the increased diversity of prey types consumed by carp and native fishes in Aug. resulted in decreased diet overlap. Transitions between developmental stages, as mouth gape increases and individuals are able to diversify their diets, may lead to decreased dietary overlap among some species (Matthews *et al.*, 1992; Sutton and Ney, 2002; Probst and Eckmann, 2009). Although diet overlap between carp and native fishes was very low in Aug., consumption rates increase as juvenile fishes become larger (Tonkin *et al.*, 2006). Thus, even species having low diet overlap may compete for increasingly limited resources (Persson, 1987; Deus and Petrere-Junior, 2003).

Because we collected diet analysis and stable isotope samples in different years, direct comparisons between the two approaches were not possible. However, stable isotope analysis provided a time-integrated perspective, showing greater spatial and temporal diversity of prey use by juvenile fishes in 2009, which indicated that juvenile fishes came to rely more on benthic invertebrates later in the year. In Brant Lake in 2009, isotopic signatures for juvenile fishes showed a more distinct transition from zooplankton to benthic invertebrates as compared to Lake Sinai, where less pronounced shifts were due to high variation in isotopic signatures among fishes. Shifts less than a full trophic level were likely biologically insignificant. Rapid shifts in isotopic signatures, reflecting ontogenetic diet shifts, are common in age-0 fishes due to high turnover rates of tissues in young individuals (typically 8–18 d; Weidel *et al.*, 2011). Similarity among  $\delta^{13}\text{C}$  signatures of all fishes in Brant Lake during both Aug. and Sep. suggests that all fishes were using similar prey resources. In comparison carp in Lake Sinai had less negative  $\delta^{13}\text{C}$  signatures than did native fishes during both months, suggesting carp consistently relied more on benthic invertebrate prey. Differences in isotopic signatures reflecting differences in consumption patterns for juvenile fishes between lakes Brant and Sinai may also reflect differences in prey resource availability, habitat types, or foraging conditions. Although we collected zooplankton and benthic invertebrates for isotopic analysis, we did not evaluate densities of either prey group in either lake to test this hypothesis. However, regardless of the mechanism, extant lake differences in resource use by juvenile fishes are likely an important predictor for interactions between carp and native species.

Invasive species can have multiple, complex effects on ecosystems and native fishes (Weber and Brown, 2009). Characterization of food webs can engender a more complete understanding of food web linkages between native and invasive species and have implications for restoration of native species and invaded ecosystems. Diet data provided a detailed snapshot of juvenile fish diets whereas stable isotopes revealed what resources were assimilated over longer temporal periods (8–18 d; Weidel *et al.*, 2011). Diet overlap indicated that shared resources between carp and native fishes can be high, but change temporally, whereas stable isotopes indicated that shared resources among these species can fluctuate monthly and among lake populations. Although resource overlap provides an approach to quantify commonalities of prey among fishes (Schoener, 1971; Schleuter and Eckmann, 2007), high resource overlap does not provide direct evidence that carp compete with native fishes for those resources (Pianka, 1974; Porter and Dueser, 1982), as competition can only occur when resources are limiting (Wiens, 1977). Thus, future research should explore ecological conditions that are likely to result in competition among these species.

*Acknowledgements.*—We thank S. Chipps for diet analysis insights and M. Hennen, K. Rounds, B. Johnson, C. Funk, A. Wiering and C. Mortensen for assistance in the field and laboratory. We thank



D. Clay, S. Hansen, and the SDSU Soils Laboratory for assistance with stable isotope samples and analysis. Partial funding for this project was provided by the Griffith Undergraduate Research Award through the Agricultural Experiment Station at South Dakota State University and through the Federal Aid in Sport Fish Restoration Act Study 1513 (Project F-15-R-42) administered by the South Dakota Department of Game, Fish, and Parks.

## LITERATURE CITED

- AMUNDSEN, P. A., H. M. GABLER, AND F. J. STALDVIK. 1996. A new approach to graphical analysis of feeding strategy from stomach contents data – modification of the Costello (1990) method. *J. Fish Biol.*, **48**:607–614.
- BENKE, A. C., A. D. HURYN, L. A. SMOCK, AND J. B. WALLACE. 1999. Length-mass relationships for freshwater macroinvertebrates in North America with particular reference to the southeastern United States. *J. N. Am. Benthol. Soc.*, **18**:308–343.
- BRITTON, J. R., R. R. BOAR, J. GREY, J. FOSTER, J. LUGONZO, AND D. M. HARPER. 2007. From introduction to fishery dominance: the initial impacts of the invasive carp *Cyprinus carpio* in Lake Naivasha, Kenya, 1999 to 2006. *J. Fish Biol.*, **71**:239–257.
- CAREY, M. P. AND D. H. WAHL. 2010. Native fish diversity alters the effects of an invasive species on food webs. *Ecology*, **91**:2965–2974.
- CHIPPS, S. R. AND J. E. GARVEY. 2007. Assessment of diets and feeding patterns, p. 473–514. In: C. S. Guy and M. L. Brown (eds.). *Analysis and Interpretation of Freshwater Fisheries Data*. American Fisheries Society, Bethesda, Maryland, U.S.A.
- COLLINGSWORTH, P. D. AND C. C. KOHLER. 2010. Abundance and habitat use of juvenile sunfish among different macrophyte stands. *Lake Reservoir Manage.*, **26**:35–42.
- COSTELLO, M. J. 1990. Predator feeding strategy and prey importance: a new graphical analysis. *J. Fish Biol.*, **36**:261–263.
- CRIVELLI, A. J. 1983. The destruction of aquatic vegetation by carp: a comparison between southern France and the United States. *Hydrobiol.*, **106**:37–41.
- CULVER, D. A., M. M. BOUCHERLE, D. J. BEAN, AND J. W. FLETCHER. 1985. Biomass of freshwater crustacean zooplankton from length-weight regressions. *Can. J. Fish. Aquat. Sci.*, **42**:1380–1390.
- CUSHING, D. H. 1990. Plankton production and year class strength in fish populations: an update of the match/mismatch hypothesis. *Adv. Mar. Biol.*, **26**:249–293.
- DEUS, C. P. AND M. PETRERE-JUNIOR. 2003. Seasonal diet shifts of seven fish species in an Atlantic rainforest stream in southeastern Brazil. *Braz. J. Biol.*, **63**:579–588.
- FISHER, S. J. AND D. W. WILLIS. 1997. Early life history of yellow perch in two South Dakota glacial lakes. *J. Freshwat. Ecol.*, **12**:421–429.
- FRANCE, R. L. 1995. Differentiation between littoral and pelagic food webs in lakes using stable carbon isotopes. *Limnol. Oceanogr.*, **40**:1310–1313.
- GRAEB, B. D. S., J. M. DETTMERS, D. H. WAHL, AND C. E. CACERES. 2004. Fish size and prey availability affect growth, survival, prey selection, and foraging behavior of larval yellow perch. *T. Am. Fish. Soc.*, **133**:504–514.
- , T. GALAROWICZ, D. H. WAHL, J. M. DETTMERS, AND M. J. SIMPSON. 2005. Foraging behavior, morphology, and life history variation determine the ontogeny of piscivory in two closely related predators. *Can. J. Fish. Aquat. Sci.*, **62**:1–11.
- JACKSON, Z. J., M. C. QUIST, J. A. DOWNING, AND J. G. LARSCHEID. 2010. Common carp (*Cyprinus carpio*), sport fishes, and water quality: Ecological thresholds in agriculturally eutrophic lakes. *Lake Reservoir Manage.*, **26**:14–22.
- KAHN, T. A. 2003. Dietary studies on exotic carp (*Cyprinus carpio* L.) from two lakes of western Victoria, Australia. *Aquat. Sci.*, **65**:272–286.
- , M. E. WILSON, AND M. T. KAHN. 2003. Evidence for invasive cap mediated trophic cascade in shallow lakes of western Victoria, Australia. *Hydrobiol.*, **506–509**:465–472.
- KOEHN, J. D. 2004. Carp (*Cyprinus carpio*) as a powerful invader in Australian waterways. *Freshwat. Biol.*, **49**:882–894.
- KREBS, C. J. 1989. *Ecological Methodology*. Harper and Row Publishers, New York. 654 p.



- LOWE, S., M. BROWNE, S. BOUDJELAS, AND M. DE POORTER. 2004. 100 of the world's worst invasive alien species: a selection from the Global Invasive Species Database. Auckland, New Zealand: The Invasive Species Specialist Group, World Conservation Union.
- MATTHEWS, W. J., F. P. GELWICK, AND J. J. HOOVER. 1992. Food of and habitat use by juveniles of species of *Micropterus* and *Morone* in a southwestern reservoir. *T. Am. Fish. Soc.* **121**:54–66.
- MEIJER, M.-L., E. H. R. R. LAMMENS, A. J. P. RAAT, M. P. GRIMM, AND S. H. HOSPER. 1990. Impact of cyprinids on zooplankton and algae in ten drainable ponds. *Hydrobiol.* **191**:275–284.
- MILLER, H. C. 1963. The behavior of the pumpkinseed sunfish, *Lepomis gibbosus* (Linnaeus), with notes on the behavior of other species of *Lepomis* and the pigmy sunfish, *Elassoma evergladei*. *Behaviour*, **22**:88–151.
- MILLS, E. L., J. L. CONFER, AND R. C. READY. 1984. Prey selection by young yellow perch: the influence of capture success, visual acuity, and prey choice. *T. Am. Fish. Soc.* **113**:579–587.
- , J. L. FORNEY, AND K. J. WAGNER. 1987. Fish predation and its cascading effect on the Oneida Lake food chain, p. 118–131. *In*: W. C. Kerfoot and A. Sih (eds.). *Predation: Direct and Indirect Impacts on Aquatic Communities*. University Press of New England.
- MITTELBACH, G. G. 1984. Predation and resource partitioning in two sunfishes (Centrarchidae). *Ecology*, **65**:499–513.
- MORISITA, M. 1959. Measuring of interspecific association and similarity between communities. *Mem. Fac. Sci. Kyushu Univ. Ser. E*, **3**:65–80.
- PANEK, F. M. 1987. Biology and ecology of carp, p. 1–5. *In*: *Carp in North America*. E. L. Cooper (ed.) American Fisheries Society. Bethesda, Maryland.
- PARKER, I. M., D. SIMBERLOFF, W. M. LONSDALE, K. GOODELL, W. WONHAM, P. M. KAREIVA, M. H. WILLIAMSON, B. VON HOLLE, P. B. MOYLE, J. E. BYERS, AND L. GOLDWASSER. 1999. Impact: towards a framework for understanding the ecological effects of invaders. *Biol. Invasions*, **1**:3–19.
- PARKOS, J. J., III, V. J. SANTUCCI, JR, AND D. H. WAHL. 2003. Effects of adult common carp (*Cyprinus carpio*) on multiple trophic levels in shallow aquatic ecosystems. *Can. J. Fish. Aquat. Sci.* **60**:182–192.
- PERSSON, L. 1987. Competition-induced switch in young of the year perch, *Perca fluviatilis*: an experimental test of resource limitation. *Environ. Biol. Fish.*, **19**:235–239.
- PETERSON, B. J. AND B. FRY. 1987. Stable isotopes in ecosystem studies. *Annu. Rev. Ecol. Syst.*, **18**:293–320.
- PHELPS, Q. E., B. D. S. GRAEB, AND D. W. WILLIS. 2008. First year growth and survival of common carp in two glacial lakes. *Fish. Manage. Ecol.*, **15**:85–91.
- PIANKA, E. R. 1974. Niche overlap and diffuse competition. *P. Natl. Acad. USA*, **71**:2141–2145.
- POPE, K. L. AND D. W. WILLIS. 1998. Early life history and recruitment of black crappie (*Pomoxis nigromaculatus*) in two South Dakota waters. *Ecol. Freshwat. Fish*, **7**:56–68.
- PORTER, J. H. AND R. D. DUESER. 1982. Niche overlap and competition in an insular small mammal fauna: a test of the niche overlap hypothesis. *Oikos*, **39**:228–236.
- PROBST, W. N. AND R. ECKMANN. 2009. Diet overlap between young-of-the-year perch, *Perca fluviatilis* L., and burbot, *Lota lota* (L.), during early life-history stages. *Ecol. Freshwat. Fish*, **18**:527–537.
- RAHMAN, M. M., M. Y. HOSSAIN, Q. JO, S. KIM, J. OHTOMI, AND C. MEYER. 2009. Ontogenetic shift in dietary preference and low dietary overlap in rohu (*Labeo rohita*) and common carp (*Cyprinus carpio*) in semi-intensive polyculture ponds. *Ichthyol. Res.*, **56**:28–36.
- SCHLEUTER, D. AND R. ECKMANN. 2007. Generalist versus specialist: the performances of perch and ruffe in a lake of low productivity. *Ecol. Freshwat. Fish*, **17**:86–99.
- SCHOENER, T. W. 1971. Theory of feeding strategies. *Annu. Rev. Ecol. Syst.*, **2**:396–404.
- SIVAKUMARAN, K. P., P. BROWN, D. STOESSEL, AND A. GILES. 2003. Maturation and reproductive biology of female wild carp, *Cyprinus carpio*, in Victoria, Australia. *Environ. Biol. Fish.*, **68**:321–332.
- ST. SAUVER, T., D. LUCCHESI, B. JOHNSON, K. HOFFMANN, AND J. STAHL. 2009. Statewide fisheries surveys. 2009: Surveys of public waters. South Dakota Department of Game, Fish and Parks Annual Report F-21R-42. Project 2102. Pierre.
- STEIN, R. A., D. R. DEVRIES, AND J. M. DETTMERS. 1995. Food-web regulation by a planktivore - exploring the generality of the trophic cascade hypothesis. *Can. J. Fish. Aquat. Sci.* **52**:2518–2526.
- SUTTON, T. M. AND J. J. NEY. 2002. Trophic resource overlap between age-0 striped bass and largemouth bass in Smith Mountain Lake, Virginia. *N. Am. J. Fish. Manage.* **22**:1250–1259.

- TONKIN, Z. D., P. HUMPHRIES, AND P. A. PRIDMORE. 2006. Ontogeny of feeding in two native and one alien fish species from the Murray-Darling Basin, Australia. *Environ. Biol. Fish.*, **76**:303–315.
- VANDER ZANDEN, M. J., S. CHANDRA, B. C. ALLEN, J. E. REUTER, AND C. R. GOLDMAN. 2003. Historical food web structure and restoration of native aquatic communities in the Lake Tahoe (California-Nevada) basin. *Ecosystems*, **6**:274–288.
- WEBER, M. J. AND M. L. BROWN. 2013a. Spatiotemporal variation of juvenile common carp foraging patterns as inferred from stable isotope analysis. *Trans. Am. Fish. Soc.*, **142**:1179–1191.
- . 2013b. Density-dependence and environmental conditions regulate recruitment and first year-growth of common carp in shallow lakes. *Trans. Am. Fish. Soc.*, **142**:471–482.
- . 2012a. Diel and temporal habitat use of four juvenile fishes in a complex glacial lake. *Lake Reservoir Manage.*, **28**:120–129.
- . 2012b. Maternal effect of common carp *Cyprinus carpio* on fecundity and energy content. *J. Freshwat. Ecol.*, doi 10.1080/02705060.2012.666890.
- . 2011. Relationships among invasive common carp, native fishes, and physicochemical characteristics in upper Midwest (U.S.A.) lakes. *Ecol. Freshwat. Fish.*, **20**:270–278.
- . 2009. Effects of common carp on aquatic ecosystems 80 years after 'Carp as a dominant': Ecological insights for fisheries management. *Rev. Fish. Sci.*, **17**:1–14.
- , J. M. DETTMERS, AND D. H. WAHL. 2011. Growth and survival of age-0 yellow perch across habitats in southwestern Lake Michigan: early life history in a large freshwater environment. *T. Am. Fish. Soc.*, **140**:1172–1185.
- , M. J. HENNEN, AND M. L. BROWN. 2011. Simulated population responses of common carp to commercial exploitation. *N. Am. J. Fish. Manage.*, **31**:269–279.
- WEIDEL, B. C., S. R. CARPENTER, J. F. KITCHELL, AND M. J. VANDER ZANDEN. 2011. Rates and components of carbon turnover in fish muscle: insights from bioenergetics models and a whole-lake <sup>13</sup>C addition. *Can. J. Fish. Aquat. Sci.*, **68**:387–399.
- WERNER, E. E. AND D. J. HALL. 1988. Habitat shifts in bluegill: the foraging rate-predation risk trade-off. *Ecology*, **69**:1352–1366.
- . 1977. Competition and habitat shift in two sunfishes (Centrarchidae). *Ecology*, **58**:869–876.
- WIENS, J. A. 1977. On competition and variable environments. *Am. Sci.*, **65**:590–597.
- WOLDA, H. 1981. Similarity indices, sample size, and diversity. *Oecologia*, **50**:296–302.
- WOLFE, M. D., V. J. SANTUCCI, JR., L. M. EINFALT, AND D. H. WAHL. 2009. Effects of common carp on reproduction, growth, and survival of largemouth bass and bluegills. *T. Am. Fish. Soc.*, **138**:975–983.