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ARTICLE

Live-bait industry as a pathway for movement of nonnative and invasive species: Implications for conservation of native Texas fishes

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Abstract

Objective: Live-bait species are widely used in recreational fishing throughout the United States. However, the use of invasive fish species as live bait has been identified as a common pathway for their introduction into aquatic ecosystems. We assessed the role that the live-bait industry has in facilitating the introduction of nonnative and invasive species into Texas rivers. We focused on two invasive cyprinodontid species, the Sheepshead Minnow *Cyprinodon variegatus* and Gulf Killifish *Fundulus grandis*, which are believed to have been introduced into inland Texas rivers via bait-bucket releases by anglers.

Methods: We conducted telephone and in-person surveys of live-bait shops in Texas on a seasonal basis (summer, fall, winter, spring) for 1 year. Locally owned bait shops and regional aquaculture facilities and hatcheries were included in the surveys.

Result: Surveys did not reveal the presence of these invasive cyprinodontids in inland bait shops but did reveal the sale of nonnative Goldfish *Carassius auratus* and their black color morph, the black salty goldfish. Surveys conducted among inland and coastal live bait shops confirmed the sale of only one nonnative bait fish and six bait items native only to certain regions of Texas. Telephone surveys with aquaculture industry experts revealed that the aquaculture industry was also facilitating the movement of nonnative game and nongame fish species throughout the state.

Conclusion: Given the potential for nonnative and invasive species to negatively affect recipient aquatic ecosystems, the continued distribution of such species within the aquaculture industry represents a potential threat in Texas. Our findings highlight the need for close monitoring of the live-bait industry in the state to prevent further introductions into inland waters and reduce potential ecological risks to native fish populations and overall ecosystem functions and services.

KEYWORDS
cyprinodontids, imperiled species, inland fisheries, nonindigenous species, riparian and stream

INTRODUCTION

The use of live bait by anglers has resulted in the introduction of aquatic invasive species throughout the United States, resulting in both ecological and economic effects on recipient communities (LoVullo and Stauffer 1993). The live-bait trade represents one major pathway of introduction because invasive species are often unknowingly

transported and sold by retail bait shops (Kilian et al. 2012; Nathan et al. 2014). Up to 97% of retailers are unable to identify the species sold by their business or the status (native versus nonnative) of those species (DiStefano et al. 2009). This knowledge gap results in aquatic invasive species being sold directly to anglers for recreational purposes. Once purchased, anglers can facilitate the movement of invasive live baits within or across watershed boundaries by disposing of unused bait in surrounding waters (Nathan et al. 2014). Although regulations are often in place to prevent the improper disposal of live bait, anglers are often unaware of such regulations or they believe that the release of unused bait is beneficial to the surrounding ecosystem (Kilian et al. 2012). Once released, nonnative bait species can establish populations that could damage recipient environments and native species (Cucherousset and Olden 2011; Kilian et al. 2012). Therefore, to prevent these introductions, nonnative bait species must be detected and stopped before reaching anglers' bait buckets.

Regulations concerning the import, export, and sale of bait species vary greatly from state to state, making it difficult for live-bait industry vendors to stay in compliance (Cohen 2012; Gunderson 2019). Even within state boundaries, regulations are not always followed by licensed bait dealers due to a lack of knowledge on species identification and local regulations (LoVullo and Stauffer 1993; Nathan et al. 2014; Passarelli and Pernet 2019). Understanding which live-bait species are sold and distributed across states is critical for developing effective regulations and public education campaigns to prevent the introduction of invasive bait species (Keller and Lodge 2007; Kilian et al. 2012). In Texas, recreational fishing in inland waters may represent a source of introduction for invasive species via bait-bucket releases (Howells 2001). However, research assessing the live-bait industry as a potential pathway of introduction is lacking in Texas. Despite this information gap, there are several fish species that are believed to have been introduced into Texas rivers via bait-bucket releases (Hillis et al. 1980; Echelle and Connor 1989; Hubbs et al. 2008). Two of these fishes are cyprinodontids: the Gulf Killifish *Fundulus grandis* and the Sheepshead Minnow *Cyprinodon variegatus* (Hillis et al. 1980; Echelle and Connor 1989). Both species are native to coastal areas within Texas and have been introduced into various freshwater basins throughout the state (Hillis et al. 1980; Echelle and Connor 1989). The introduction of the Gulf Killifish into the Pecos River resulted in drastic declines in its native congener, the Plains Killifish *Fundulus zebrinus*, due to competition for food and direct predation (Cheek and Taylor 2016; Vaughan et al. 2016). Similarly, after being introduced into both the Pecos River and Lake Balmorhea, the Sheepshead Minnow hybridized with two native congeners, the Pecos Pupfish *Cyprinodon pecosensis* and the Comanche Springs Pupfish *Cyprinodon elegans*, thus precipitating their decline (Echelle and Connor 1989; Echelle and Echelle 1994).

Impact statement

The use of live bait in recreational fishing has been identified as a pathway for introduction of invasive species because they are often unknowingly transported and sold by retail bait shops and introduced bait-bucket releases. Surveys on inland and coastal live-bait shops in Texas were conducted over 1 year to learn about potential pathways of introduction of invasive coastal fishes (i.e., cyprinodontids) on to inland waters. While invasive cyprinodontids were not being sold as a live bait, other nonnative species were sold and being moved across the state. These results can be utilized by natural resource agencies to continue monitoring the live-bait industry in the state to prevent further introductions into inland waters and reduce the potential ecological risks to native fish populations.

With the discovery of Sheepshead Minnow populations in the Brazos River at Possum Kingdom Reservoir, Texas, in 2011 (Wilde 2015) and the discovery of Gulf Killifish in the Wichita River, Texas, in 2016 (Robertson et al. 2019), it has become necessary to assess the live-bait industry as a potential pathway of continued introduction for these and other nonnative fishes. Both the Sheepshead Minnow and the Gulf Killifish pose major threats to their native congeners, the Red River Pupfish *Cyprinodon rubrofluviatilis* and the Plains Killifish, but there is a lack of information and quantitative data to support the live-bait pathway as the likely means of introduction into inland Texas streams. In 2020, the Texas Parks and Wildlife Department (TPWD) listed the Red River Pupfish as a threatened species in the state of Texas (TPWD 2020). Invasive fish species such as the Sheepshead Minnow and Gulf Killifish are now common in the middle Brazos River, and their presence could result in negative effects on the native populations throughout this portion of the system. Understanding how these species are introduced into novel ecosystems can inform efforts seeking to disrupt the vectors facilitating their introduction and spread.

In this study, we surveyed the live-bait industry in Texas, with an emphasis on portions of the Brazos and Red River basins, where invasive populations of Gulf Killifish and Sheepshead Minnow were recently reported. Across 1 year, we conducted telephone and in-person surveys of live-bait shops in Texas on a seasonal

basis to explore whether bait shops constitute a potential pathway of introduction of these nonnative fishes into inland sites. We hypothesized that Gulf Killifish and Sheepshead Minnow were being sold at inland bait shops, thus facilitating their introduction into inland systems. Additional objectives of this study were to verify (1) the types of bait being sold at bait shops, (2) where baitfish were being sourced, and (3) where aquaculture facilities were distributing their bait products throughout Texas. Through contact with locally owned bait shops, we expected to gain a better understanding of the types of bait sold in the focal basins. We also contacted regional aquaculture facilities and hatcheries to gain insight into the Texas aquaculture industry by determining which species are being raised and distributed to the live-bait trade throughout the state. Our findings are beneficial for identifying the types of live-bait products that are being distributed throughout Texas to better understand the role that the live-bait industry plays in the introduction of the Gulf Killifish, Sheepshead Minnow, and other nonnative aquatic species within the state.

METHODS

Expert opinions

Live bait is either sourced from wild populations or produced in aquaculture facilities. To assess the status of the aquaculture industry as a source of bait for the live-bait industry, we contacted 21 aquaculture industry experts, including both in-state and out-of-state (i.e., adjacent states providing live bait to Texas) institutions (i.e., aquaculture facilities, fisheries and pond management centers, and regional wholesale businesses) and personnel (see Table S1 available in the Supplement in the online version of this article). These institutions were contacted from May 8 to September 30, 2020. In some cases, repeated callbacks were necessary. These experts were asked about the diversity of bait being produced at local facilities in Texas, distribution within the state, bait seasonal availability, bait producers, and specific knowledge of the two invasive species, the Gulf Killifish and Sheepshead Minnow. Industry experts were also able to provide information on other aquaculture products, including fish species being produced for stocking and other recreational purposes (i.e., sportfishing). All reported fish species were recorded, and their status within Texas (i.e., native or nonnative) was then investigated using the U.S. Geological Survey (USGS) Nonindigenous Aquatic Species database (USGS 2023). Additional information on available aquaculture products was collected from the institutions' websites when available.

To supplement the expert opinions, we consulted published information on baitfish production, aquaculture statistics, species, and the quantity of baitfish being produced in the state of Texas. These sources included reports published by TPWD, Texas A&M University AgriLife Extension, U.S. Department of Agriculture (USDA), Southern Regional Aquaculture Center, and Louisiana Department of Wildlife and Fisheries (see Table S2). Information regarding the species and quantity of baitfish being produced was also recorded. Published information provided insight into regulations that are pertinent to the import, export, sale, and use of aquatic live bait. Likewise, expert opinions and published data provided insights into which species are being produced for bait in aquaculture facilities, the demand for species, distributors, consumers, and baitfish regulations in Texas.

Bait shop telephone surveys and in-person visits

To document native and nonnative species being sold as bait in Texas shops, we contacted locally owned bait shops within the study regions (defined below) over the phone (Table S3). The contacted bait shops were found either from a list provided by TPWD or via Internet searches. Efforts focused on surveying (1) bait shops in the Brazos and Red River basins, where invasive cyprinodontids have been recently introduced; and (2) bait shops in coastal areas, where our focal invasive cyprinodontids are native. Additional bait shops located primarily in major metropolitan areas surrounding our focal basins were also surveyed because of the high likelihood that anglers are traveling between these areas and transporting their bait. Areas in western Texas were not included in this sampling effort. Bait shops were categorized by region: Red River, Brazos River, Coastal, and Other. Red River and Brazos River shops were located within those river basins, Coastal shops were located close to the Gulf of Mexico coast of Texas, and Other included all other shops, located primarily in eastern Texas.

The names and locations of 239 persons holding a bait license were originally provided by TPWD, and an additional 89 bait shops were identified through Internet searches and through the smartphone application BaitFinder (Version 2.0.257; AvailabilityFinders, LLC). From February 2020 to May 2021, informal calls were made to contact each bait shop on a seasonal basis. These shops were contacted via the phone to inquire about current types of bait being sold during the summer (June–August), fall (September–November), winter (December–February), and spring (March–May). In some cases, repeated calls within each season were necessary,

and some businesses were unavailable for sampling during certain seasons. Bait shop managers or workers were informally questioned about the types of live bait currently being sold at their shop. Although information on live and dead bait was recorded, we report only information about live-bait items, as these are the propagules of introductions. Information on bait availability as determined from each bait shop's website was also recorded when accessible. All responses were summarized and categorized by season and by basin of bait shop location (Red River, Brazos River, Coastal, or Other; Figure 1). All reported bait items were counted by location, and this information was used to evaluate general trends in bait item popularity as well as variation in bait items between seasons and basins of origin. Differences in the number of bait items reported by shops per season were assessed using a one-way analysis of variance (ANOVA) in RStudio version 4.2.2. A two-tailed *t*-test in RStudio was also used to evaluate whether there was significant variation in the number of bait items being sold in inland shops (i.e., Red River, Brazos River, or Other) versus Coastal shops.

To confirm the identity of bait items, we visited 61 small, locally owned bait shops located within the Brazos and Red River basins between summer 2020 and spring 2021, and we purchased live bait when available. Several shops were visited multiple times throughout the sampling period (see Table S5). The shops were selected from a list compiled from sources including the TPWD, Internet resources, and the BaitFinder application. Selected shops were first contacted via the telephone and then were visited in person. During shop visits, researchers visually examined tanks to try to identify the species being sold. All bait items being sold were recorded; when possible, baitfish were identified to the lowest feasible taxonomic resolution (typically species). Baitfish that could not be identified in the store were purchased, euthanized using clove oil, preserved in 10% formalin, and identified in the laboratory. At least 12 of each type of unidentified bait item were purchased for further laboratory identification. We calculated the variation in bait items across seasons and regions by using Microsoft Excel 2021.

RESULTS

Expert opinions

Aquaculture experts from 21 different commercial facilities distributed across Texas ($n = 18$), Oklahoma ($n = 1$), and Arkansas ($n = 2$) were successfully contacted. Experts provided both the common names and the scientific names of the species that they sold (Table 1).

Aquaculture industry fishes

In total, aquaculture experts named 21 different fish species that they distributed across Texas for live bait

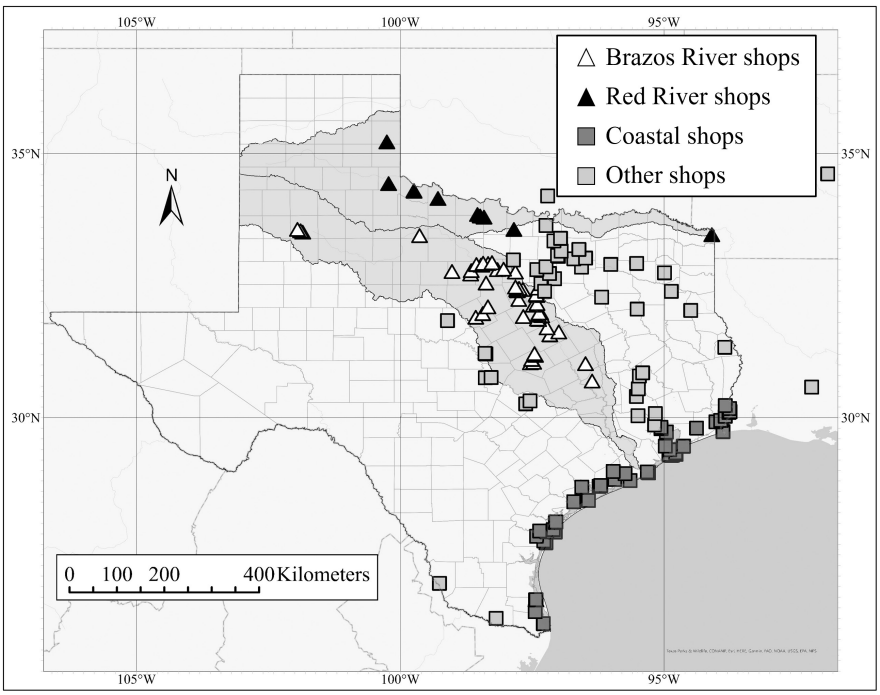

FIGURE 1 Distribution of locally owned bait shops by region in Texas (Brazos River: $n = 59$; Red River: $n = 10$; Coastal: $n = 58$; Other: $n = 44$), which were surveyed via phone calls during 2020–2021. The geographic coordinates and bait shop names are provided in Table S3.

TABLE 1 Aquaculture products that were reported by contacted aquaculture industry experts in Texas, Arkansas, and Oklahoma, with the number and percentage of institutions (out of the total of 21 surveyed institutions) that reported each item. The status of each species within Texas was confirmed using the USGS Nonindigenous Aquatic Species database (USGS 2023).

Product type	Common name	Species	Number of institutions	Percentage of institutions	Status in Texas
Fish	Fathead Minnow	*Pimephales promelas*	18	86	Native
	Largemouth Bass	*Micropterus nigricans*	15	71	Native
	Channel Catfish	*Ictalurus punctatus*	15	71	Native
	Golden Shiner	*Notemigonus crysoleucas*	13	62	Native
	Coppernose Bluegill	*Lepomis macrochirus purpurescens*	11	52	Nonnative
	Grass Carp	*Ctenopharyngodon idella*	11	52	Nonnative
	Redear Sunfish	*Lepomis microlophus*	9	43	Native
	Mozambique Tilapia	*Oreochromis mossambicus*	9	43	Nonnative
	Striped Bass	*Morone saxatilis*	8	38	Native
	Rainbow Trout	*Oncorhynchus mykiss*	8	38	Nonnative
	Goldfish	*Carassius auratus*	8	38	Nonnative
	Bluegill	*Lepomis macrochirus*	6	29	Native
	Threadfin Shad	*Dorosoma petenense*	6	29	Native (southeast)
	Black Crappie	*Pomoxis nigromaculatus*	4	19	Native (east/central)
	Blue Catfish	*Ictalurus furcatus*	4	19	Native (southeast)
	Smallmouth Bass	*Micropterus dolomieu*	3	14	Nonnative
	Black salty goldfish	Color morph of Goldfish	3	14	Nonnative
	Koi	Ornamental variant of Amur Carp *Cyprinus rubrofuscus*	2	10	Nonnative
	Koi fingerlings	Ornamental variant of Amur Carp	2	10	Nonnative
	Gizzard Shad	*Dorosoma cepedianum*	2	10	Native
	Rosy red minnow	Color morph of Fathead Minnow	2	10	Native
	Walleye	*Sander vitreus*	1	5	Nonnative
Hybrid fish	Sunshine bass	White Bass *Morone chrysops* × Striped Bass *Morone saxatilis*	3	14	Nonnative
	Koi/carp hybrid	Amur Carp *Cyprinus rubrofuscus* × Common Carp *Cyprinus carpio*	2	10	Nonnative
	Saugeye	Walleye *Sander vitreus* × Sauger *Sander canadensis*	1	5	Nonnative
	Hybrid Bluegill	Bluegill *Lepomis macrochirus* × Green Sunfish *Lepomis cyanellus*	1	5	Nonnative
Other	Crayfish	Unknown	5	24	Unknown
	Worms	Unknown	1	5	Unknown
	Crickets	Unknown	1	5	Unknown
	American bullfrog tadpoles	*Lithobates catesbeianus*	1	5	Native

or fish stocking. The most commonly reported species, which are all native throughout Texas (Table 1), were the Fathead Minnow, reported to be distributed by 18 of the 21 institutions (86%); Largemouth Bass and Channel Catfish, both reported by 15 institutions (71%); and Golden Shiner, reported by 13 institutions (62%). Thirteen of the 21 fish species reported from aquaculture facilities were either nonnative to the state or were only native to certain regions (e.g., southeastern, eastern, or central Texas; Table 1). For this study, hybrid fishes were considered nonnative, as they are not known to occur naturally in Texas. All 21 institutions reported producing or selling at least one nonnative species. The most commonly reported nonnative fish species (Table 1) were the Coppernose Bluegill and Grass Carp, both reported by 11 institutions (52%); Mozambique Tilapia, reported by nine institutions (43%); and Rainbow Trout and Goldfish, both reported by eight institutions (38%). According to experts, most species distributed by these institutions are fishes used for stocking lakes and ponds around the state for recreational purposes. Of the commonly reported nonnative fish, two species (Grass Carp and Mozambique Tilapia) are sold for stocking with the purpose of vegetation and/or algae control or as forage species. Fathead Minnows, "rosy red minnows" (color morph of the Fathead Minnow), Golden Shiners, Goldfish, and "black salty goldfish" (color morph of the Goldfish) were the only fishes mentioned as being produced specifically for the live-bait trade (Table 1).

Other bait types from aquaculture

Nonfish aquaculture products consisted of four taxa: crayfish, reported by five institutions (24%); and nightcrawlers/earthworms, crickets, and American bullfrog tadpoles, each of which was reported by only one expert institution (Table 1). According to experts, these are commonly produced and distributed as live bait or stocked in ponds as forage items. Invertebrate groups were not identified to species, so their status within Texas was recorded as unknown. The American bullfrog is native to eastern and central portions of the state (Schalk et al. 2018).

Bait shop telephone surveys and in-person visits

From the list of TPWD bait license holders, a total of 124 unique bait shop businesses were identified. Among these, 41 shops were eliminated because of their permanent closure or disconnected telephone number. To increase the number of live-bait shops to be contacted, an additional 89 shops were identified through Internet searches and through BaitFinder. In total, 170 different bait shop businesses were successfully contacted between spring 2020 and spring 2021 via telephone calls (Figure 1).

In total, 305 successful telephone calls were made to live-bait shops across all four seasons (summer: $n = 143$; fall: $n = 69$; winter: $n = 6$; spring: $n = 87$). Shop responses about the types of bait sold did not provide scientific names of species; only common names or categories were submitted (e.g., minnows, perch [Texas colloquial name for sunfish]; Table 2). The number of bait shops contacted varied across our four sampling regions (Red River: $n = 10$; Brazos River: $n = 58$; Coastal: $n = 58$; Other: $n = 44$; Figure 1). To confirm the identity of species being sold, 40 different shops located in the Brazos and Red River basins were surveyed in person for the types of bait sold. Several shops were visited multiple times, resulting in 61 successful visits that were made from summer 2020 to spring 2021 (summer: $n = 22$; fall: $n = 18$; spring: $n = 21$).

Bait species sold

Twenty-four types of fish were reported across all 170 live-bait shop locations in Texas. The most commonly reported live baitfish were "minnows" of various sizes, with 71 shops (42%) reporting "small minnows," 27 shops (16%) reporting "medium minnows," 57 shops (34%) reporting "large minnows," and four shops (2%) reporting "extra-large minnows" (Table 2). In-person surveys confirmed minnows as either Golden Shiners or Fathead Minnows (Table 2). Golden Shiners were reported by name at 34 shops (20%), and Fathead Minnows were reported by name at 27 shops (16%). Fathead Minnows are native across the entire state of Texas, and Golden Shiners, while not historically native across the entire state, have been widely introduced and are now found statewide (Thomas et al. 2007). Goldfish were stocked at 40 shops (24%), and "black salty goldfish" were stocked at 11 shops (6%). Both "Goldfish" and "black salty goldfish" refer to the same species (*Carassius auratus*), which is nonnative in North America. "Croaker" (likely Atlantic Croaker) and "mudminnows" were both relatively popular bait items in coastal areas, being reported in 32 (19%) and 22 (13%) live-bait shops, respectively (Table 2). Based on the descriptions provided by various bait shop employees and information on the TPWD website, we suspect that the mudminnow was our focal species, the Gulf Killifish. Additional fishes that were reported by locally owned bait shops included

TABLE 2 Live-bait items reported by locally owned shops during the telephone surveys. Species common names were reported by the owner/employee, and suspected species identifications were based on in-person surveys and online databases (TPWD fishing guides). Status of each species within Texas was confirmed using the USGS Nonindigenous Aquatic Species database (USGS 2023). Status is listed as unknown if we were not able to accurately identify the species.

Bait type	Common name reported	Suspected species	Total number of stores carrying item ($n = 170$)	Confirmed via in-person surveys	Status in Texas
Fish	Mudminnow	Gulf Killifish *Fundulus grandis*	22		Native (coastal)
	Extra-large minnow	Golden Shiner *Notemigonus crysoleucas*/Fathead Minnow *Pimephales promelas*	4	×	Native
	Large minnow	Golden Shiner/Fathead Minnow	57	×	Native
	Medium minnow	Golden Shiner/Fathead Minnow	27	×	Native
	Small minnow	Golden Shiner/Fathead Minnow	71	×	Native
	Golden Shiner	Golden Shiner	34	×	Native
	Fathead Minnow	Fathead Minnow	27	×	Native
	Goldfish	Goldfish *Carassius auratus*	40	×	Nonnative
	Black salty goldfish	Goldfish (color morph)	11	×	Nonnative
	Croaker	Atlantic Croaker *Micropogonias undulatus*	32		Native (coastal)
	Mullet	Mullet *Mugil* spp.	27		Unknown
	Shad	Shad *Dorosoma* spp.	10		Unknown
	Rosy red minnow	Fathead Minnow (color morph)	6	×	Native
	Perch	Sunfish *Lepomis* spp.	35	×	Unknown
	Bluegill	Bluegill *Lepomis macrochirus*	7	×	Native
	Green Sunfish	Green Sunfish *Lepomis cyanellus*	2	×	Native
	Redear Sunfish	Redear Sunfish *Lepomis microlophus*	2		Native
	Piggy perch	Pinfish *Lagodon rhomboides*	4		Native (coastal)
	Red Shiner minnow	Red Shiner *Cyprinella lutrensis*	1		Native
	Redhorse minnow	Red Shiner	1		Native
	Bream bait	Unknown	1		Unknown
	Crappie minnow	Golden Shiner/Fathead Minnow	2	×	Native
	Spottail Shiner	Unknown	1		Unknown
	Chub	Unknown	1		Unknown
Crustaceans	Shrimp	Unknown	52		Unknown
	Grass shrimp	Unknown	2		Unknown
	Sea lice	Unknown	3		Native
	Crayfish	Unknown	7		Unknown
	Crab	Blue crab *Callinectes sapidus*	17		Native
Other	Earthworms/ nightcrawlers	Earthworms *Lumbricus* spp.	83		Unknown
	Leeches	Unknown	1		Unknown
	Crickets	Unknown	1		Unknown
	Salamanders	Unknown	1		Unknown

species such as "perch," "shad," "Bluegill," "Green Sunfish," and "Redear Sunfish," yet they were reported relatively infrequently (Table 2). Bait shop owners' taxonomic knowledge was not assessed during this survey, so the true species identity of these additional items is unknown.

The most popular nonfish live-bait item sold across all 171 shops was "earthworms/nightcrawlers," which

were reported in 83 shops (49%; Table 2). Fifty-two shops (31%) reported carrying live "shrimp" as bait. At least four species of shrimp are known to be sold as live bait in Texas, including the brown shrimp *Farfantepenaeus aztecus*, white shrimp *Litopenaeus setiferus*, pink shrimp *Farfantepenaeus duorarum*, and grass shrimp *Palaemonetes pugio* (TPWD 2002). All four species are native to coastal waters in Texas. Grass shrimp were reported by name at two (1%) of the bait shops. Other non-fish bait species included "crab," "crayfish," and "leeches," although they were reported by shops infrequently (17 shops, 7 shops, and 1 shop, respectively; Table 2).

Regional distribution of bait items

All live-bait shops identified within the inland Texas regions (Red River, Brazos River, and Other) appeared to sell similar live-bait types. The most popular inland baits included "earthworms/nightcrawlers," "minnows" of different sizes, and Goldfish (Table 3). Coastal bait shops sold four baits that were not available in inland shops: "croaker," "mudminnows" (suspected Gulf Killifish), "piggy perch" (suspected Pinfish), and "sea lice" (colloquial name for mantis shrimp, likely sold dead; Table 3). Unlike inland shops, live "shrimp" and "mullet" (*Mugil* spp.) were some of the most popular coastal live baits, reported in 38 (63%) and 26 (43%) coastal shops, respectively. A report from TPWD also indicated that shrimp species sold in Texas are native only to marine waters off the coast (TPWD 2002). The use of nonnative shrimp as bait, dead or alive, is against state regulations. "Shrimp" and "mullet" were also reported in several inland shops, although relatively infrequently. Inland bait shops carried a greater variety of bait items (30 total items) compared to coastal shops (18 total items). A two-way *t*-test revealed that inland shops sold, on average, a significantly greater number of bait items per shop ($\mu = 3.86$, $SD = 2.68$) compared to coastal shops ($\mu = 2.93$, $SD = 2.30$; *t*-test: $t_{131} = -2.32$, $p = 0.02$).

Seasonal variation in bait

Live-bait items sold within study areas did not appear to vary among seasons. Throughout all four seasons, both "earthworms/nightcrawlers" (summer: 42%; fall: 30%; winter: 67%; spring: 34%) and "shrimp" (summer: 33%; fall: 29%; winter: 33%; spring: 27%) were among the most popular bait items sold by stores (see Table S4). Similarly, "small minnows," identified as either Golden Shiners or Fathead Minnows, were the most popular bait items sold throughout the year (summer: 40%; fall: 23%; winter: 67%; spring: 35%; Table S4). In every season except winter, "large minnows" were commonly reported in bait shops (summer: 30%; fall: 29%; spring: 25%). A one-way ANOVA did reveal that the numbers of bait items being carried in bait shops were significantly different among seasons (ANOVA: $F_{3,301} = 4.37$, $p = 0.005$). A post hoc Tukey's test revealed significant differences ($p = 0.003$) in the variety of bait items carried in stores during the summer and fall seasons, but no other differences between seasons were detected. However, the most popular bait items reported, such as "earthworms/nightcrawlers," "shrimp," and "minnows," stayed consistent between the summer and fall seasons.

In-person survey results

To confirm the identity of bait species being sold, 40 different shops located in the Brazos and Red River basins were surveyed in person to inquire about the types of bait being sold. In total, 61 shop visits were made across three seasons (summer: $n = 24$; fall: $n = 17$; spring: $n = 20$); winter was excluded because of COVID travel restrictions during that sampling period. Seven different bait items were identified during in-person surveys: "large minnows" ($n = 46$), "medium minnows" ($n = 4$), "small minnows" ($n = 20$), "perch" ($n = 9$), Goldfish ($n = 10$), "worms" ($n = 20$), and "shrimp" ($n = 3$; Table S5). Species identity was verified in person or, when necessary, live bait was purchased and transported back to the Aquatic Ecology Laboratory at Stephen F. Austin State University for identification. In total, 281 baitfish were purchased across the entire sampling period. Based on both in-person and laboratory identification, "minnows" of all sizes were identified as either Golden Shiners or Fathead Minnows, while "perch" were either Green Sunfish or Bluegill. Worms and shrimp were not identified to species from this survey.

DISCUSSION

These findings did not support our hypothesis that the Gulf Killifish and Sheepshead Minnow are currently being sold at inland bait shops in Texas. The Sheepshead Minnow and Gulf Killifish have been introduced into the middle and upper reaches of the Brazos and Red River basins. While previous reports speculated that both cyprinodontids were introduced into inland Texas basins via bait-bucket releases (Hillis et al. 1980; Echelle and Connor 1989), we did not find evidence from our surveys to support this claim. Telephone surveys from coastal areas of Texas reported the sale of "mudminnows," a species that is suspected to be Gulf Killifish (Wallace and

TABLE 3 Regional variation in live-bait items reported from telephone surveys, as depicted by the total number of shops (*n*) contacted per region in Texas and the frequency of occurrence (%) of the bait items across all shops surveyed. The suspected species of each reported bait is described in Table 2.

		Region							
		Red River ($n = 10$)		Brazos River ($n = 59$)		Coastal ($n = 58$)		Other ($n = 44$)	
Bait type	Bait reported	Number	Percent	Number	Percent	Number	Percent	Number	Percent
Fish	Small minnow	7	70	36	60	3	5	26	65
	Large minnow	4	40	32	53	4	7	18	45
	Goldfish	2	20	22	37	1	2	16	40
	Perch	2	20	18	30	6	10	9	23
	Golden Shiner	2	20	20	33	1	2	11	28
	Croaker	0	0	0	0	32	53	0	0
	Medium minnow	0	0	14	23	2	3	11	28
	Mullet	0	0	0	0	26	43	1	3
	Fathead Minnow	2	20	17	28	1	2	7	18
	Mudminnow	0	0	0	0	22	67	0	0
	Black salty goldfish	0	0	5	8	0	0	6	15
	Shad	1	10	1	2	4	7	4	10
	Bluegill	1	10	3	5	0	0	3	8
	Rosy red minnow	1	10	1	2	0	0	4	10
	Extra-large minnow	0	0	0	0	0	0	4	10
	Piggy perch	0	0	0	0	4	7	0	0
	Green Sunfish	0	0	2	3	0	0	0	0
	Redear Sunfish	0	0	1	2	0	0	1	3
	Crappie minnow	1	10	0	0	0	0	1	3
	Red Shiner minnow	0	0	1	2	0	0	0	0
	Redhorse minnow	0	0	1	2	0	0	0	0
	Bream bait	0	0	0	0	0	0	1	3
	Spottail shiner	0	0	0	0	0	0	1	3
	Chub	0	0	1	2	0	0	0	0
Crustaceans	Shrimp	0	0	10	17	38	63	5	13
	Crab	0	0	0	0	16	27	1	3
	Crayfish	0	0	1	2	2	3	4	10
	Sea lice	0	0	0	0	3	5	0	0
	Grass shrimp	0	0	0	0	1	2	1	3
Other	Earthworms	4	40	45	75	4	7	30	75
	Leeches	0	0	0	0	0	0	1	3
	Crickets	0	0	0	0	0	0	1	3
	Salamanders	0	0	1	2	0	0	1	3

Waters 2004). Although the sale of Gulf Killifish on the coast does not suggest a strong likelihood of its introduction into inland waters, its sale as live bait could still indicate that it historically was and still potentially is being moved as a live-bait species into inland Texas waters. We did, however, find evidence that the aquaculture industry

may be facilitating the movement of other nonnative bait and aquaculture products.

Live-bait species of Texas

Nonnative and invasive species of fish have been documented in live-bait shops across the United States (LoVullo and Stauffer 1993; Kerr et al. 2005; Keller and Lodge 2007; Kilian et al. 2012; Drake and Mandrak 2014). Aquaculture facilities reported commonly producing Golden Shiners, Fathead Minnows, and Goldfish to be sold as live bait in locally owned shops. Results from our surveys of Texas live-bait shops further confirmed the popularity of these live baitfish throughout the state. Our surveys of bait shops found that the only nonnative baitfish being sold in Texas shops were Goldfish and their black color morph, the "black salty goldfish." "Black salty goldfish" are typically marketed as a variety of Goldfish with a high salt tolerance; "black salty goldfish" are likely the same species (*Carassius auratus*), as Goldfish are known to be tolerant of high salinity (Schofield et al. 2006). Golden Shiners, commonly sold in bait shops, are not native to all of Texas but have been introduced statewide (Thomas et al. 2007), likely through bait-bucket transfers. Our surveys of the live-bait industry throughout Texas also identified some trends in the diversity of live-bait species being sold in inland versus coastal shops, with inland live-bait shops carrying a larger variety of live-bait items. Additionally, inland shops typically carried baits that were grown in hatcheries, while the coastal shops harvested their bait locally from coastal brackish or saline environments. Although we did contact shops across multiple seasons, general trends of the surveys suggested low variation in live-bait items being sold throughout the year.

At a regional scale (i.e., inland versus coastal), there were differences in popular live-bait species. Across all inland locations, either Golden Shiners or Fathead Minnows (i.e., "minnows") and Goldfish were commonly reported, which agrees with previous surveys conducted by the USDA and the Southern Regional Aquaculture Center (Stone and Thromforde 2001; USDA 2019). Fathead Minnows are native throughout the state, and Golden Shiners, although originally not native statewide, have been widely introduced. Goldfish are not native to the United States and are considered by some researchers to be invasive (Thomas et al. 2007; Nathan et al. 2014; Gunderson 2019). Goldfish may be one of the most popular baitfish species produced in the United States, but they are an illegal baitfish in 28 states (Nathan et al. 2014; Gunderson 2019; USDA 2019). However, the use of Goldfish as live bait is permitted in Texas. Although Fathead Minnows are native throughout Texas and Golden Shiners have already been widely introduced throughout the state, their use as live bait is also not without risk (Gunderson 2018). There are several baitfish farms within Texas, but most live baitfish sold in Texas are imported from Arkansas (Gunderson 2019; USDA 2019). Both Golden Shiners and Fathead Minnows produced in Arkansas have been shown to carry harmful pathogens, such as the Golden Shiner virus and Fathead Minnow nidovirus (Gunderson 2019). Neither virus is regulated by the Arkansas Commercial Bait and Ornamental Fish Certification Program, and both have the potential to harm native populations of these species in Texas if introduced (Faisal et al. 2016; Gunderson 2019).

Invasive cyprinodontids

The Gulf Killifish was first reported in the Brazos River basin just below Lake Whitney Dam in 1978 (Hillis et al. 1980). Hillis et al. (1980) speculated that the Gulf Killifish was introduced by anglers that purchased it from local bait shops in the Brazos River area. It is unclear whether Gulf Killifish were historically sold in inland bait shops. During our contemporary surveys, we did not observe Gulf Killifish being sold at inland bait shops in Texas. The Gulf Killifish is a popular coastal live-bait item often called either "bull minnow" or "cocahoe minnow," but in Texas it is colloquially known as the "mudminnow" (Strawn et al. 1986; Wallace and Waters 2004; Ohs et al. 2013). Despite claims that Gulf Killifish would be a lucrative aquaculture product (Strawn et al. 1986; Wallace and Waters 2004), no facilities have yet produced them for commercial use. Therefore, the Gulf Killifish currently being sold are likely wild-caught fish obtained from locations off the coast. Although regulations exist in Texas to designate the native freshwater species or genera that can be harvested and sold as wild-caught bait (TPWD 2022a), similar limitations for coastal bait species do not exist and regulations do not prohibit sale outside of the native range of the bait species.

Anglers harvesting live bait for their own purposes could also potentially be facilitating the movement of nonnative species in Texas. Kilian et al. (2012) reported that anglers are typically unaware of or ignore regulations about the transportation and disposal of live-bait items. Anglers will often release unused bait into surrounding waters because it is convenient and thought to be beneficial to the surrounding ecosystem (Kilian et al. 2012). Texas regulations in general do not prohibit the release of live bait, although regulations exist stipulating that bait that has come into contact with public freshwater can be used only on that water body (TPWD 2022b). Additionally,

regulations prohibit the transfer of live nongame fish from certain freshwater systems where invasive Bighead Carp *Hypophthalmichthys nobilis* or Silver Carp *H. molitrix* have been detected to prevent their transfer as live bait (TPWD 2022b). However, no such regulations apply to the transfer of live bait from coastal waters. Therefore, anglers traveling from the coast to inland locations may be bringing nonnative bait, such as the Gulf Killifish, for fishing in inland waters, thus putting those ecosystems at risk.

Our surveys did not confirm the sale of Sheepshead Minnows at either inland or coastal live-bait shop locations—a finding that was inconsistent with previous reports suggesting that this species was a popular baitfish in Texas (Echelle and Connor 1989; Wilde and Echelle 1992). The selected bait shops were not surveyed during this time to confirm anecdotal reports. Although the use of Sheepshead Minnows as bait, as observed by Echelle and Connor (1989), might have explained historic introductions, it does not seem to adequately identify their pathway of introduction into the Brazos River in 2011. Hubbs et al. (1978) suggested that estuarine fish such as the Sheepshead Minnow may have made their way to inland water bodies via being harvested as bycatch and then transported alongside marine fishes (e.g., Red Drum *Sciaenops ocellatus*) that were stocked in inland reservoirs for recreational purposes. In addition to the hypothesis of Hubbs et al. (1978), it is possible that Sheepshead Minnows were transported along with wild-caught Gulf Killifish, as the two species are shown to regularly occur together in coastal marshes (Perschbacher and Strawn 1986). These alternative pathways of introduction for the Gulf Killifish and Sheepshead Minnow should be investigated in the future to help prevent their spread into novel inland Texas ecosystems.

Additional aquaculture products

Much of the research on the Texas aquaculture industry has focused primarily on the economic status of the production, distribution, and sale of its products (Green 2007; USDA 2019). Our surveys with aquaculture experts revealed information about both live baitfish and other fish species being used for stocking purposes around Texas. Almost all of the baitfish produced by the Texas aquaculture industry are native or naturalized, whereas several fish species produced for stocking purposes are not native to the state. The ecological consequences of stocking popular nonnative and invasive species are often ignored given that the economic benefits provided by these species are considered to outweigh any ecological effects in the recipient freshwater environments. Well-known examples include the Rainbow Trout and Mozambique Tilapia (Lowe et al. 2000; Russell et al. 2012; Thibault and Dobson 2013), two species that also were identified in our surveys.

Rainbow Trout are commonly stocked in small lakes and ponds throughout Texas, as well as in the Guadalupe River, due to their popularity with anglers. One of the most significant harmful impacts resulting from Rainbow Trout introductions is hybridization with native trout species (Rinne 1995). In Texas, Rainbow Trout replaced native Rocky Mountain Cutthroat Trout *Oncorhynchus virginalis* and are now established in McKittrick Creek in west Texas (Garrett and Matlock 1991). There are currently no native trout species in Texas (Thomas et al. 2007); thus, the effects of introduction would not include hybridization. Although other effects (e.g., competition, predation, and disease) associated with Rainbow Trout are possible, those effects have not been documented or studied in Texas. Rainbow Trout may be capable of oversummer survival in cool waters where they have been stocked in the dam tailraces immediately downstream of two Texas lakes and in private spring headwaters, but otherwise, the stocking of Rainbow Trout creates a put-and-take fishery in Texas and the species is not capable of surviving summer temperatures (Howells 2001).

Mozambique Tilapia are commonly stocked in private ponds in Texas for filamentous algae control and as forage for sport fish, but their stocking in public waters is not permitted. Mozambique Tilapia have been documented in public waters in Texas, although they appear to have become hybridized with Blue Tilapia *Oreochromis aureus* and there is little information about their effects within the state (Howells 2001; U.S. Fish and Wildlife Service 2011). However, regulations were promulgated in 2021 that seek to minimize the risk of escape from private ponds and subsequent effects on imperiled native fishes based on a spatial conservation assessment that balanced prioritizing oversight of private pond stocking in habitats containing imperiled fishes that may be negatively affected against the economic benefits of pond stocking (McGarrity 2019).

CONCLUSIONS

Although the live-bait industry in the United States generates tremendous economic benefits (Gunderson 2019), discussions regarding the transport and release of live bait and the potential for introduction of nonnative and invasive species via the live-bait pathway need to be considered to prevent negative ecological effects in recipient environments. Even though we did not find evidence that Gulf Killifish and Sheepshead Minnows are currently being sold in inland bait shops, this pathway may still be responsible for their dispersal in low incidence. The incidence of introductions does not need to be high to result in the establishment of nonnative species. Invasive species, such as the

Gulf Killifish and Sheepshead Minnow, have been shown to impose devastating effects on native communities; after the introductions of these species, populations of native Cyprinodontiformes drastically declined. It is widely acknowledged that eradicating invasive species is nearly impossible, so prevention is our most effective form of management (Kerr et al. 2005; Vander Zanden and Olden 2008; Kilian et al. 2012). Identifying and closing the pathways of introduction are essential for preventing future introductions and ensuring the preservation of freshwater biodiversity. Although we identified several potential pathways of introduction surrounding the transportation of live bait and other aquaculture products throughout Texas, further research should seek to address these pathways in order to better understand their role in introducing nonnative and invasive species into inland waters.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are included in the article; further inquiries can be directed to the corresponding author upon reasonable request.

ETHICS STATEMENT

Fish specimen collection was conducted under TPWD Scientific Collection Permit SPR-0217-046. Fish collection and manipulation followed the protocols of the Institutional Animal Care and Use Committee approved by committee at Stephen F. Austin State University, Protocol Number 2019-12.

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