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Two Decades of Advancement in Flathead Catfish Research

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Abstract

We summarized advancements in Flathead Catfish *Pylodictis olivaris* biology, fisheries, and management published from 1999 to 2021. Our goal was to highlight recent advancements in Flathead Catfish research and address information needs for this species to encourage future research. We identified and reviewed 140 papers from 33 peer-reviewed journals, 27 theses/dissertations, and 13 technical reports on Flathead Catfish over the 23-year period. Most studies focused on introduced Flathead Catfish populations, age and growth, movements, diet, sampling methods, and human dimensions of Flathead Catfish fisheries. The number of studies published on riverine Flathead Catfish populations was greater than the number published on reservoir populations, and many studied negative effects of populations introduced outside of the species' native range. Flathead Catfish are most commonly found in shallow (<3-m) locations with large woody debris or riprap and substrates with a hard bottom. Flathead Catfish movement studies identified three distinct migration periods: overwintering, prespawn/spawn, and late summer/fall, with little movement between these migrations. Flathead Catfish are typically lightly exploited (0–19% annual exploitation) and have typical (for a long-lived species) annual total mortality rates of 11–37%, ranging as high as 62%. Flathead Catfish are most commonly sampled using low-frequency electrofishing. Despite an increase in published literature on Flathead Catfish, information remains inadequate such that most state agencies do not follow a standardized protocol for sampling Flathead Catfish and information to guide management approaches for the species is limited. Minimal research on Flathead Catfish reproduction and spawning has occurred since 1999. Additional research is needed on these and other topics to provide information critical to managing this important species.

The Flathead Catfish *Pylodictis olivaris* is a popular sport fish throughout the United States (Jackson 1999; Arterburn et al. 2002). However, there has been little research conducted on this species relative to other sport fishes. Jackson (1999) contributed a review article for *Catfish 2000: Proceedings of the International Ictalurid Symposium* (hereafter, Catfish 2000; American Fisheries Society Symposium 24; Erwin et al. 1999b) that highlighted research conducted on the species up to that time. As with the entire Catfish 2000 conference and published proceedings, Jackson's (1999) primer on Flathead Catfish was intended to guide additional research. Kwak et al. (2011) summarized literature for *Conservation, Ecology, and Management of Catfish: the Second International Symposium* (hereafter, Catfish 2010; American Fisheries Society Symposium 77; Michaletz and Travnichek 2011) that highlighted research on catfish science (order Siluriformes) in the following decade (2000–2010), and the quantity of information on Flathead Catfish still lagged that of the other sport catfishes. New research has been conducted in the 21 years since Catfish 2000, but advances in Flathead Catfish research have not been as numerous as those for the other large-bodied catfishes (i.e., Blue Catfish *Ictalurus furcatus* and Channel Catfish *I. punctatus*). Our goal was to review the published and gray literature research conducted on Flathead Catfish since 1999 to summarize significant advancements made during that period and to highlight areas that require additional study to

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further our knowledge of Flathead Catfish biology and management.

To conduct our review, we used Google Scholar with the search term "Flathead Catfish" during the years 1999–2020 (the search was run on May 10, 2020, but our review also includes articles from this special issue, which were not returned by the Google Scholar search and were published in 2021). This resulted in 6,300 documents, which is relatively less literature than has been published on other sport fish during this time frame. For comparison, Google Scholar produced 48,900 documents from a search of "Channel Catfish" and 31,600 documents from a search of "Blue Catfish" over the same period. From the 6,300 Flathead Catfish search results, we reviewed all documents in which the Flathead Catfish was a central focus (i.e., we did not include those that tangentially mention Flathead Catfish). Although we include theses, agency reports, and other gray literature (i.e., non-peer-reviewed manuscripts) here, we designate non-peer-reviewed sources with asterisks (*) throughout our review to make this distinction. Our search produced a total of 182 documents with a Flathead Catfish focus that came from 140 articles published in 33 peer-reviewed journals, 27 theses/dissertations, and 13 technical reports (Table 1). Among the years examined, the most documents were published in 2011 (14.0%; most from Catfish 2010, two additional papers in *Transactions of the American Fisheries Society*, and one technical report), followed by 2021 (8.4%; Catfish 2020 proceedings [this special issue]) and 1999 (6.7%; Catfish 2000, one paper in *Fisheries*, one paper in the *Journal of the Southeastern Association of Fish and Wildlife Agencies*, and two theses), with a notable number (≥5%) of papers also published in 2004–2006, 2009, and 2015–2017 (Figure 1). Clearly, the decadal international catfish symposia have yielded many of the publications (28.7% of all publications during this 23-year interval), but a large proportion (19.2%) of papers have also been published in the *North American Journal of Fisheries Management*. No other publication outside the two previous decadal conference proceedings and the *North American Journal of Fisheries Management* published more than 8% of the total papers from this period (Table 1). Herein, we summarize the relevant findings from this literature compilation by topic and address what we see as some important knowledge gaps that remain.

TABLE 1. Number of articles published in journals or symposium proceedings from 1999 to 2021 that were focused on Flathead Catfish research based on a Google Scholar search conducted on May 10, 2020.

Journal or symposium proceedings	Number of articles
North American Journal of Fisheries Management	27
Catfish 2010 (Michaletz and Travnichek 2011)	23
Catfish 2020 (this special issue)	14
Journal of the Southeastern Association of Fish and Wildlife Agencies	11
Transactions of the American Fisheries Society	10
Catfish 2000 (Erwin et al. 1999b)	9
Journal of Freshwater Ecology	7
Fisheries	4
Proceedings of the Annual Conference Southeastern Association of Fish and Wildlife Agencies	4
Fisheries Management and Ecology	3
Journal of Fish and Wildlife Management	2
Northeastern Naturalist	2
Parasitology Research	2
River Research and Applications	2
American Midland Naturalist	2
18 other journals	1

HABITAT AND THE ENVIRONMENT

We identified 24 publications that addressed environmental effects on Flathead Catfish populations (Table 2). During summer, Flathead Catfish are most commonly found in shallow (<3 m) locations with large woody debris, riprap, or hard-bottom substrates (Weller and Winter 2001; Vrtiska et al. 2004; Daugherty and Sutton 2005a; Malindzak 2006*; Huck 2014*; Blank et al. 2021, this special issue), but in winter they move to water depths exceeding 4 m in deep, main-channel pools (Daugherty and Sutton 2005a). Nighttime habitat use includes a greater proportion of open-water habitat away from wood and rock (Daugherty and Sutton 2005a) than daytime

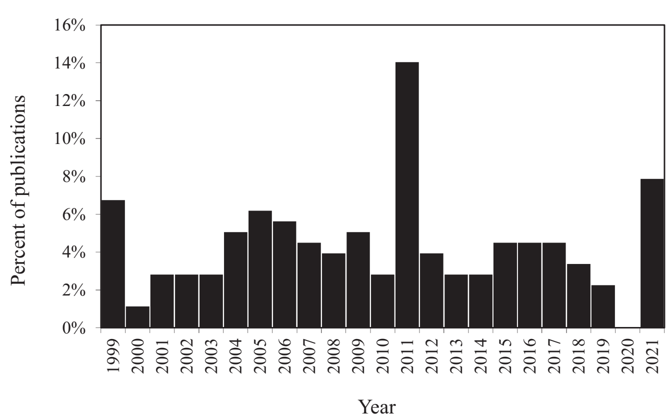

FIGURE 1. Percentage of published documents by year that focus on Flathead Catfish research based on a Google Scholar search conducted on May 10, 2020, searching publications from 1999 to 2020.

TABLE 2. Topically arranged literature focusing on Flathead Catfish research from 1999 to 2021 based on a Google Scholar search conducted on May 10, 2020. Non-peer-reviewed literature is denoted with an asterisk (*).

Topic	Subtopic	References
Biology/ecology		
Habitat and the environment	Overall habitat selection	Weller and Winter 2001; Vokoun 2003*; Vrtiska et al. 2003; Daugherty 2004*; Bringolf et al. 2005; Daugherty and Sutton 2005a; USGS 2007*; McCain et al. 2011; Porter et al. 2011; Stanley et al. 2012; Huck 2014*; Blank et al. 2021; Hamel et al. 2021, this special issue
	Juvenile habitat selection	Irwin et al. 1999a; Brewer 2004*; Brewer and Rabeni 2008; Baumann and Kwak 2011; Daugherty et al. 2011
	Urbanization effects on habitat selection	Gutreuter et al. 2006; Makinster 2006*; Heimann et al. 2007*; Paukert and Makinster 2009; White et al. 2009; Porter et al. 2011; Raabe and Hightower 2014
Diet	General diet and predatory control by Flathead Catfish	Mayo and Schramm 1999; Odenkirk et al. 1999; Eggleton 2001*; Haas et al. 2001; Jolley and Irwin 2003, 2011; Vrtiska et al. 2003; Eggleton and Schramm 2004; Waters et al. 2004; Pine et al. 2005; Jones and Noltie 2007; Baumann and Kwak 2011; Weber and Brown 2012; Walker et al. 2015; Hogberg and Pegg 2016; Turner 2017*; Schmitt et al. 2019
	Gape limitation	Slaughter and Jacobson 2008
	Effects of temperature on diet	Bourret et al. 2008
Movements	Diel patterns	Vokoun 2003*; Daugherty 2004*; Daugherty and Sutton 2005b; Malindzak 2006*; Vokoun and Rabeni 2006; Hedden and Gibo 2016
	Seasonal patterns/ migrations	Dobbins et al. 1999; Pugh and Schramm 1999; Weller and Winter 2001; Bayne et al. 2002; Vokoun 2003*; Travnichek 2004; Vokoun and Rabeni 2005a; Vokoun and Rabeni 2005b; Meerbeek 2007*; Barada 2009*; Garrett 2010*; Garrett and Rabeni 2011; Gelwicks and Simmons 2011; Piette and Niebur 2011; Shroyer 2011; Aadland 2015*; Hedden and Gibo 2016
	Fish passage	Raabe 2012*; Aadland 2015*; Raabe et al. 2019; Smith et al. 2021, this special issue
Reproduction	Fecundity	Colehour 2009*; Gima 2009*
Other	Microorganisms	Tarle et al. 2015; Leis et al. 2017, 2018
	World record	Neely and Lynott 2016
	Genetics	Padhi 2014; Arce-H. et al. 2017
	Climate change	Whitney et al. 2014
	Catfish symposium reviews	Jackson 1999; Kwak et al. 2011
Fisheries management		
Age and growth	Choice of aging structure	Nash and Irwin 1999; Sakaris 2006*; Koch et al. 2011; Olive et al. 2011; Sakaris et al. 2011; Steuck and Schnitzler 2011; Sakaris and Bonvechio 2021, this special issue
	Growth rate and size at age	Mayo 1999*; Nash 1999*; Grabowski et al. 2004; Holley 2006*; Kwak et al. 2006; Sakaris et al. 2006; Donabauer 2009*; Marshall et al. 2009a, 2009b; Rypel 2011, 2013; Steuck and Schnitzler 2011; Bonvechio et al. 2016; Lucchesi et al. 2017; Massie et al. 2018; Hilling et al. 2019

TABLE 2. Continued.

Topic	Subtopic	References
Sampling	Low-frequency electrofishing	Stauffer and Koenen 1999; Cunningham 2000, 2004; Daugherty and Sutton 2005d; Cailteux and Strickland 2007; Ford et al. 2011; McCain et al. 2011; Travnichek 2011b; Mitchell 2016*; Morris 2018*
	Hoop nets	Willenberg 2000*; Ford et al. 2011; Gelwicks and Simmons 2011*; Sindt 2018
	Trotlines	Stauffer and Koenen 1999; Arterburn 2001*; Arterburn and Berry 2002; Gelwicks and Simmons 2011*; Dickinson et al. 2018
	Other gears	Arterburn and Berry 2002; Sullivan 2014; Dean et al. 2021, this special issue
	Review of gears	Bodine et al. 2013
	Tagging methods	Daugherty and Buckmeier 2009; Neely et al. 2021, this special issue
Mortality and exploitation	Mortality in introduced riverine populations	Kwak et al. 2006; Sakaris et al. 2006; Kaeser et al. 2011; Rachels and Ricks 2015*; Bonvechio et al. 2016; Hilling et al. 2019
	Mortality in native riverine populations	Daugherty and Sutton 2005c; Makinster 2006*; Sakaris et al. 2006; Makinster and Paukert 2008; Hamel et al. 2021; Muhlbauer and Krogman 2021, this special issue; Schall and Lucchesi 2021, this special issue
	Mortality in reservoirs	Winkelman 2011; Stubbs et al. 2015; Lucchesi et al. 2017; Muhlbauer and Krogman 2021
	Exploitation rate	Marshall 2008*; Marshall et al. 2009; Sullivan and Vining 2011; Travnichek 2011a; Bodine et al. 2016; Schall and Lucchesi 2021; Winders and McMullen 2021, this special issue
Harvest management	Noodling	Winkelman 2003*; Reitz and Travnichek 2005; Morgan 2006, 2008; Brandes 2008*; Winkelman 2011; Bodine et al. 2016 and 2021, this special issue; Bennett et al. 2017
	Modeling regulations	Sakaris et al. 2006; Pine et al. 2007; Makinster and Paukert 2008; Sakaris and Irwin 2010; Moody-Carpenter 2013*; Stewart et al. 2016; Moody-Carpenter et al. 2017; Oliver et al. 2021, this special issue
	Manager opinions	Arterburn et al. 2002; Brown 2007a, 2007b*
Human dimensions		Michaletz and Dillard 1999; Travnichek and Clemons 2001; Dames et al. 2003*; Mestl 2003*; Hurley and Duppong-Hurley 2005*; Reitz and Travnichek 2006; Hunt and Hutt 2010*; Page et al. 2012; Stewart et al. 2012; Hutt et al. 2013; Hunt et al. 2012; Fisk et al. 2019; Krogman and Stubbs 2021, this special issue; Schlechte et al. 2021, this special issue
Introduced populations	Range expansions	Brown et al. 2005; Granfors 2014; Fuller and Whelan 2018; Rachels 2021, this special issue; Smith et al. 2021
	Predatory effects and diets of invasive populations	Weller and Robbins 1999; Herndon and Waters 2002; Kwak et al. 2004*; Pine 2004*; Pine et al. 2005; Brewster 2007*; Slaughter and Jacobson 2008; Bonvechio et al. 2009; Tetzlaff et al. 2010; Baumann and Kwak 2011; Flowers et al. 2011; Dobbins et al. 2012; Ward and Figiel 2013; Evans et al. 2014; Hedden 2015*; Steffenson et al. 2015; Walker et al. 2015; Hedden et al. 2016; Lucchesi et al. 2017; Schmitt et al. 2017, 2019
	Management of invasive populations	Weller and Geihsler 1999; Herndon and Waters 2002; Pine et al. 2007; Bonvechio et al. 2011, 2016; Propst et al. 2015

habitat. Larger fish (quality size or greater, ≥410 mm) are more inclined to use rocky habitat with shallow-water access, whereas smaller fish are more likely to use rocky habitat with deepwater access (Vrtiska et al. 2003). Flathead Catfish are known as fluvial generalists (Jackson 1999) but have a preference for free-flowing, unimpounded main-channel habitat in rivers (McCain et al. 2011). Only two studies evaluated habitat selection in reservoir habitat rather than in rivers (Weller and Winter 2001; Vrtiska et al. 2003), but habitat selection in reservoirs appears similar to that described for rivers (primarily rocky habitat, with some use of wood). Reservoir Flathead Catfish populations exhibit high resiliency even after unfavorable riverine hydrologic conditions (Sakaris and Irwin 2010), and flooding can provide additional suitable habitat for juveniles, thereby increasing recruitment during high-water years (Stanley et al. 2012; Hamel et al. 2021). Although the Flathead Catfish is a freshwater species, these fish can tolerate salinity levels up to 11‰, making them tolerant of estuarine habitat (Bringolf et al. 2005).

Juvenile Flathead Catfish occupy different habitats than adults. Juvenile Flathead Catfish are usually found in shallow riffle areas of streams with coarse substrate (Irwin et al. 1999a; Jackson 1999) and select microhabitat based on their body size (Daugherty et al. 2011). Smaller juveniles (<60 mm TL) select smaller interstitial microhabitats than larger juveniles (>60 mm TL; Daugherty et al. 2011), and larger juveniles select deeper habitats (Irwin et al. 1999a). However, juvenile Flathead Catfish in a Midwestern U.S. river utilized a broader range of velocities and showed little difference in diel microhabitat preferences (Brewer and Rabeni 2008). Juvenile Flathead Catfish have a preference for riprap (rock revetment), an anthropogenic substrate (White et al. 2009).

The degree of urbanization affects the growth and abundance of Flathead Catfish. Flathead Catfish grow faster in areas of low urbanization (i.e., areas with mature riparian habitat) and have a higher relative abundance in areas with agricultural land use than urban use (urban aquatic habitat is often characterized by dredging, channelization, and degraded riparian zones; Paukert and Makinster 2009; Hamel et al. 2021). Agricultural areas often have higher nutrient loading rates that increase the productivity of aquatic habitats, which in turn may increase prey abundance for Flathead Catfish. Impoundments result in a decline in juvenile Flathead Catfish habitat and can alter their development (Heimann et al. 2007*). Flathead Catfish are able to migrate upstream from barriers, such as fishways, and can use dams as a staging area to forage before migrating (Raabe and Hightower 2014; Raabe et al. 2019; Smith et al. 2021). Flathead Catfish populations are unaffected by boat traffic disturbance in commercial navigation channels (Gutreuter et al. 2006).

Given what has been published on Flathead Catfish habitat use, it appears that improving the quantity and quality of unimpounded rivers with mature riparian zones should provide optimal conditions to maximize Flathead Catfish populations. Additionally, increasing the quantity of riprap, boulders, and other hard substrates or the amount of coarse woody debris is recommended to provide additional preferred habitat (Porter et al. 2011). Enhancing habitat for Flathead Catfish may also benefit other fish species in the ecosystem. This recently published habitat information is also important for fisheries managers focusing on Flathead Catfish because it can guide them to productive sampling areas and may suggest potential competitive or predatory interactions.

DIET

Flathead Catfish are among the least gape-limited apex predators (Slaughter and Jacobson 2008) and are opportunistic feeders that frequently consume shads, centrarchids, moronid bass, and crayfish (Weller and Robbins 1999; Vrtiska et al. 2003; Eggleton and Schramm 2004; Pine et al. 2005; Baumann and Kwak 2011; Schmitt et al. 2019). They also consume a diverse range of prey items, including macroinvertebrates and other fish species when abundant, as well as threatened and endangered species (Jolley and Irwin 2003; Pine et al. 2005; Baumann and Kwak 2011; Flowers et al. 2011; Walker et al. 2015; Schmitt et al. 2019). Flathead Catfish undergo an ontogenetic shift from eating macroinvertebrates and crayfish as juveniles to eating piscine prey when they reach about 300 mm TL (Jackson 1999; Baumann and Kwak 2011). Due to their predatory and piscivorous nature, Flathead Catfish can be used to control overabundant fish species (Odenkirk et al. 1999; Haas et al. 2001; Vrtiska et al. 2003; Schmitt et al. 2019). Prey selection generally appears to be opportunistic, with fish species being consumed in proportion to their abundance (Pine et al. 2005). However, Flathead Catfish may selectively feed on fish that share their benthic habitat (Turner 2017). Sampling of Flathead Catfish stomach contents is most efficiently done by using gastric lavage (Waters et al. 2004).

Flathead Catfish diets vary with changes in environmental conditions. Flathead Catfish primarily feed nocturnally (Weber and Brown 2012). Feeding rates decrease when water temperatures drop below 15°C and completely stop when water temperatures are below 7°C (Bourret et al. 2008). High water levels apparently increase food availability and can provide energetic benefits to Flathead Catfish (Mayo and Schramm 1999; Jones and Noltie 2007; Hogberg and Pegg 2016). Flathead Catfish diets are less variable among habitats than what is observed for other catfish species (i.e., Blue Catfish; Eggleton and Schramm 2004). Climate change can increase Flathead Catfish population sizes and affect their growth, resulting in increased predation on native fishes that may already be in decline as a result of changing environmental conditions (Rypel 2011; Whitney et al. 2014; Massie et al. 2018).

These diet studies are important for predicting the competitive and predatory effects of Flathead Catfish. Many of the diet studies published over the past two decades were conducted in the context of concerns that introduced Flathead Catfish could negatively affect native species through predatory impacts. However, even within their native range, diet studies are important and suggest that the generalist behavior of Flathead Catfish not only leads to its adaptability and success, but also makes it a potential competitor with many other piscivorous species.

MOVEMENTS

In the past two decades, there have been 23 published papers on the use of radiotelemetry or mark–recapture techniques to track movements of Flathead Catfish (Table 2). The majority of movement studies have been conducted in lotic systems on introduced populations of Flathead Catfish because fisheries managers were concerned about the spread of the species (i.e., Flathead Catfish can travel over 100 km in a year; Vokoun and Rabeni 2005b; Piette and Niebur 2011). However, Flathead Catfish are also highly mobile in reservoirs (Bayne et al. 2002).

Flathead Catfish are typically sedentary during the daytime and are most active at night (Daugherty and Sutton 2005b; Malindzak 2006; Vokoun and Rabeni 2006; Hedden and Gibo 2016). This information is consistent with the literature prior to 2000, which indicates that Flathead Catfish remain sedentary in dense cover and then move short distances to shallower water during the night to feed (Jackson 1999). Flathead Catfish exhibit their greatest diel movement during the summer season (Huck 2014*).

Based on literature published up to that time, Jackson (1999) and Pugh and Schramm (1999) reported that Flathead Catfish were largely sedentary and that movement was thought to be random, but research published since 2000 demonstrated three distinct migration periods (overwintering, prespawn/spawn, and late summer/fall), each followed by a low-movement period (Vokoun and Rabeni 2005b; Barada 2009; Garrett and Rabeni 2011; Gelwicks and Simmons 2011; Piette and Niebur 2011). The timing of these migration events is more dependent on water temperature than on calendar date (Piette and Niebur 2011; Hedden and Gibo 2016). Flathead Catfish congregate in deep (>4-m) holes and move little during winter when water temperatures are less than 14°C (Weller and Winter 2001; Meerbeek 2007). Flathead Catfish move from overwintering locations to shallower spring habitats when water temperatures reach 12–15°C in preparation for spawning. They remain in shallower habitat during summer and then move to deeper pool habitat (>4 m deep) when water temperature drops below 15–20°C in the fall (Piette and Niebur 2011). However, several studies noted that not all fish were involved in migrations (Dobbins et al. 1999; Vokoun and Rabeni 2005a; Gelwicks and Simmons 2011; Huck 2014; Hedden and Gibo 2016). Site fidelity is very high across years, although the specific sites used by individuals vary seasonally (Gelwicks and Simmons 2011; Piette and Niebur 2011; Shroyer 2011; Hedden and Gibo 2016). Site fidelity is observed even for fish that make long migrations (Piette and Niebur 2011; Hedden and Gibo 2016).

These recent movement studies provide valuable information that can assist fisheries managers in managing Flathead Catfish populations. First, these newly published movement patterns indicate that Flathead Catfish can be found in shallower water when the water temperature is above 20°C, which suggests that they can be most effectively sampled using low-frequency electrofishing (LFE) during that time. Second, the potential for long-range migrations suggests a mechanism by which invasive populations could spread. If barriers or manual removal methods are to be employed to limit invasive populations, these movement studies will be important because they provide evidence for the temporal and geographic extent of migration. However, studies addressing the effects of dams on Flathead Catfish have shown inconsistent findings. Aadland (2015*) found that Flathead Catfish were absent above dams in Minnesota, but Smith et al. (2021) found that Flathead Catfish have the ability to disperse despite the presence of dams. Lastly, there has historically been some question regarding whether Flathead Catfish populations should be managed riverwide or by river reach (Travnichek 2004). Although many fish are sedentary for portions of the year, recent studies (Travnichek 2004; Hamel et al. 2021) suggest that annual movement is sufficient to necessitate management of populations at the riverwide level.

SPAWNING AND REPRODUCTION

There has been little additional literature (two studies) on Flathead Catfish spawning biology since 2000. Flathead Catfish can produce 100,000 eggs or more, and they spawn in nesting cavities when the water temperature reaches 19–24°C in summer months (Jackson 1999). Flathead Catfish fecundity in the Mississippi River typically ranges from 1,637 to 5,025 eggs/kg (mean = 3,783 eggs/kg: Gima 2009), with female fish weighing 0.8–28.2 kg on average (mean = 8.0 kg: Gima 2009). They typically reach sexual maturity when they are 390 mm in length (Munger et al. 1994). Flathead Catfish utilize low-velocity areas with large structure (wing dikes, riprap, etc.) for spawning (Garrett 2010*). There has been no research addressing the proportion of adults in a population that spawn in a given year, whether the spawning pairs are monogamous, or whether the available spawning habitat could lead to a limitation of how many fish can spawn.

AGE AND GROWTH

There continue to be discrepancies in the literature regarding which aging structure produces the most accurate and precise age estimates for Flathead Catfish. Although, to our knowledge, no validation studies exist for Flathead Catfish annuli on any structure, daily rings on otoliths can be accurate up to 72 d but become less accurate as the fish ages (Sakaris et al. 2011). Otoliths are generally considered the most accurate and precise aging structure (Nash and Irwin 1999; Steuck and Schnitzler 2011) and have been used to age fish up to 34 years (Marshall et al. 2009a), although the assumption that otoliths produce accurate ages is speculative, as no validation data on otoliths have been published. While preparing otoliths for aging, both cutting and grinding methods produce high reader agreement, but cutting is more efficient (Sakaris and Bonvechio 2021). Pectoral spines typically produce younger age estimates than otoliths for older fish, suggesting that spines are less accurate (presumably due to the loss of growth rings in the central lumen of the spine, as occurs with Channel Catfish; Buckmeier et al. 2002). When pectoral spines are used, the basal recess section is easier to read than the articulating process (Jackson 1999; Koch et al. 2011).

The age at which differences in age estimates become apparent ranges from as early as age 1 to as late as age 17 (Olive et al. 2011; Steuck and Schnitzler 2011), with Nash and Irwin (1999) finding intermediate results (disagreements in their study began at age 5). There is no clear explanation for why investigators found different ages at which otolith- and spine-derived estimates begin to diverge, but it may be related to varying environmental conditions of the populations studied. Age accuracy with pectoral spine-based estimates for all but young fish is a clear concern, and there is a need for Flathead Catfish age validation studies.

There has been a modest amount of literature (15 publications) related to growth rates of Flathead Catfish in the past two decades (Table 2), with some generalizations. There is generally no difference in growth between sexes in rivers (Grabowski et al. 2004; Steuck and Schnitzler 2011), but males can grow longer than females in reservoirs (Marshall et al. 2009b). Flathead Catfish generally grow faster in rivers where they are introduced than in rivers where they are native (Grabowski et al. 2004; Kwak et al. 2006; Sakaris et al. 2006; Rypel 2013; Bonvechio et al. 2016; Hilling et al. 2019). Within their native range, Flathead Catfish generally grow faster in reservoirs than in rivers (Kwak et al. 2006; Lucchesi et al. 2017), but invasive riverine populations typically grow faster than fish in either habitat within the species' natural range (Kwak et al. 2006; Sakaris et al. 2006). Flathead Catfish can grow larger, older, and faster in areas where there is no commercial harvest compared to areas with commercial harvest (Donabauer 2009).

SAMPLING

Flathead Catfish are susceptible to capture by multiple gears, including LFE, hoop nets, gill nets, bank poles, and hook and line, but LFE is the most efficient sampling gear (Stauffer and Koenen 1999; McCain et al. 2011; Bodine et al. 2013; Mitchell 2016), with catch rates typically ranging from 19 to 62 fish/h (Bodine et al. 2013). Catch rates with LFE are highest in tailwater river reaches, habitats associated with riprap, and the main channels of free-flowing rivers (Jolley and Irwin 2011; McCain et al. 2011; Travnichek 2011b). The highest LFE catch rates are achieved using 15 pulses/s (pps) rather than 7.5 or 30.0 pps (Cailteux and Strickland 2007) and by sampling when water temperatures are over 20°C (Cunningham 2000). Morris (2018*) found no difference in the amount of power needed to immobilize Flathead Catfish at pulse rates from 8 to 80 pps yet concluded that 15 pps was the most efficient because it produced a larger field size and lower fish size bias (i.e., smaller fish required more power than large fish for immobilization). A chase boat is commonly used when sampling for Flathead Catfish with LFE in rivers (Daugherty and Sutton 2005d), but chase boats do not add to the efficiency of LFE sampling in lentic habitat (Cunningham 2004). Only one study has quantified the capture probability of LFE for Flathead Catfish (i.e., with a known or marked population); however, it was unable to assess the size bias of the gear (Pine 2003*) due to the model not converging with the small number of recaptures available. It has been suggested that LFE length-frequency data may underestimate the abundance of fish larger than 600 mm TL (Stauffer and Koenen 1999; Brown 2007a; Ford et al. 2011), but this remains untested.

Several other gears have also been evaluated in the past 23 years (Table 2). Hoop-net catch rates range from 0.03 to 0.33 fish/net set (Willenberg 2000; Bodine et al. 2013), and the nets are typically set unbaited from May through October (Ford et al. 2011) when the water reaches spawning season temperatures (26–28°C; Travnichek 2011b). However, the amount of sampling effort needed to catch enough fish for age and growth analyses and detect small population changes may be difficult to attain with hoop nets (Sindt 2018). Hook and line, bank poles, and high-frequency electrofishing are also methods used to sample Flathead Catfish, but catch rates are lower than those achieved with LFE (Bodine et al. 2013; Sullivan 2014;

Dean et al. 2021). Hoop nets and trotlines baited with live baitfish can be an effective method for collecting Flathead Catfish that are larger than 450 mm—size-classes for which other gears are thought to be less effective (Stauffer and Koenen 1999; Arterburn and Berry 2002; Gelwicks and Steuck 2011; Dickinson et al. 2018). Fishing tournament data can also be used to examine populations over time (Travnichek and Clemons 2001).

Most state agencies do not have a standardized sampling protocol for Flathead Catfish and report that they do not actively manage for Flathead Catfish populations (Michaletz and Dillard 1999). For agencies that follow a Flathead Catfish sampling protocol, LFE is the most common sampling gear used (Brown 2007a). Quantitative information on the gear bias of LFE or other gears used to sample Flathead Catfish is limited (Brown 2007a). Future studies involving gear performance evaluations are warranted to quantify the biases associated with each sampling gear for Flathead Catfish. To test the accuracy of a gear, a population of known size must be sampled. Passive integrated transponder tags have high retention when implanted in the dorsal musculature (Daugherty and Buckmeier 2009; Neely et al. 2021) and can be used to effectively mark Flathead Catfish populations for mark–recapture studies. Further research is also needed to determine why LFE causes fish to surface so far from the boat and what power level is needed to achieve this behavior (i.e., the behavior is difficult to induce under laboratory conditions; Morris 2018*).

MORTALITY RATES AND EXPLOITATION

Flathead Catfish populations that have been studied in the past two decades have low total mortality rates and are lightly exploited. Annual total mortality rates (A) of Flathead Catfish typically range from 0.14 to 0.62 in rivers where they are native (Willenberg 2000*; Daugherty and Sutton 2005c; Sakaris et al. 2006; Makinster and Paukert 2008; Hamel et al. 2021; Schall and Lucchesi 2021), from 0.11 to 0.40 in reservoirs (Winkelman 2011; Stubbs et al. 2015; Lucchesi et al. 2017; Muhlbauer and Krogman 2021), and from 0.16 to 0.37 in rivers where they have been introduced (Kwak et al. 2006; Sakaris et al. 2006; Kaeser et al. 2011; Rachels and Ricks 2015; Bonvechio et al. 2016; Hilling et al. 2019). One exception is the Satilla River, Georgia, where A was reported as 0.62 (Bonvechio et al. 2016) and 0.45 (Sakaris et al. 2006), presumably due to the years of electrofishing removals conducted in this system.

Annual exploitation rates in rivers range from 4.5% to 19.0% (Schall and Lucchesi 2021; Winders and McMullen 2021), and those in reservoirs range from 0% to 13% (Marshall et al. 2009a; Sullivan and Vining 2011; Travnichek 2011a; Bodine et al. 2016). These low annual mortality and exploitation rates are consistent with long-lived species (e.g., 34 years as reported by Marshall et al. 2009b), and this further suggests that overharvest is possible if angling pressure is high in a given location. However, changes in population dynamics (increased recruitment and earlier age at maturation) observed in invasive populations that are heavily harvested (manual removals by biologists) indicate that high harvest pressure may need to be sustained to maintain control of these invasive populations (Bonvechio et al. 2011).

HARVEST MANAGEMENT

The Flathead Catfish is popular among anglers, many of whom target trophy-sized fish (>864 mm; Arterburn et al. 2002; Dames et al. 2003*; Hurley and Duppong-Hurley 2005*). Flathead Catfish anglers are generally harvest oriented and use several methods to catch fish, including trotlines, juglines, limblines, rod-and-reel angling, and hand fishing ("noodling"; Jackson 1999; Reitz and Travnichek 2005; Hunt et al. 2012; Stewart et al. 2012). There is increasing interest in fishing for trophy catfish, and most Flathead Catfish anglers consider fish size to be more important than the quantity of fish caught (Arterburn et al. 2002). In addition, 75% of catfish anglers liked the idea of developing trophy catfish fisheries (Arterburn et al. 2002). However, literature focusing on methods to better manage this species for trophy production is scarce.

Noodling is a unique way to fish for Flathead Catfish wherein anglers use their hands to catch fish from their spawning cavities (Jackson 1999). Noodling can generate a negative perception because it can target large fish that may not otherwise be vulnerable to harvest, it potentially harms the reproductive success of nesting fish, and some feel that the method is not "sporting," thus leading to only limited participation in this activity among anglers (Jackson 1999; Reitz and Travnichek 2005; Brandes 2008). However, from the studies conducted on noodling since 2000, this harvest method does not appear to have a substantial negative impact on Flathead Catfish populations (Winkelman 2011; Bodine et al. 2016, 2021), so it can be a sustainable fishing method in areas where it is legal. Noodlers, despite being highly dedicated to their noodling pursuits, only fish 13–15 times per year on average and harvest few fish (1–3) per day (Morgan 2006, 2008; Bennett et al. 2017), resulting in low fishing mortality rates for noodling (Bodine et al. 2016). Jackson (1999) noted that commercial hoop nets set during the spawning season may have greater impacts on exploitation than noodling.

Modeling to assess the effects of length regulations has become more common in the past two decades. Overall, modeling suggests that regulations have little impact on Flathead Catfish populations because most populations have low fishing and natural mortality rates such that reducing harvest further has minimal benefit in shaping size structure (Oliver et al. 2021; Schall and Lucchesi 2021), a finding similar to those of modeling studies examining other ictalurid species (Stewart et al. 2016). However, regulations can be effective at changing Flathead Catfish populations under some conditions. For example, Makinster and Paukert (2008) simulated the effect of minimum length limits on population size structure in the Kansas River, Kansas, and found that the population could sustain up to 60% mortality before proportional stock density levels were affected. Moody-Carpenter et al. (2017) modeled regulations in the exploited Wabash River, Illinois–Indiana, and recommended that the minimum length regulation be raised to increase yield and reduce exploitation in a fishery with high commercial harvest (average annual mortality was about 50%). Furthermore, Muhlbauer and Krogman (2021) found that regulations could produce slight (1–2%) increases in the proportional stock density of Flathead Catfish populations. Models have also been used to determine that if angling mortality is sufficiently high, then angling harvest may substantially reduce the biomass of introduced Flathead Catfish populations (Sakaris et al. 2006; Pine et al. 2007), which could allow native fish communities to be restored. However, reductions in the age at maturation and increases in recruitment may produce feedback that makes this more difficult than models would suggest (Bonvechio et al. 2011). These modeling studies illustrate the utility of modeling in Flathead Catfish management, but there remains a need for empirical research evaluating regulation effectiveness and better guidance on how to enhance trophy production of Flathead Catfish.

HUMAN DIMENSIONS

Studies of human dimensions have become more common with regard to the three major ictalurid sport fish species (Channel, Blue, and Flathead catfish). Flathead Catfish are less popular with anglers than Blue and Channel catfish (Hutt et al. 2013), and only a small proportion of anglers correctly identified Flathead Catfish (most anglers commonly misidentified Flathead Catfish as Channel Catfish; Page et al. 2012). Demographically, catfish anglers are more likely to be middle-aged males who grew up in rural areas (Krogman and Stubbs 2021).

Most Flathead Catfish anglers prefer management for trophy sizes even though the majority of them are also harvest oriented (Dames et al. 2003; Reitz and Travnichek 2006; Hunt et al. 2012; Stewart et al. 2012; Hutt et al. 2013), and active Flathead Catfish anglers are more likely to be trophy oriented than lapsed anglers or anglers that do not specifically target the species (Krogman and Stubbs 2021). However, catfish anglers in Texas were more interested in having adequate catch rates than in catching trophy-sized fish (Schlechte et al. 2021), and the smaller group of Texas anglers that were trophy oriented were from distinctly rural areas, whereas more harvest-oriented anglers were urban.

Quality fishing locations are important for recruiting and retaining catfish anglers, so fisheries managers should focus on providing anglers with convenient fishing access areas and education about where and how to catch fish (Krogman and Stubbs 2021). Some managers are focusing on developing statewide "R3" (recruitment, retention, and reactivation) management plans to bolster catfish angling (Schlechte et al. 2021).

INTRODUCED POPULATIONS

More Flathead Catfish literature has been published in the past two decades on the topic of introduced populations than on any other topic (32 articles; Table 2). The northern extent of the Flathead Catfish's native range is the lower Great Lakes and Mississippi River basin from western Pennsylvania in the east to the White–Little Missouri River system in the west (USGS 2020). The southern portion of the species' native range extends south to the Gulf Slope from the Mobile Bay drainage in the east across to Mexico in the west (USGS 2020). Jackson (1999) provided a map of introduced populations as they were distributed at that time, which included several isolated sections of the Atlantic Slope, the Snake River basin, the Gila River basin extending into a small part of the Colorado River, and three sections extending upstream from the western edge of the native range into the North Platte, South Platte, and Arkansas rivers in Colorado and Wyoming. Since Jackson's (1999) article, Flathead Catfish have invaded the Great Lakes basin (originally by stocking in the 1800s; Fuller and Whelan 2018) and are now found in Lakes Erie, St. Clair, Huron, and Michigan, including nearly all Lake Michigan drainages on the Michigan side and the Fox/Wolf and Milwaukee River drainages on the Wisconsin side (Fuller and Whelan 2018). Flathead Catfish have also expanded into additional Chesapeake Bay tributaries (Schmitt et al. 2019) and are now also more extensively established along the Atlantic Slope (USGS 2020; Rachels 2021; Smith et al. 2021). The species' range also expanded from the native range along the Gulf Coast into parts of Alabama, Georgia, and Florida (USGS 2020). In short, Flathead Catfish now occur in all U.S. states except Alaska, Hawaii, Montana, Utah, and the New England states. Flathead Catfish often quickly establish a population and become abundant in areas where they have been introduced (Brown et al. 2005; Granfors 2014).

In their introduced range, Flathead Catfish nonselectively consume a diverse range of prey items consisting of macroinvertebrates, crayfish, and a variety of fish species (Weller and Robbins 1999; Pine et al. 2005; Baumann and Kwak 2011; Walker et al. 2015; Schmitt et al. 2019), which likely cascade into important food web effects. Introduced Flathead Catfish produce predation pressure that can negatively impact native fish communities (Bonvechio et al. 2009; Baumann and Kwak 2011; Dobbins et al. 2012; Steffenson et al. 2015; Lucchesi et al. 2017). Researchers can use bioenergetics modeling to assess the impacts of Flathead Catfish predation on native fish species and to estimate their consumptive demand (Tetzlaff et al. 2010; Evans et al. 2014; Hedden et al. 2016). Interestingly, Flathead Catfish have the highest energetic efficiency (i.e., lowest grams of prey required to grow a specific amount of predator biomass) among common piscivores in southern reservoirs (Evans et al. 2014), suggesting that they would not have as large of an effect on the prey community as other predators. However, Flathead Catfish often consume large quantities of prey such that they can produce noticeable assemblage changes in systems where they have been introduced. This may be due, in part, to the fact that Flathead Catfish can eat much larger prey than many other piscivores, allowing them to exert predation pressure on several year-classes of their prey species (Slaughter and Jacobson 2008). Furthermore, the presence of Flathead Catfish can change the behavior of native fishes in ways that also produce deleterious effects beyond direct consumption (Ward and Figiel 2013).

Most diet studies of invasive Flathead Catfish populations have focused on direct predation effects, with little consideration of competitive interactions (e.g., Herndon and Waters 2000; Pine et al. 2005; Walker et al. 2015; Hedden et al. 2016; Lucchesi et al. 2017; Schmitt et al. 2017, 2019). The focus on direct consumption likely stems from the large prey sizes that Flathead Catfish can consume (i.e., the lack of gape limitation; Slaughter and Jacobson 2008), which means that they can directly consume even modest-size adult sport fish (e.g., Largemouth Bass *Micropterus salmoides*) and that native species of concern may be vulnerable to predation for several years before they gain a size refuge, if ever. However, it seems that any direct predation effects of Flathead Catfish that have population-level consequences for their prey would surely also produce food web effects by affecting other piscivores in the system through competition, especially given that Flathead Catfish are nonselective for their prey (Pine et al. 2005). Two studies discussed possible effects of competition between invasive Flathead Catfish and native piscivores (Bonvechio et al. 2009; Baumann and Kwak 2011), but neither paper specifically studied this aspect using field data, so competitive effects remain speculative. Further research is needed to determine how invasive Flathead Catfish populations affect systems at the assemblage and food web levels.

In areas where Flathead Catfish are invasive, anglers and managers favor management efforts that reduce their abundance (Weller and Geihsler 1999). Recreational hand-crank electrofishing is an encouraged, legal form of harvest for invasive Flathead Catfish in North Carolina, but this practice has not proven effective at reducing population size (Moser and Roberts 1999; Fisk et al. 2019). Fisheries managers attempting to limit invasive Flathead Catfish population size have promoted unrestricted angling harvest (Jackson 1999) or have used LFE to manually remove Flathead Catfish and protect the native fish assemblages, such as native centrarchids and bullheads (Herndon and Waters 2000; Bonvechio et al. 2011, 2016). Modeling suggests that with sustained exploitation of nonnative Flathead Catfish populations (6–25%), native fish communities can be restored (Pine et al. 2007; Propst et al. 2015). These removal methods effectively reduced the biomass, population age structure, and number of large fish in the population, indicating that the methods are somewhat beneficial, but there is evidence that heavily exploited Flathead Catfish populations mature earlier and have increased recruitment, suggesting that removal efforts would need to be continued for population control (Bonvechio et al. 2011). Research is warranted to find effective and economically viable methods for controlling invasive Flathead Catfish populations.

CONCLUSION

The Flathead Catfish is a species sought by many anglers (Arterburn et al. 2002). Despite the increase in research on this species since 1999, there are information gaps on the biology and management of the Flathead Catfish, which is arguably the least studied of the large North American ictalurids (i.e., Blue, Channel, and Flathead catfish). During the past two decades, much has been learned about the movements and migrations of Flathead Catfish populations and the negative effects of Flathead Catfish on native fish species in systems where they have been introduced. Much less research has been conducted to guide management of the species as a sport fish. Many states do not recognize the Flathead Catfish as a sport fish and do not have a standardized protocol for sampling Flathead Catfish (largely because there is little information about the capture probability of sampling methods), and there has been little research conducted on the reproduction or spawning behavior of the species. Additional research is warranted to develop better trophy management strategies that many anglers desire. It is our hope that this review inspires research into this important but poorly studied sport fish and invasive species.

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