

## TEMPORAL AND SIZE-RELATED TRENDS IN FOOD HABITS OF INTRODUCED WESTERN MOSQUITOFISH AND NATIVE TOPMINNONS

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**ABSTRACT.** Western mosquitofish (*Gambusia affinis*) are stocked in Indiana waters for the biological control of mosquitoes. However, this species has the potential to negatively impact native fishes. We examined the food habits and diet overlap of adult western mosquitofish, northern starhead topminnow (*Fundulus dispar*), northern studfish (*F. catenatus*), blackstripe topminnow (*F. notatus*), and banded killifish (*F. diaphanus*) in Indiana from April through October 2005 to evaluate trophic resource use by month and body length. Food habits for each species were similar, with the largest percentage of the diet composed of zooplankton (Cladocera) and non-culicid diptera (Chironomidae and Ceratopogonidae). There was no trend in the percentage of culicids (mosquito larvae) consumed by species, regardless of month and body length (range, 0–27%). Diet overlap index values between western mosquitofish and the topminnow species were high but there was no clear trend, regardless of month (range, 0.25–0.87) or body length category (range, 0.49–0.83). Because food habits for the fishes examined in this study were similar and there exists the high potential for negative behavioral impacts by western mosquitofish, we do not recommend stocking this species into Indiana waters that contain native topminnows.

**Keywords:** Western mosquitofish, Northern starhead topminnow, Northern studfish, Blackstripe topminnow, Banded killifish, Food habits, Diet overlap

The introduction of non-native fishes can lead to large-scale changes in aquatic communities (Fuller et al. 1999). However, long-term impacts to community structure resulting from these introductions are often unknown (Bonar et al. 2005). On a global scale, introductions of non-native fishes are one of the primary causes for ongoing declines of native fishes (Simberloff 2004; Vitule et al. 2008). These introductions may have far-reaching consequences, and can lead to the extirpation of native species (Rogowski & Stockwell 2006; Vitule et al. 2008).

The western mosquitofish (*Gambusia affinis*), and its congener the eastern mosquitofish (*G. holbrooki*), are the most widely distributed larvivorous fishes in the world (Courtenay

and Meffe 1989). These species were broadly stocked outside their native distribution for mosquito control and often outcompete native fishes for habitat and trophic resources (Fuller et al. 1999; Rehage et al. 2005; Laha & Mattingly 2007; Matthews & Marsh-Matthews 2011). Although mosquitofish are efficient at mosquito control (Hoy and Reed 1971; Bence 1988), more recent studies suggest that they do not preferentially prey on mosquito larvae and that native fishes may more effectively control mosquitoes (Castleberry and Cech 1990; Blaustein 1992; Hurst et al. 2004). As a result, there is a need to evaluate the food habits of introduced mosquitofish relative to other native fishes.

Topminnows occupy a similar ecological niche as mosquitofish and are often negatively impacted by introductions of this species (Meffe 1985; Laha & Mattingly 2007). For example, when Sonoran topminnows (*Poeciliopsis occidentalis sonoriensis*) were exposed to western mosquitofish in laboratory experiments, the topminnows ceased to feed, retreated to areas with structure to escape aggression

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Table 1.—Fish species collected at Indiana sites from April - October 2005, and associated site numbers for Figure 1. Species are western mosquitofish (MSQ), blackstripe topminnow (BST), northern studfish (NSF), northern starhead topminnow (NST), and banded killifish (BAK).

Site number	Site name	Latitude	Longitude	Fish species	System type	Land-use type
1	Loomis Lake	41.5200° N	87.0550° W	NST	Lake	Fallow Fields
2	Pine Lake	41.6203° N	86.7478° W	NST	Lake	Fallow Fields/ Residential
3	Upper Fish Lake	41.5714° N	86.5439° W	NST	Lake	Fallow Fields/ Residential
4	Silver Lake	41.6303° N	85.0644° W	BAK	Lake	Fallow Fields/ Residential
5	Golden Lake	41.6037° N	85.0650° W	BST	Lake	Residential
6	Lake Wawasee	41.4006° N	85.7022° W	BAK	Lake	Residential
7	Waubee Lake	41.3875° N	85.8292° W	BAK	Lake	Fallow Fields/ Residential
8	Moots Creek	40.5378° N	86.7804° W	BST	Stream	Agriculture
9	Martell Forest Pond	40.4534° N	87.0542° W	MSQ	Pond	Fallow Fields/Forest
10	Greenfield Bayou	39.1930° N	87.3237° W	MSQ	Wetland	Fallow Fields/ Agriculture
11	Connelly Ditch	39.1524° N	87.0908° W	MSQ	Stream	Agriculture
11	Connelly Ditch	39.1524° N	87.0908° W	BST	Stream	Agriculture
12	Sugar Creek	39.3043° N	85.5812° W	NSF	Stream	Fallow Fields/Forest
13	Flatrock River	39.2149° N	85.5118° W	NSF	River	Fallow Fields/Forest
14	Lewis Creek	39.2355° N	85.4938° W	NSF	Stream	Fallow Fields/Forest

and predation, and experienced declines in growth, increases in mortality, and reductions in reproductive potential (Schoenherr 1981). Sutton et al. (2009, 2013) found that western mosquitofish initiated agonistic behaviors (i.e., chases and nips) on four native Indiana topminnow species (banded killifish [*Fundulus diaphanus*], northern studfish [*F. catenatus*], northern starhead topminnow [*F. dispar*], and blackstripe topminnow [*F. notatus*]) and caused changes in topminnow behavior in mixed-species microcosms. The first three topminnow species have restricted ranges in Indiana, while the latter species is ubiquitous throughout the state.

We evaluated the food habits of populations of introduced western mosquitofish and four species of native Indiana topminnows to determine similarity in prey consumption. We examined: (1) temporal and size-related patterns in food habits; (2) the percent consumption of mosquitoes in the diet; and (3) temporal and size-related patterns in diet overlap. This research will allow greater understanding of how western mosquitofish could potentially impact native topminnows in Indiana if they were to co-occur in the same aquatic systems.

## METHODS

Western mosquitofish and topminnows were collected from Indiana waters from April through October 2005 (Table 1; Figure 1). Fish sampling was conducted monthly at three sites per species (14 sites total; one site was sampled for two species each month). The wetland site (Greenfield Bayou) contained silt substrate and no aquatic vegetation, and only supported western mosquitofish. The pond site (Martell Forest Pond) contained silt substrate and coontail (*Ceratophyllum demersum*), and the dominant fish species was green sunfish (*Lepomis cyanellus*). Lake-edge sites contained gravel, sand, and silt substrates and supported water lilies (*Nymphaea* spp.), with the exception of Waubee Lake and Lake Wawasee which lacked aquatic vegetation. These sites contained diverse fish assemblages, with the most abundant species being bluegill (*L. macrochirus*), largemouth bass (*Micropterus salmoides*), and various minnow species. Stream and river-edge sites contained silt and gravel substrates and supported diverse fish assemblages, and were dominated by native minnows. Regardless of sampling site, fish were always collected in shallow water habitats,

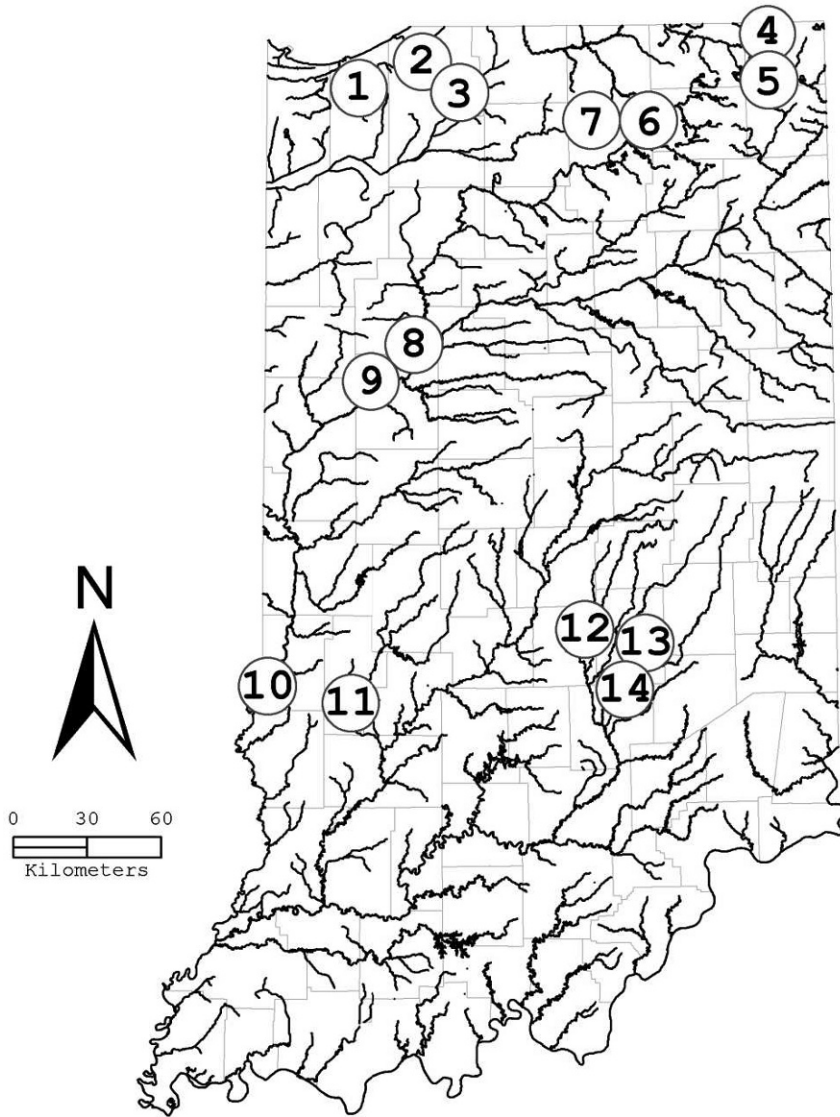


Figure 1.—Map of Indiana, with field sites sampled from April through October 2005 identified by the three-letter abbreviation. For the name of each site, see TABLE 1.

either backwater or side channels in stream and river-edge sites with no flow or shoreline areas of wetland, pond, and lake sites. Habitat types supporting these fishes were similar among sites.

A maximum of 20 adult fish of each species was collected each month from each sampling site. Sampling gears included a 3.18-mm mesh seine (length: 3.05 m; depth: 1.22 m) and a 3.18-mm mesh dip net (diameter: 40 cm). Fish were euthanized with an overdose of tricaine methanesulfonate and placed on ice to slow the

digestion of stomach contents. In the laboratory, fish were measured for total length to the nearest 0.05 mm, weighed to the nearest 0.01 g, and fixed in 10% formalin pending laboratory analysis of stomach contents.

Stomach contents were extracted from each fish, blotted to remove excess formalin, and weighed to the nearest 0.0001 g. Consumed prey were examined under 2.5 X magnification with a stereomicroscope, and individual items were identified to family for diptera and order for all other prey types. The percentage of each

consumed prey type in relation to the entire stomach contents for each fish was recorded as the percent composition by weight following methods described in Garvey and Chipps (2012). Stomach contents were further analyzed to determine the proportion of mosquito (Culicidae) larvae consumed by fish species. To facilitate examination of trends in food habits, data from all three sampling sites for each fish species were combined for each sampling month because stomach contents did not differ for each species among sites (Chi Square, all  $P > 0.08$ ). Because there was no difference in stomach contents between males and females for each species (Chi Square, all  $P > 0.24$ ), both sexes were pooled for all analyses for each species.

The diets of western mosquitofish were compared each month and by 5-mm total-length category to the diets of each topminnow species using Schoener's diet overlap index (1970):

$$C_{xy} = 1 - 0.5 \left( \sum |p_{xi} - p_{yi}| \right),$$

where  $C_{xy}$  was the index value,  $p_{xi}$  was the proportion of food type  $i$  consumed by species  $x$ , and  $p_{yi}$  was the proportion of food type  $i$  consumed by species  $y$ . Calculated values ranged from 0.0 (no diet overlap) to 1.0 (complete diet overlap for consumed prey). Although this index cannot be used to make statistical comparisons of diet, index values greater than 0.60 indicate significant prey consumption overlap (Schoener 1970).

## RESULTS

A total of 1,816 fish was collected from April through October 2005. Western mosquitofish ( $n = 394$ ) had a mean length of 32.25 mm and a mean weight of 0.54 g. Northern starhead topminnows ( $n = 346$ ) were larger than mosquitofish, with a mean length of 40.16 mm and a mean weight of 0.88 g. Both blackstripe topminnows ( $n = 370$ ) and banded killifish ( $n = 287$ ) were similar in size to northern starhead topminnows. Blackstripe topminnows had a mean length of 42.63 mm and a mean weight of 0.98 g, while banded killifish had a mean length of 46.98 mm and a mean weight of 1.21 g. Northern studfish ( $n = 417$ ) were the largest species, with a mean length of 49.71 mm and a mean weight of 2.01 g.

Non-culicid diptera (primarily chironomidae and ceratopogonidae) dominated the prey items

consumed by topminnows and western mosquitofish each month (Figure 2). For northern starhead topminnows, non-culicid diptera comprised 34% of the diet, with the highest consumption in April (51%), May (47%), and October (61%). The highest percentage of culicid diptera consumed by this species occurred in May (23%) and September (18%). For northern studfish, non-culicid diptera comprised at least 40% of the diet each month, except during July and August when ephemeroptera, coleoptera, and other prey items (gastropods and nematodes) accounted for the majority of consumed prey items. The highest percentage of culicid diptera consumption for northern studfish occurred in April (20%) and August (10%). Non-culicid diptera comprised at least 38%, and coleoptera and hymenoptera comprised at least 25% of the stomach contents for blackstripe topminnows, regardless of month. Culicid diptera comprised their highest percentage of the diet in April (17%) for this species. Cladocera and non-culicid diptera composed the largest percentages of prey consumed by western mosquitofish (33 and 34%, respectively). The highest percentages of culicid diptera were consumed by this species in May (27%) and June (18%). Banded killifish consumed variable percentages of cladocera and non-culicid diptera, with the greatest consumption of non-culicid diptera in June. Culicid diptera were always a low percentage component of the diet for banded killifish.

Diet composition of topminnows and western mosquitofish varied by length category, but largely consisted of non-culicid diptera (chironomidae and ceratopogonidae) and zooplankton (mostly cladocera; Figure 3). The percentage of zooplankton consumed by northern starhead topminnows declined for larger fish, whereas the percentage of non-culicid diptera remained high for individuals  $> 30$  mm. More culicid diptera were consumed by this topminnow than any other species at lengths of 25 mm (17%) and 30 mm (21%). Nearly half of the prey items (49%) in northern studfish diets were comprised of non-culicid diptera, but the percentage of ephemeroptera and hemiptera consumed increased with fish length. This topminnow species consumed its highest percentage of culicid diptera at 20 mm in length (18%). Although most sizes of blackstripe topminnows contained similar percentages of prey items, non-culicid diptera comprised more

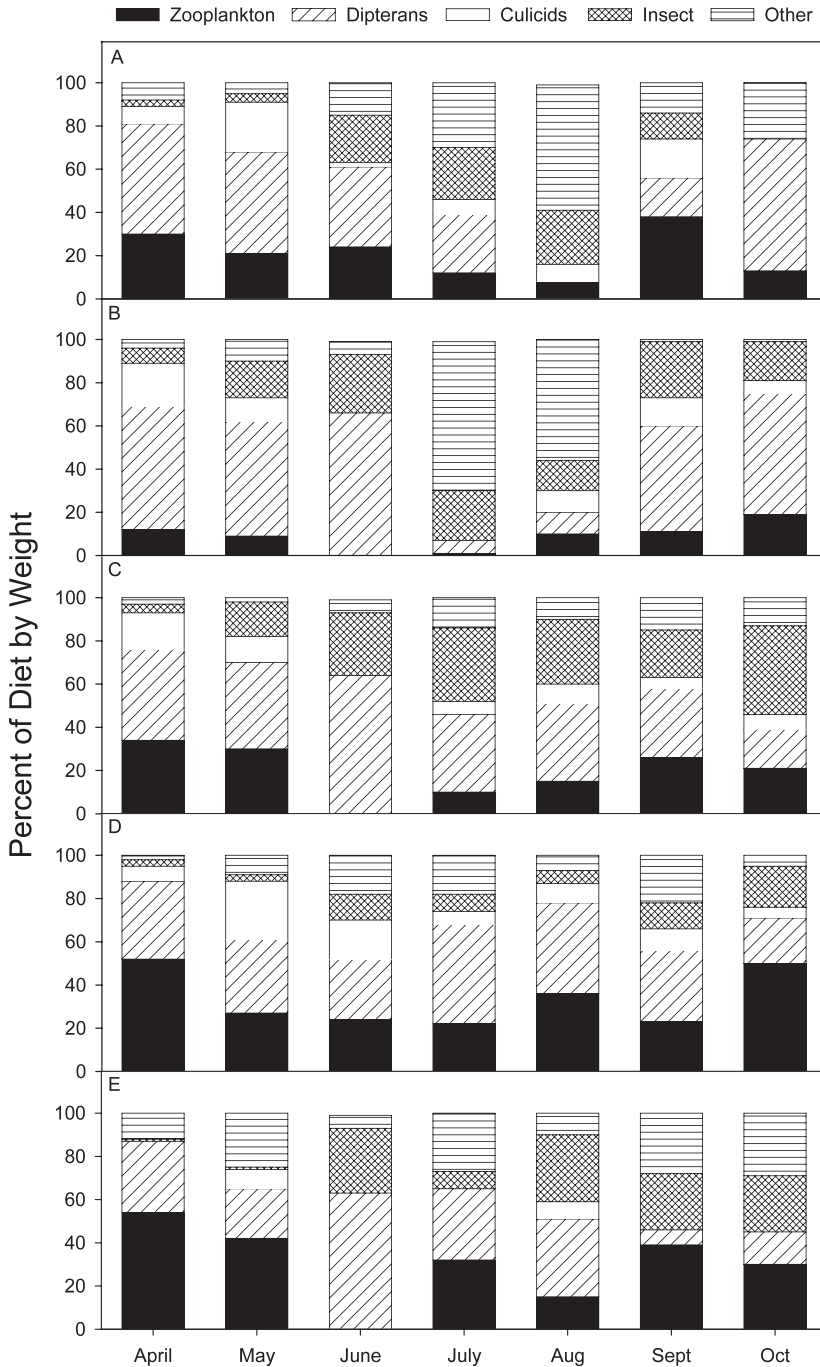


Figure 2.—Percent of diet by weight for (A) northern starhead topminnows, (B) northern studfish, (C) blackstripe topminnows, (D) western mosquitofish, and (E) banded killifish each month.

than half (55%) of the diet for 25-mm fish. Length classes for this species that consumed the most culicid diptera ranged from 35 to 45 mm (10% to 13%). Western mosquitofish of size 20

to 30 mm consumed similar percentages of zooplankton and non-culicid diptera (42% and 36%, respectively), but these prey items composed a lower dietary percentage for fish 35 to

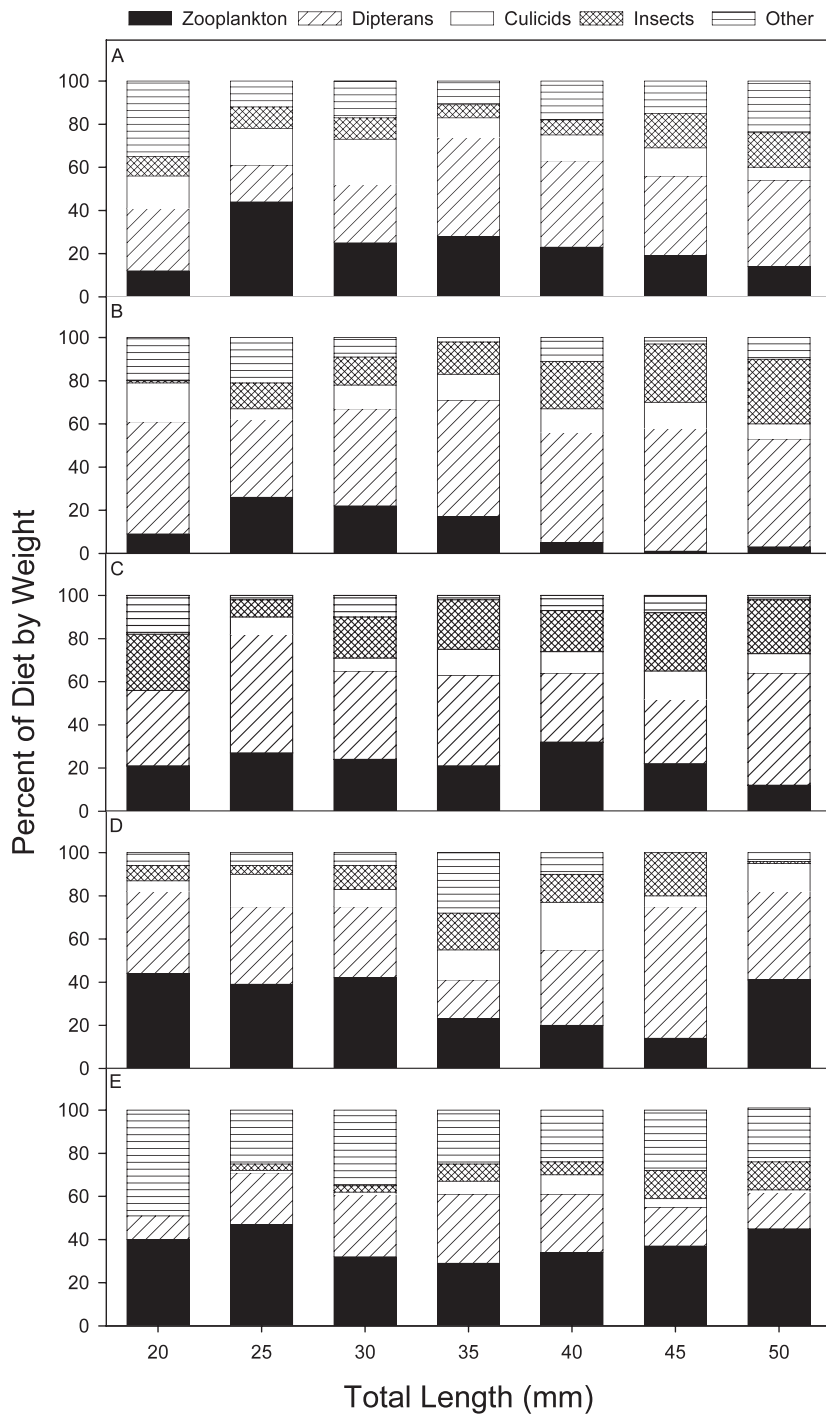


Figure 3.—Percent of diet by weight for (A) northern starhead topminnows, (B) northern studfish, (C) blackstripe topminnows, (D) western mosquitofish, and (E) banded killifish in each size category.

40 mm (mean = 22% and 27%, respectively). Non-culicid and culicid diptera were consumed at higher percentages by 35 (28% and 14%, respectively) and 40 mm (51% and 22%, respectively) fish. Banded killifish consumed mostly zooplankton (38%), except 20-mm fish where other prey items (amphipods) were the primary prey type (49%). Culicid diptera never comprised more than 9% of the diet for any length class of banded killifish.

There was no clear trend in diet overlap between western mosquitofish and topminnows from April through October 2005 (Table 2). Although no species pairings had significant diet overlap ( $> 0.60$ ) for all months, western mosquitofish and blackstripe topminnows had significant overlap for all months except June (0.47). Diet overlap of western mosquitofish with banded killifish, northern starhead topminnows, and northern studfish was significant for five, four, and three months, respectively. The only month where diet overlap was significant between western mosquitofish and all topminnow species was May.

Diet overlap between western mosquitofish and topminnows did not follow a clear length-related trend (Table 3). For the 25- through 40-mm length categories, diet overlap was significant for all mosquitofish-topminnow pairings. Only the western mosquitofish-blackstripe topminnow pairing had significant diet overlap for all size categories. Diet overlap was not significant for the smallest and/or largest size categories between western mosquitofish and northern starhead topminnow (20 mm), northern studfish (20 and 50 mm), and banded killifish (20 and 45 mm).

## DISCUSSION

The food habits documented in this study for western mosquitofish and native Indiana topminnows are similar to the results of dietary studies reported for mosquitofish species in other evaluations. Although western mosquitofish consume culicids, they often consume other insects, small crustaceans, arachnids, and rotifera (Pflieger 1997). Eastern mosquitofish will switch from mosquitoes to other prey types with availability (Jenkins and Burkhead 1994). Northern starhead topminnows consumed insects, chironomidae, crustaceans, plant material, and algae, while blackstripe topminnows often ingested large percentages of insects, molluscs, cladocera, and copepods (Gunning

and Lewis 1955; Schwartz and Hasler 1966). Northern studfish utilized more ephemeroptera, trichoptera, gastropods, and pelecypoda than other fish species, but also consumed diptera, nematodes, and coleoptera (McCaskill et al. 1972; Fisher 1981). Banded killifish consumed a variety of prey items, including small crustaceans, amphipods, cladocera, nematodes, chironomidae, and plant material (Becker 1983). All fishes examined in our study also consume terrestrial insects at the water surface (Becker 1983; Pflieger 1997), which was observed in our analyses.

Prey availability may be more important in prey selection of mosquitofish and topminnow than preferences for particular food items. For example, differences in the diet composition of mummichogs (*Fundulus heteroclitus*) reflected prey availability, regardless of habitat type occupied by this species (James-Pirri et al. 2001). In California rice fields, western mosquitofish reduced the abundance of mosquitoes, but preference for this prey type diminished in the presence of abundant zooplankton (Bence 1988). Native topminnows, such as the Plains killifish (*Fundulus zebrinus*), consumed mosquito larvae at rates equal to mosquitofish in outdoor mesocosms (Nelson and Keenan 1992). Prey availability data were not collected during this study, but it is well documented that fish are opportunistic feeders (Specziar 2004; Hinz et al. 2005; Quist et al. 2006). As a result, the lack of preference for mosquito larvae by western mosquitofish and similarity in food habits among the five species examined in this study may be more a function of availability rather than predilection for particular prey types.

Similarities in feeding strategies, behavior, and habitat use for western mosquitofish and topminnows may increase their potential for high niche overlap. All species examined in this study have an upturned mouth and flattened head to facilitate prey consumption at the water surface (Pflieger 1997). All five species occur at shallow depths ( $< 15$  cm) near aquatic vegetation, with the exception of banded killifish and northern studfish which occur over gravel and sand substrates devoid of plant material. These similarities could facilitate interspecific competition when they co-occur. For example, western mosquitofish and blackstripe topminnows were often collected during this study in the same seine haul from Connelly Ditch, indicating co-occurrence in the same system.

Table 2.—Diet overlap values for April - October 2005 between western mosquitofish (MSQ) and blackstripe topminnow (BST), northern studfish (NSF), northern starhead topminnow (NST), and banded killifish (BAK).

Month	MOSQ- BST	MOSQ- NSF	MOSQ- NST	MOSQ- BAK
April	0.81	0.59	0.77	0.87
May	0.77	0.62	0.83	0.68
June	0.47	0.47	0.74	0.47
July	0.70	0.25	0.56	0.64
August	0.70	0.41	0.26	0.69
September	0.72	0.66	0.63	0.54
October	0.67	0.64	0.35	0.66

Both western and eastern mosquitofish have been shown to negatively impact native fish species where resource overlap is high. For example, western mosquitofish had a significant negative effect on the abundance and biomass of the threatened White Sands pupfish (*Cyprinodon tularosa*; Rogowski and Stockwell 2006). Sympatric populations of western mosquitofish and blackstripe topminnows in Indiana were observed to consume similar prey items, indicating the potential for high diet overlap between these two species (Clem and Whitaker 1995). In our study, the similarity in food habits (i.e., high diet overlap) indicates that these fishes have the potential for significant competition in prey consumption. The high similarity in food habits, coupled with the aggressive behaviors that western mosquitofish exhibit towards other fishes (Schoenherr, 1981; Laha and Mattingly 2007; Sutton et al. 2009,

Table 3.—Diet overlap values by length category between western mosquitofish (MSQ) and blackstripe topminnow (BST), northern studfish (NSF), northern starhead topminnow (NST), and banded killifish (BAK). Length categories were 20 (20.01–25 mm), 25 (25.01–30.0 mm), 30 (30.01–35.0 mm), 35 (35.01–35.0 mm), 40 (40.01–45.0 mm), 45 (45.01–50.0 mm), and 50 (50.01–55.0 mm) mm.

Size Category	MOSQ- BST	MOSQ- NSF	MOSQ- NST	MOSQ- BAK
20	0.63	0.56	0.53	0.54
25	0.77	0.75	0.75	0.71
30	0.79	0.79	0.72	0.67
35	0.70	0.64	0.64	0.64
40	0.81	0.70	0.82	0.72
45	0.69	0.83	0.72	0.49
50	0.64	0.55	0.62	0.60

2013), suggest that introductions of this species could lead to deleterious results for native Indiana topminnows.

The potential impacts of western mosquitofish on native Indiana topminnows proposed in this study need to be interpreted with caution because rarely was the former species found in the same systems as topminnows. Western mosquitofish were only found at one site (Connelly Ditch) during this study that also contained a native topminnow species (blackstripe topminnow). Diet overlap between these two species at this site was high (month: range, 0.53–0.86; length: range, 0.60 to 0.85; Zeiber 2007), suggesting that the potential for trophic competition is also high. Although western mosquitofish are native to southern and southwestern Indiana, they have been stocked throughout much of the state to reduce West Nile Virus *Flavivirus* transmission by mosquitoes (G. Polston, Marion County Health Department, personal communication). As a result, the potential for trophic competition is high and could result in niche shifts due to changes in behavior and/or prey/habitat utilization, which may have deleterious effects on native Indiana topminnows as has been shown in other studies (Schaeffer et al. 1994; Arthington and Marshall 1999; Fuller et al. 1999; Rehage et al. 2005; Laha and Mattingly 2007; Matthews & Marsh-Matthews 2011). Additional research is required to determine if these potential impacts will lead to realized outcomes if western mosquitofish are introduced or escape into aquatic systems in Indiana which currently support topminnow species.

Western mosquitofish and the Indiana topminnows examined in this study appear to be trophic equivalents and have nearly identical habitat requirements. These similarities, coupled with the unknown potential impacts of resource competition and aggressive and deleterious behaviors often exhibited by mosquitofish toward topminnows, make it likely that western mosquitofish would negatively impact topminnow species in Indiana waters if they co-occurred in the same aquatic system. We do not recommend stocking mosquitofish into permanent or even ephemeral water bodies where the possibility of escapement by mosquitofish into nearby waterways exists. If there is a need for mosquito control in Indiana waters, we suggest that blackstripe topminnow be considered as an alternative to western mosquitofish because



they are the most trophically similar topminnow species in Indiana. Sutton et al. (2012) observed that blackstripe topminnows exhibited almost no aggressive behaviors toward northern starhead topminnows, northern studfish, and banded killifish and did not change the behavior of these fishes in laboratory evaluations. However, this recommendation also requires additional research to ensure that blackstripe topminnows would not negatively impact other fishes if introduced into aquatic systems in which they are not native.

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#### LITERATURE CITED

- Arthington, A.H. & C.J. Marshall. 1999. Diet of the exotic mosquitofish *Gambusia holbrooki* in an Australian lake and potential for competition with indigenous fish species. *Asian Fisheries Science* 12:1–16.
- Becker, G.C. 1983. *The Fishes of Wisconsin*. The University of Wisconsin Press, Madison, Wisconsin.
- Bence, J.R. 1988. Indirect effects and biological control of mosquitoes by mosquitofish. *Journal of Applied Ecology* 25:505–521.
- Blaustein, L. 1992. Larvivorous fishes fail to control mosquitoes in experimental rice plots. *Hydrobiologia* 232:219–232.
- Bonar, S.A., B.D. Bolding, M. Divens & W. Meyer. 2005. Effects of introduced fishes on wild juvenile coho salmon in three shallow Pacific Northwest lakes. *Transactions of the American Fisheries Society* 134:641–652.
- Castleberry, D.T. & J.J. Cech, Jr. 1990. Mosquito control in wastewater: a controlled and quantitative comparison of pupfish (*Cyprinodon nevadensis amargosae*), mosquitofish (*Gambusia affinis*) and guppies (*Poecilia reticulata*) in sago pondweed marshes. *Journal of the American Mosquito Control Association* 6:223–228.
- Clem, P.D. & J.O. Whitaker, Jr. 1995. Distribution of the mosquitofish, *Gambusia affinis* (Baird & Girard), in Indiana, with comments on resource competition. *Proceedings of the Indiana Academy of Sciences* 104:249–258.
- Courtenay, W.R. & G.K. Meffe. 1989. Small fishes in strange places: a review of introduced poeciliids. Pp. 319–331. *In Ecology and evolution of livebearing fishes (Poeciliidae)* (G.K. Meffe & F.F. Snelson, eds.). Prentice Hall, New Jersey.
- Fisher, J.W. 1981. Ecology of *Fundulus catenatus* in three interconnected streams. *American Midland Naturalist* 106:372–378.
- Fuller, P.L., L.G. Nico & J.D. Williams. 1999. Nonindigenous fishes introduced into inland waters of the United States. *American Fisheries Society, Special Publication* 27, Bethesda, Maryland.
- Garvey, J.E. & S.R. Chipps. 2012. Diets and energy flow. Pp. 733–779. *In Fisheries Techniques*, Third Edition (A.V. Zale, D.L. Parrish & T.M. Sutton, eds.). American Fisheries Society, Bethesda, Maryland.
- Gunning, G.E. & W.M. Lewis. 1955. The fish population of a spring-fed swamp in the Mississippi bottoms of southern Illinois *Ecology*: 36:552–558.
- Hinz, H., I. Kroencke & S. Ehrich. 2005. The feeding strategy of dab *Limanda limanda* in the southern North Sea: linking stomach contents to prey availability in the environment. *Journal of Fish Biology* 67:125–145.
- Hoy, J.B. & D.E. Reed. 1971. The efficacy of mosquitofish for control of *Culex tarsalis* in California rice fields. *Mosquito News* 31:567–572.
- Hurst, T.P., M.D. Brown & B.H. Kay. 2004. Laboratory evaluation of the predation efficacy of native Australian fish on *Culex annulirostris* (Diptera: Culicidae). *Journal of the American Mosquito Control Association* 20:286–291.
- James-Pirri, M.J., K.B. Raposa & J.G. Catena. 2001. Diet composition of mummichogs *Fundulus heteroclitus*, from restoring and unrestricted regions of a New England (U.S.A.) salt marsh. *Estuarine, Coastal, and Shelf Science* 53:205–213.
- Jenkins, R.E. & N.M. Burkhead. 1994. *Freshwater fishes of Virginia*. American Fisheries Society, Bethesda, Maryland.
- Laha, M. & H.T. Mattingly. 2007. Ex situ evaluation of impacts of invasive mosquitofish on the imperiled Barrens topminnow. *Environmental Biology of Fishes* 78:1–11.
- Matthews, W.J. & E. Marsh-Matthews. 2011. An invasive fish species within its native range: community effects and population dynamics of

- Gambusia affinis* in the central United States. *Freshwater Biology* 56:2609–2619.
- McCaskill, M.L., J.E. Thomerson & P.R. Mills. 1972. Food of the northern studfish, *Fundulus catenatus*, in the Missouri Ozarks. *Transactions of the American Fisheries Society* 96:70–74.
- Meffe, G.K. 1985. Predation and species replacement in American southwest fishes: a case study. *The Southwestern Naturalist* 30:173–187.
- Nelson, S.M. & L.C. Keenan. 1992. Use of an indigenous fish species *Fundulus zebrinus*, in a mosquito abatement program: a field comparison with the mosquitofish, *Gambusia affinis*. *Journal of the American Mosquito Control Association* 8:301–304.
- Pflieger, W.L. 1997. *The Fishes of Missouri*. Missouri Department of Conservation, Jefferson City, Missouri.
- Quist, M.C., M.R. Bower & W.A. Hubert. 2006. Summer food habits and trophic overlap of roundtail chub and creek chub in Muddy Creek, Wyoming. *Southwestern Naturalist* 51:22–27.
- Rehage, J.S., B.K. Barnett & A. Sih. 2005. Behavioral responses to a novel predator and competitor of invasive mosquitofish and their non-invasive relatives (*Gambusia* sp.). *Behavioral Ecology and Sociobiology* 57:256–266.
- Rogowski, D.L. & C.A. Stockwell. 2006. Assessment of population impacts of exotic species on populations of a threatened species, White Sands pupfish, *Cyprinodon tularosa*. *Biological Invasions* 18:79–87.
- Schaefer, J.F., S.T. Heulett & T.M. Farrell. 1994. Interactions between two poeciliid fishes (*Gambusia holbrooki* and *Heterandia formosa*) and their prey in a Florida marsh. *Copeia* 2:516–520.
- Schoenherr, A.A. 1981. The role of competition in the replacement of native fishes by introduced species. Pp. 173–203. In *Fishes in North American Deserts* (R.J. Naiman & D.L. Soltz, eds.). John Wiley, New York, New York.
- Schwartz, E. & A.D. Hasler. 1966. Perception of surface waves by the blackstripe topminnow, *Fundulus notatus*. *Journal of Fisheries Research Board of Canada* 23:1331–1352.
- Simberloff, D. 2004. A rising tide of species and literature: a review of some recent books on biological invasions. *BioScience* 54:247–254.
- Specziar, A. 2004. Life history pattern and feeding ecology of the introduced eastern mosquitofish, *Gambusia holbrooki*, in a thermal spa under temperate climate, of Lake Heviz, Hungary. *Hydrobiologia* 522:249–260.
- Sutton, T.M., R.A. Zeiber & B.E. Fisher. 2009. Mesocosm evaluation of western mosquitofish impacts on northern starhead topminnows. *Proceedings of the Indiana Academy of Sciences* 118:88–95.
- Sutton, T.M., R.A. Zeiber & B.E. Fisher. 2012. Behavioral interactions between blackstripe topminnow and other native Indiana topminnows. *Proceedings of the Indiana Academy of Sciences* 121:62–70.
- Sutton, T.M., R.A. Zeiber & B.E. Fisher. 2013. Agonistic behavioral interactions between introduced western mosquitofish and topminnows. *Journal of Freshwater Ecology* 28:1–16.
- Vitule, J.R.S., C.A. Freire & D. Simberloff. 2008. Introduction of non-native freshwater fish can certainly be bad. *Fish and Fisheries* 10:98–108.
- Zeiber, R.A. 2007. Effects of western mosquitofish on Indiana aquatic communities. Master's thesis, Purdue University, West Lafayette, Indiana.
- Zeiber, R.A., T.M. Sutton & B.E. Fisher. 2008. Western mosquitofish predation on native amphibian eggs and larvae. *Journal of Freshwater Ecology* 23:663–671.

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