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Demographic and Life History Characteristics of Black Bullheads *Ameiurus melas* in a North Temperate USA Lake

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Abstract: Black bullheads *Ameiurus melas* are an environmentally tolerant omnivorous fish species that are found throughout much of North America and parts of Europe. Despite their prevalence, black bullheads are an infrequently studied species making their biology, ecology, and life history poorly understood. Although limited information has been published on black bullheads, evidence suggests that bullheads can dominate the fish biomass and have profound influences on the fish community in some north temperate USA lakes. The goal of our study was to provide additional information on black bullhead population demographics, growth rates, life history characteristics, and seasonal diet preferences in a northern Wisconsin lake. Using common fish collection gears (fyke netting, electrofishing), fish aging protocols, fecundity assessments, and diet indices, our results suggested that black bullheads exhibited relatively fast growth rates, early ages at maturity, moderate fecundity, and a diverse omnivorous diet. Due to these demographic and life history characteristics, black bullheads have the potential to dominate fish community biomass in their native and introduced range. Results from our study may inform the management of black bullhead as native and invasive species.

Keywords: bullhead; black bullhead; ameiurus; *Ameiurus melas*; life history; growth; reproductive potential; fecundity; maturity; sex ratio

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1. Introduction

Black bullhead *Ameiurus melas* are an ictalurid species that are common but often overlooked throughout their native range. Black bullheads are endemic to the Mississippi River drainages of North America, with populations extending from southern Saskatchewan to the Gulf of Mexico drainage near northern Mexico [1–3]. Black bullhead populations have become prevalent and widespread outside of their native range, notably across the western United States and Europe [4]. In these non-native systems, black bullheads are frequently considered invasive and (or) a nuisance [5–9] primarily due to driving undesired ecological effects [10,11]. In non-native systems, most introductions have been unintentional [5,6,10]. Following colonization, bullheads can dominate fish community biomasses, alter fish community composition, and have been shown to increase turbidity in small impoundments [10–12]. Colonization and invasive potential are often attributed to their environmental tolerance and omnivorous diet [4,5,10].

The prevalence of black bullheads can be attributed to their plastic habitat requirements and tolerance to suboptimal abiotic conditions. For example, black bullheads are tolerant to high water temperatures ($\leq$35 °C; [13]), low dissolved oxygen concentrations (>3.0 mg L^{-1}; [14]), and degraded water quality [12,13,15]. This plasticity in habitat requirements allows black bullheads to persist in most aquatic systems such as lakes (oligotrophic and eutrophic), ponds, impoundments, diked or flooded wetlands, low gradient streams, and backwaters across their native and non-native range [10,12,14]. Despite black bullhead populations being common and widespread throughout many systems across the world, they are infrequently studied, and there is a paucity of information on their demographics, life history, and ecological role in north-temperate lakes [4,16,17].

Over the past two decades, warm-water fishes such as largemouth bass *Micropterus salmoides*, bluegill *Lepomis macrochirus*, and likely black bullheads have been increasing in abundance, while cool-water species such as walleye *Sander vitreus* and yellow perch *Perca flavescens* have been decreasing [18–21]. The mechanism(s) behind the decline of these cool-water species are largely unknown but are likely variable among systems and related to climate change, habitat loss, production overharvest, invasive species, imbalances in fish communities, species-specific angler behaviors, and/or interactions among the aforementioned [11,21–26]. In concert or independently, these mechanisms are driving abiotic and biotic change [27]. Due to the black bullhead's plasticity in habitat requirements and tolerance, it seems plausible that they will thrive in these new environmental conditions and possibly fill devoid cool-water species niche space. Therefore, expanding knowledge and understanding of this understudied species is of critical importance.

The goal of our study was to provide additional information on black bullhead population demographics, growth rates, life history characteristics, and seasonal diet preferences in a north-temperate lake. The specific objectives of our study were to: (1) determine growth rates, fecundity, sex ratio, and age at maturity of black bullheads; and (2) determine seasonal diet composition of black bullheads. This type of information will increase our management and (if needed) control capabilities of this widely infrequently studied, highly tolerant species.

2. Materials and Methods

Black bullheads were sampled monthly from Howell Lake, Forest County, Wisconsin (45.9469436°, −88.9338069°). Howell Lake is an ideal system to study black bullhead demographics and life history due to the abundant nature of the population and diverse native fish community. Howell Lake is considered eutrophic with a surface area of 69 ha and maximum depth of 4 m. The fish assemblage in Howell Lake is representative of many Northern Wisconsin lakes, including black and yellow bullhead *A. natalis*, northern pike *Esox lucius*, walleye, largemouth bass, smallmouth bass *Micropterus dolomieu*, yellow perch, bluegill, black crappie *Pomoxis nigromaculatus*, pumpkinseed *Lepomis gibbosus*, rock bass *Ambloplites rupestris*, white sucker *Catostomus commersonii*, golden shiner *Notemigonus crysoleucas*, common shiner *Luxilus cornutus*, common creek chub *Semotilus atromaculatus*, and bluntnose minnow *Pimephales notatus*. Additionally, invasive rusty crayfish *Faxonius rusticus* and Chinese mystery snails *Cipangopaludina chinensis* are present in Howell Lake.

2.1. Black Bullhead Population Characteristics

Black bullhead sampling took place during May–October 2020 with standard fisheries gear including 6 fyke nets (13-mm mesh, 1.2-m tall, 1.8-m wide, and 15–23-m lead lines), 4 mini fyke nets (4.7-mm mesh, 0.9-m tall, 0.9-m wide, and 4.5–12-m lead lines), and boat-mounted AC electrofishing equipment. Fyke nets (standard and mini) were set weekly (24-h set, picked daily) at fixed locations in the littoral zone during mid-May–mid-August. Beginning in mid-April (after ice-out) and continuing through mid-October, the entire shoreline of Howell Lake was electrofished once monthly at night. As part of an ongoing removal study, all black bullheads that were captured on Howell Lake in 2020 were removed and the population of black bullheads >100 mm was estimated using a k-pass depletion estimate [28]. Up to 30 individuals per net per day and a minimum of 50 individuals from each electrofishing survey were measured for total length (TL; mm) and weight (g). From June 10–June 25, up to 10 fish per 13 mm length bin were retained for age estimation [29]. Retained fish were placed in individually labeled Ziploc bags with their respective lengths and weights, placed on ice in the field, and brought to the laboratory at the University of

Wisconsin-Stevens Point. In the laboratory, lapilli otoliths (commonly mistaken for sagittal otoliths in siluriformes; [30]) were extracted for age estimation [31]. Sex and maturity status (i.e., immature, mature) was determined by making a small incision near the vent and visually inspecting the gonads [32].

In the laboratory, otoliths were placed in distinctly numbered vials and allowed to dry for a minimum of two weeks prior to processing [33]. Individual otoliths were placed in the wells of a 24-cavity silicone baking tray and fully submerged in West System 105/206B slow hardening two-part epoxy. After curing for a minimum of 48 h, otoliths were removed and cut through the focus on a Beuhler low-speed isomet saw, were lightly hand-sanded with wetted 1000-grit carborundum sandpaper and covered with a drop of immersion oil [33]. The epoxy that contained the halved otolith was placed under a Nikon® SMZ1500N dissecting microscope (30× magnification; Nikon, Tokyo, Japan) and illuminated from the side with a 1-mm diameter, single-strand fiber optic filament connected to a light source (Fiber-Lite model 180; Dolan-Jenner Industries, Inc., St. Lawrence, MA, USA) [34]. When all annuli were illuminated, the otolith was photographed. Ages were estimated double-blind by two independent readers by enumerating the observed annuli on otoliths. Consensus age estimates were then used for subsequent analyses.

Age estimates were used to construct an age–length key for black bullheads in Howell Lake, which was used to assign ages to un-aged fish for maturity and age and growth models (Table 1; [35]). Black bullhead growth on Howell Lake was evaluated using length at age data to inform the von Bertalanffy growth relationship [36], and by estimating mean length-at-age. Bullhead size structure was determined using proportional size distribution (PSD-X) indices [37].

Table 1. Age-length key based on 197 black bullheads *Ameiurus melas* sampled and aged in June 2020 from Howell Lake, Wisconsin. The proportion of fish in each age-length combination is followed by the number fish that were sampled in that combination in ().

	Age (year)								
Length (mm)	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**
50	1.00 (3)								
60	1.00 (10)								
70	1.00 (6)								
80	1.00 (3)								
90	0.67 (2)	0.33 (1)							
100	0.33 (1)	0.67 (2)							
120		0.60 (3)	0.40 (2)						
130		0.40 (2)	0.60 (3)						
140		0.14 (1)	0.71 (5)	0.14 (1)					
150		0.40 (2)	0.40 (2)	0.20 (1)					
160			0.62 (5)	0.38 (3)					
170			0.73 (8)	0.27 (3)					
180			0.75 (6)	0.25 (2)					
190			0.33 (4)	0.67 (8)					
200			0.25 (2)	0.75 (6)					
210			0.10 (1)	0.70 (7)	0.20 (2)				
220			0.18 (2)	0.36 (4)	0.27 (3)	0.09 (1)	0.09 (1)		
230			0.11 (1)	0.33 (3)	0.22 (2)	0.33 (3)			
240				0.17 (2)	0.25 (3)	0.50 (6)	0.80 (1)		
250					0.11 (1)	0.89 (8)			
260					0.08 (1)	0.62 (8)	0.31 (4)		
270						0.60 (6)	0.20 (2)	0.10 (1)	0.10 (1)
280						0.18 (2)	0.55 (6)	0.18 (2)	0.09 (1)
290						0.14 (1)	0.29 (2)	0.29 (2)	0.29 (2)
300							0.17 (1)	0.50 (3)	0.33 (2)
310								1.00 (2)	

Weighted catch-curve regressions were used to estimate the total annual mortality of black bullheads in Howell Lake [38]. Based on the catch curve, we assumed that fish ≥ age-3 were fully recruited to the fyke nets; therefore, fish <age-3 were not included in regression analysis. The catch curve was developed from fish sampled from June 2–June 25, and we used fishes that had age estimated directly from otoliths and fish that were assigned ages based on the developed age-length key. Catch curves were developed by regressing the natural log catch of fish against age and the slope-estimated instantaneous total mortality (Z) and total annual mortality ($A = 1 - e^{-z}$; [35]). Because there is relatively little fishing pressure for bullheads in Wisconsin and Howell Lake's remote location, fishing mortality was assumed to be negligible, and any measured mortality was assumed to be natural mortality.

2.2. Spawning, Maturity, and Fecundity

The sex ratio of black bullheads in Howell Lake was estimated based on the number of males to females that were observed during sampling. The estimated sex ratio was expanded to the entire sample in a manner consistent with [29]. Sex-specific length at 50% maturity (L_{50}) and length at 90% maturity (L_{90}) was determined using logistic regression where 0 denoted immature or unknown sex fish and 1 denoted mature fish.

Ripe female black bullheads were used for fecundity and reproductive potential estimation. Sampling of these fish coincided with those that were sampled for age structures, which took place from June 10–June 25. Up to 5 females per 13 mm length bin were placed in individual Ziploc bags, labeled with their respective total lengths and weights, placed on ice in the field, and brought to the laboratory. In the laboratory, both ovaries were removed and weighed to the nearest 0.1 g. Both ovaries from each fish were agitated and rinsed to remove remnant ovarian tissue. A sub-sample of eggs were taken as a 0.5–1.5 cm cross-section from the middle of each ovary. The subsample weights varied from 10–100% of the weight of the whole ovary. The subsample of eggs was weighed and photographed for enumeration. The total number of eggs in each ovary was estimated with the equation:

$$\text{Ovary}_1 = \left(\frac{\text{Subsample Count}}{\text{Subsample Weight}}\right) \times \text{Total Ovary Weight} \tag{1}$$

and the total fecundity for each fish was estimated by adding the estimates of both ovaries together.

Fecundity estimates were paired with our population estimate, size structure, and sex ratio data to produce reproductive potential estimates for black bullheads in Howell Lake. Mean fecundity estimates were multiplied by the estimated number of females in each Gabelhouse length category [37] to determine the cumulative reproductive potential of the population.

2.3. Seasonal Diet Analysis

Up to 300 black bullheads, captured via electrofishing, were retained each month for diet analysis. Upon capture, fish were placed on ice and then brought to the WIDNR, Escanaba Lake Field Station, where they were frozen. Frozen bullheads were later brought to and processed at the University of Wisconsin-Stevens Point. After thawing, bullheads were measured for total length (mm) and weighed (g). Stomachs were extracted ventrally. Prey items were then removed, identified to the lowest possible taxonomic category (species for fishes, order or family for invertebrates), enumerated, and individual prey items were weighed wet (nearest 0.1 g).

Diets were quantified by the percentage stomachs with contents, frequency of occurrence (O_i), mean percent composition by number (MN_i), mean percent composition by weight (MW_i), and index of relative importance (IRI) for each prey taxa for each month and stratified by bullhead length (length categories from [37]) [39–42]. For analysis, each fish species in the diets were individual categories except for minnow species (common shiner and bluntnose minnow), which were pooled to create the "Cyprinid" category. Items that fell within the following categories were pooled into the appropriate category: aquatic invertebrates, terrestrial insects, and other diet items. A multivariate analysis of variance

(MANOVA) was used to test whether differences in diet were present among month of collection (May and October were excluded from the statistical analysis due to the low sample size leading to violation of the MANOVA's assumption of equal variance). If results from the MANOVA were statistically significant ($\alpha \geq 0.05$), a Tukey's HSD test for multiple comparisons was used to determine which comparisons were significantly different.

3. Results

3.1. Black Bullhead Population Characteristics

The black bullhead population (>100 mm) in Howell Lake was estimated to be 24,479 fish (95% CI = 24,171 −24,787) with an estimated density of 355/fish ha. A total of 20,952 black bullheads were sampled over the study period, ranging in length from 25 to 325 mm (mean = 197 mm; SE = 0.70; Figure 1), weight from 1 g to 474 g (mean = 121; SE = 1.34), and age from 1–9 (Figure 2). The population exhibited high natural mortality (A = 40.5%; Z = 0.52; Figure 3) and relatively fast growth rates ($L\infty$ = 381 mm; K = 0.17; $t_0 = -0.64$; Table 2; Figure 4). Mean lengths at ages 1–9 were 80, 132, 180, 196, 235, 260, 274, 297, and 292 mm, respectively (Table 2). Of 4966 fish that were sampled and measured in 2020, 90% of the fish were of stock length (>150 mm), 22% of the fish were of quality length (>230 mm), and only 1% of the fish were preferred length (Figure 1).

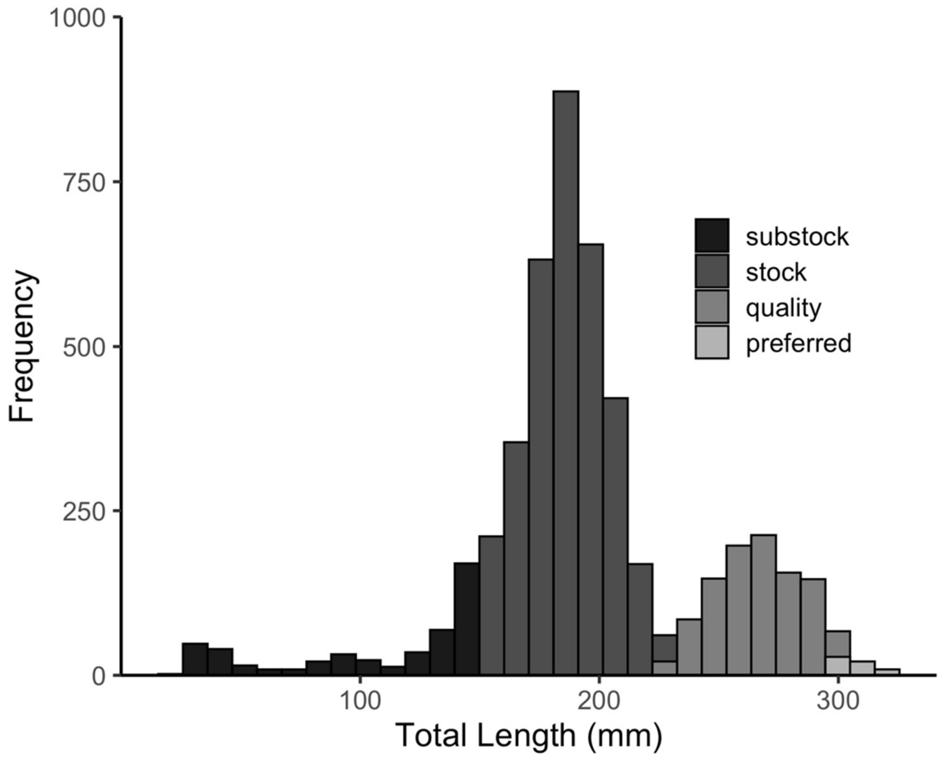

Figure 1. Length-frequency histogram for black bullheads *Ameiurus melas* (n = 4966) sampled in 2020 from Howell Lake, Wisconsin. Colors are representative of the respective Gabelhouse (1984) length categories.

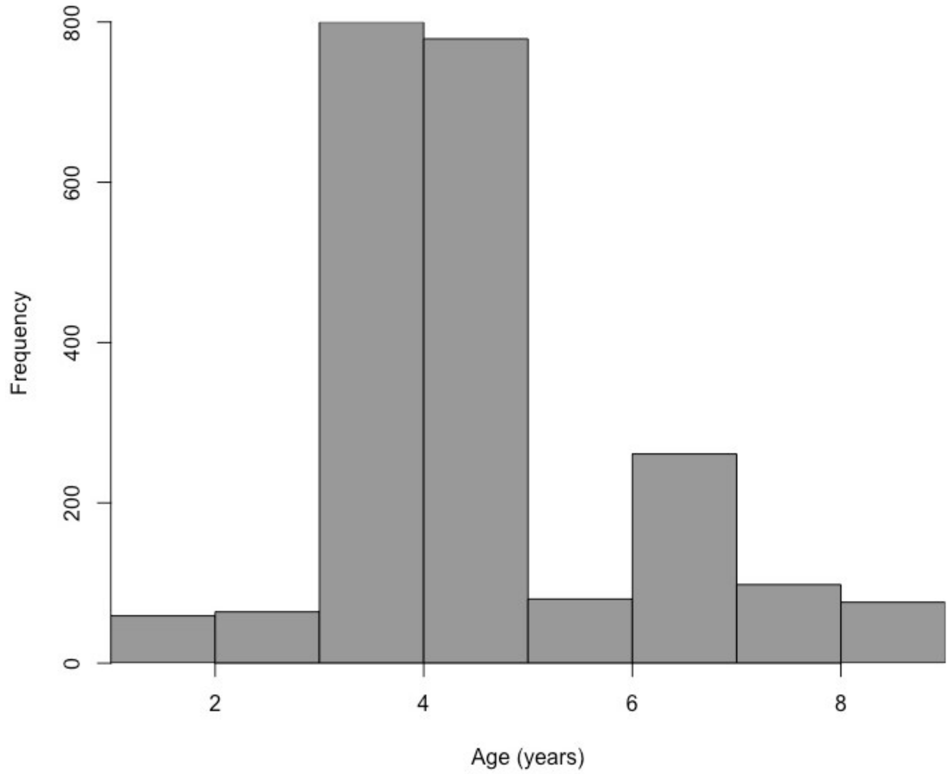

Figure 2. Age-frequency histogram for black bullheads *Ameiurus melas* (n = 4966) sampled in 2020 from Howell Lake, Wisconsin.

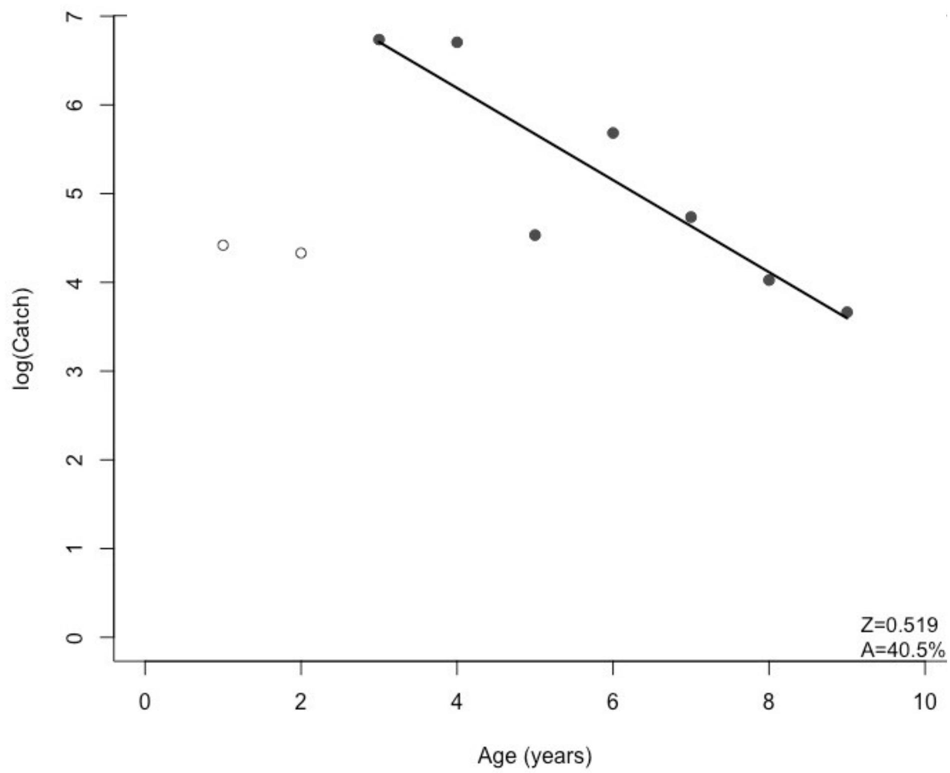

Figure 3. Catch-curve for black bullheads *Ameiurus melas* ≥age-3 sampled in June 2020 from Howell Lake, Wisconsin. Z is representative of the slope of the descending limb of the catch curve and represents instantaneous mortality and A represents the total annual mortality of the population.

Table 2. Mean length at age with standard deviation (SD) and predicted length at age from the von Bertalanffy growth function with 95% confidence intervals from black bullheads *Ameiurus melas* sampled from Howell Lake, Wisconsin.

Age (year)	N	Mean Length (mm)	Standard Deviation (SD)	Predicted Length (mm)	Lower 95% CI	Upper 95% CI
1	84	80	15.0	90	87	93
2	76	132	22.0	135	133	136
3	842	180	18.3	172	171	173
4	816	196	18.0	204	203	205
5	92	235	17.3	231	230	233
6	295	260	14.6	254	253	256
7	117	274	18.5	274	272	276
8	57	297	14.0	290	288	283
9	35	292	11.1	304	301	307

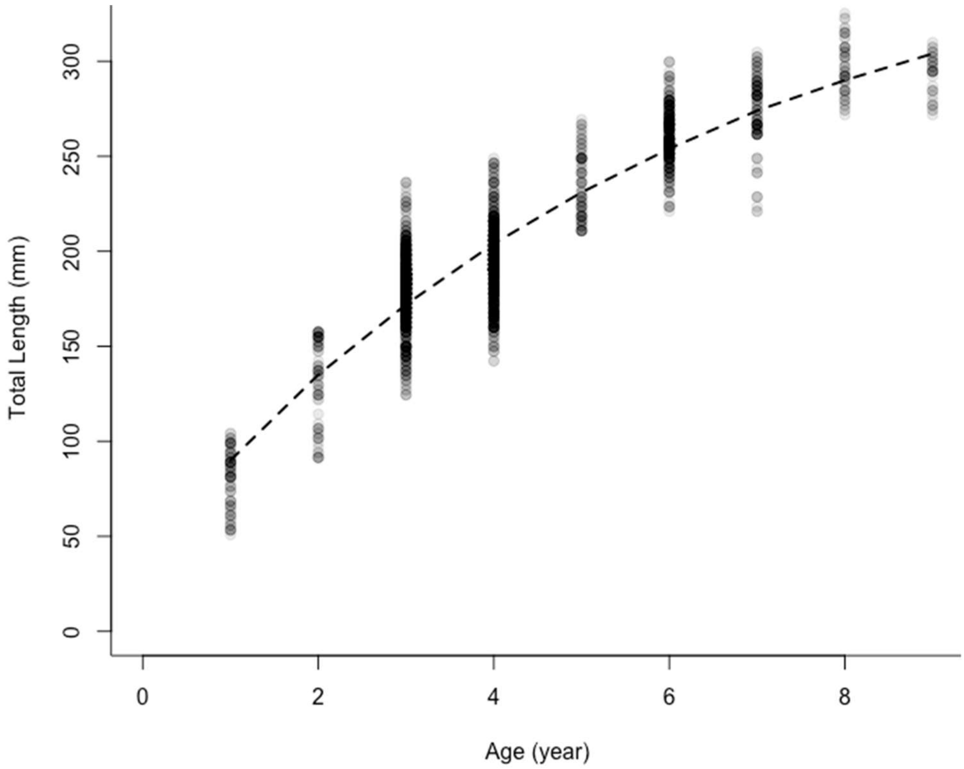

Figure 4. Best fit von Bertalanffy growth model for black bullheads *Ameiurus melas* sampled in June 2020 from Howell Lake, Wisconsin.

3.2. Spawning, Maturity, and Fecundity

In 2020, black bullhead spawning activity (nest building) was first observed on June 17 (21 °C), and fish were last observed on nests on August 3 (24 °C). Of the 959 fish sampled, the male to female ratio was nearly equal and was estimated to be 0.93:1.00 males to females. The shortest sexually mature male and female black bullheads were sampled on June 16, 2020, and were 124 mm and 127 mm, respectively. Estimated length at maturity was similar between male and female bullheads, with L_{50} = 133 mm (95% CI = 124–143 mm) for males and 134 mm (95% CI = 125–143 mm) for females. Additionally, L_{90} was 144 mm (95% CI = 126–151 mm) for males and was 144 mm (95% CI = 126–151 mm) for females (Figure 5).

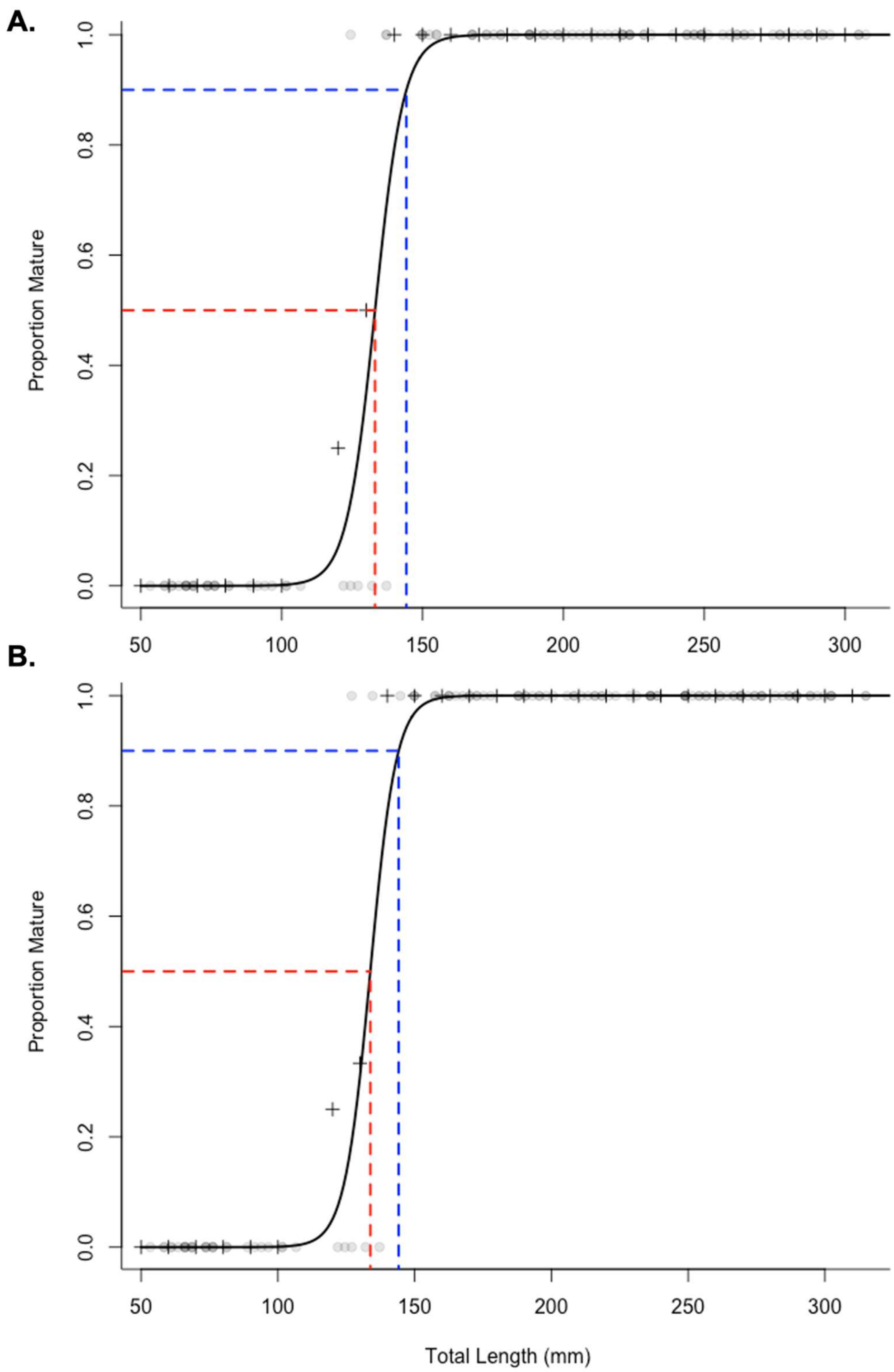

Figure 5. Logistic regression results showing length at maturity for male (**A**) and female (**B**) black bullheads *Ameiurus melas* sampled in June 2020 from Howell Lake, Wisconsin. Value 0 indicates sexually immature or unknown fish, while 1 represents sexually mature fish. The red dashed lines indicate the length at 50% maturity (L_{50}) and the blue dashed lines indicate the length at 90% maturity (L_{90}).

Ovaries of 62 sexually mature female black bullheads ranging in length from 134–308 mm (mean = 227 mm; SE = 5.81) were examined to estimate fecundity. Substock length fish (<150 mm) had a mean fecundity of 1518 eggs/female (n = 2; range = 1050–1986); stock length fish (150–230 mm) had a mean fecundity of 2,133 eggs/female (n = 30; SE = 166.72; range = 513–4128); quality length (230–300 mm) had a mean fecundity of 4319 eggs/female

(n = 27; SE = 459.29; range = 1365–12,337); and preferred length (300–390 mm) had a mean fecundity of 5,485 eggs/female (n = 3; SE = 671.78; range = 4193–6449; Figure 6). An estimated 7% of the female bullheads sampled were deemed immature. Substock length fish were estimated to comprise 3% of the sexually mature female black bullheads in Howell Lake potentially resulting in the production of an estimated 488,247 eggs (95% CI = 339,014–641,221); stock length fish were estimated to comprise 73% of the sexually mature female population, potentially resulting in the production of an estimated 17,821,634 eggs (95% CI = 4,286,216–34,490,250); quality length fish were estimated to make up 22% of the sexually mature female population, potentially resulting in the production of an estimated 10,985,501 eggs (95% CI = 3,471,917–31,379,515); and preferred length fish were estimated to make up 2% of the of the sexually mature female population, potentially resulting in the production of an estimated 784,082 eggs (95% CI = 599,390–921,886). The total reproductive potential of mature female black bullheads in Howell Lake was estimated to be 30,081,334 eggs (95% CI = 8,696,537–67,432,872).

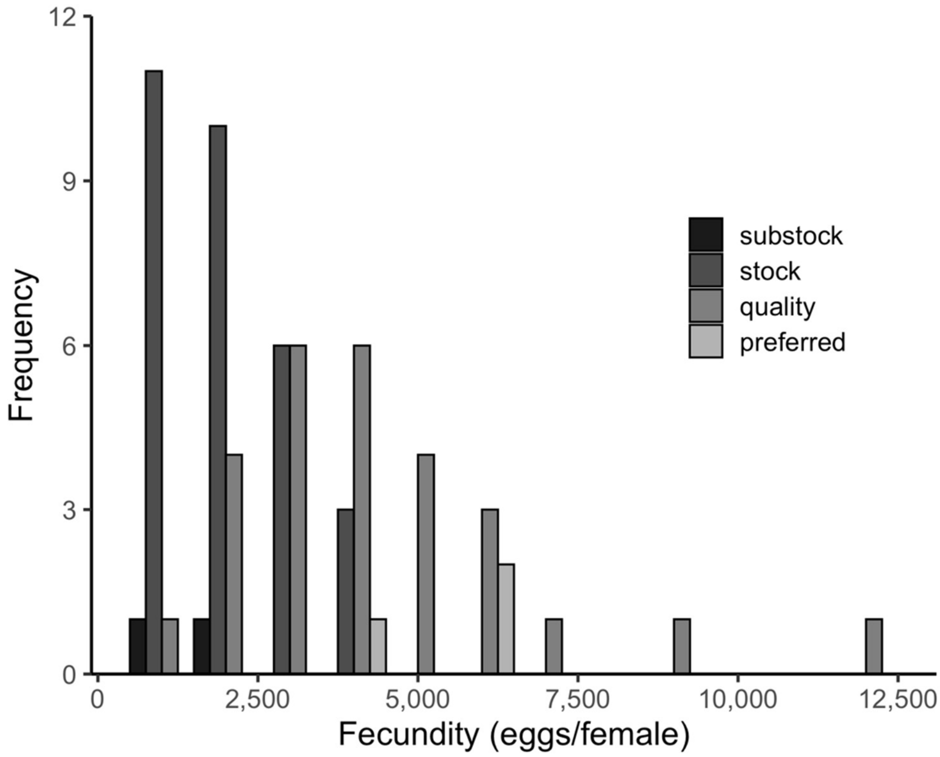

Figure 6. Frequency histogram showing black bullhead *Ameiurus melas* fecundity (eggs/female; n = 62) by Gabelhouse (1984) length category for Howell Lake, Wisconsin in June 2020.

3.3. Seasonal Diet Analysis

Of the 853 bullheads dissected for diet analysis during May–October 2020, 57% had empty stomachs (n = 452). The highest proportion of fish with empty stomachs were sampled in October at 70%, while the lowest proportion of empty stomachs were sampled in August at 47% (n = 387). Black bullheads that were dissected ranged in length from 116–308 mm (mean = 200 mm; SE = 1.03) and ranged in weight from 11–308 g (mean = 119 g; SE = 1.59). The diets of the bullheads were diverse, including seven different fish species, fish eggs, nine aquatic invertebrate taxa, three terrestrial insects, aquatic plant material, detritus, and unknown contents (Table 3). Of the diet items, snails were the most common diet item overall and yellow perch were the most common fish species for nearly every length category of bullhead during every month of sampling (Table 3; Figure 7).

Table 3. Frequency of occurrence (O_i) for seasonal diet composition of black bullheads *Ameiurus melas* collected from May–October 2020 from Howell Lake, Wisconsin. The number of fish preyed on each diet item is indicated in ().

Diet Item	May	June	July	August	October
	Oi	Oi	Oi	Oi	Oi
Fish					
Bluegill (*Lepomis macrochirus*)			0.7 (1)	1.5 (2)	16.7 (1)
Yellow Perch (*Perca flavescens*)		1.0 (1)	8.3 (12)	3.8 (5)	
Black Crappie (*Pomoxis nigromaculatus*)				0.8 (1)	
Black Bullhead (*Ameiurus melas*)					16.7 (1)
Walleye (*Sander vitreus*)	7.1 (1)				16.7 (1)
Common Shiner (*Luxilus cornutus*)		1.0 (1)		1.5 (2)	
Bluntnose Minnow (*Pimephales notatus*)				2.3 (3)	
Eggs	14.3 (2)				
Aquatic Invertebrates					
Gastropod (snails)	35.7 (5)	18.5 (19)	67.6 (98)	63.9 (85)	50 (3)
Arthropoda (crayfish)		3.9 (4)	1.4 (2)	1.5 (2)	16.7 (1)
Ephemeroptera (larvae)	7.1 (1)	4.9 (5)		0.8 (1)	
Odonota (larvae)	21.4 (3)	4.9 (5)	0.7 (1)	1.5 (2)	
Dytiscidae (beetle)		1.9 (2)			
Diptera (larvae and pupae)		1 (1)	2.6 (3)	12.8 (17)	
Trichoptera (larvae)				1.5 (2)	
Hirundea (leeches)	28.6 (4)	2.9 (3)		1.5 (2)	
Terrestrial Insects					
Odonota (adult)		1.9 (2)	0.7 (1)		
Tipulidae (adult)		1.9 (2)		0.8 (1)	
Lepidoptera (adult)		1.0 (1)			
Other					
Aquatic Vegetation		17.5 (18)	17.2 (25)	14.3 (19)	
Detritus	21.4 (3)	38.8 (40)	8.3 (12)	3.8 (5)	
Unknown		1.0 (1)			

In May, seven stock length and seven quality length bullheads with stomach contents were sampled. The diets sampled consisted of fish eggs, a walleye, and aquatic invertebrates (snails, leeches, Ephemeroptera, and Odonata; Table 3). Detritus occurred in 43%, snails in 36%, aquatic insects (Odonata) 4%, and fish eggs in 24% of the stomachs from stock length fish. Snails occurred in 29%, leeches in 5%, aquatic insects in 2% (Ephemeroptera, Odonata) in 28%, walleye in 14%, and fish eggs in 14% of quality length fish sampled in May.

In June, two sub-stock lengths, 70 stock length, 27 quality length, and four preferred length bullheads with stomach contents were sampled. The diets sampled consisted of yellow perch, common shiner, terrestrial insects (Tipulidae, Odonata, and Lepidoptera), aquatic invertebrates (snails, crayfish, leeches, Ephemeroptera, Dytiscidae, and Chironomidae), aquatic plant material, detritus, and some unknown contents (Table 3). Detritus occurred in 50% and aquatic insects in 50% of the stomachs from sub-stock length fish. Detritus occurred in 49%, aquatic plants in 14%, snails in 14%, aquatic insects in 17%, terrestrial insects in 1%, leeches in 3%, crayfish in 3%, and unknown contents in 3% of the stomachs from stock length fish. Detritus occurred in 30%, aquatic plants in 30%, snails in 33%, aquatic insects in 4%, terrestrial insects in 4%, leeches in 4%, crayfish in 7%, and yellow perch in 4% of the stomachs from quality length fish. Aquatic plants occurred in 50%, terrestrial insects in 25%, and common shiner in 25% of the stomachs from preferred length fish.

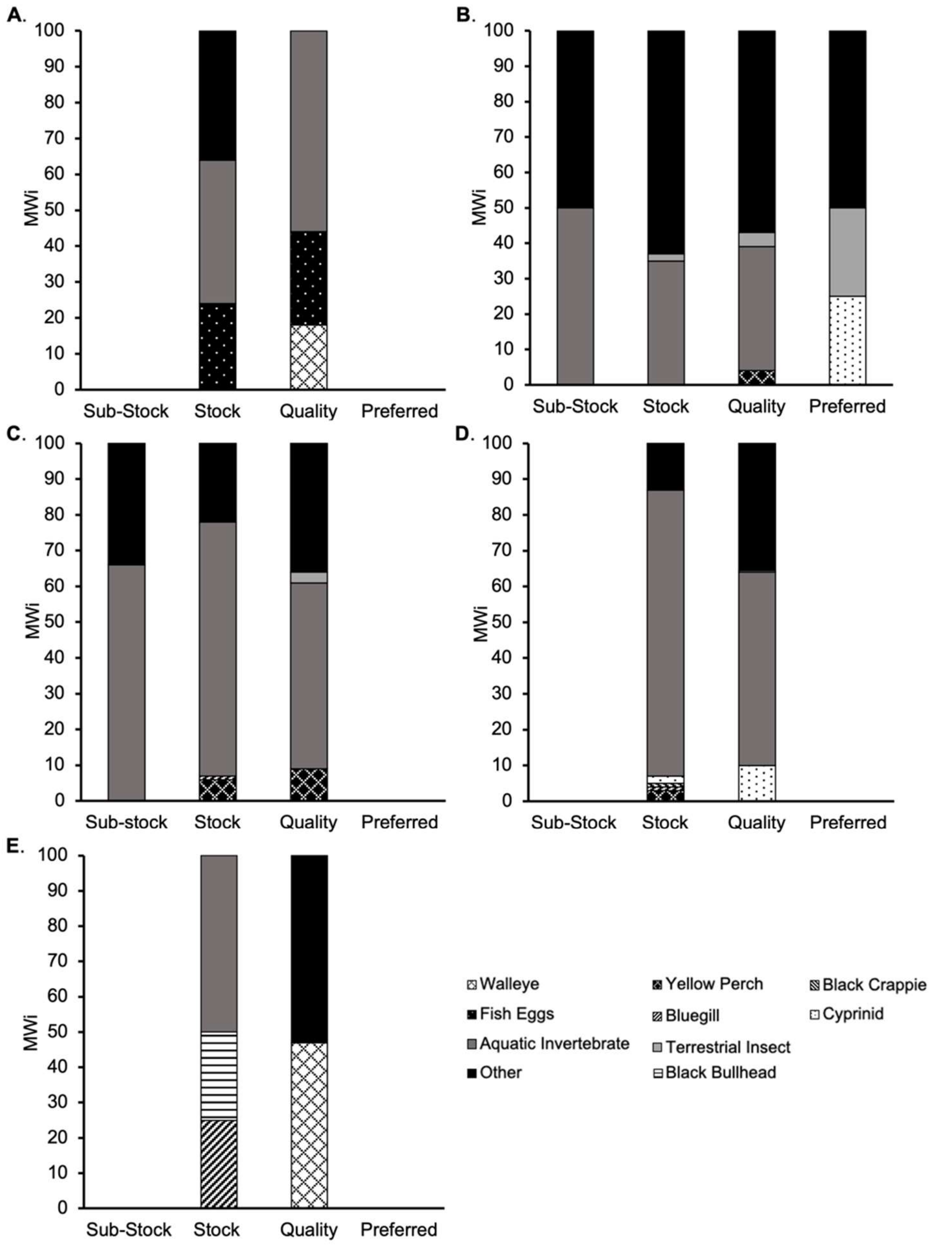

Figure 7. Mean percent composition by weight (*MWi*) of diet items from black bullheads *Ameiurus melas* separated into appropriate Gabelhouse (1984) length categories sampled from Howell Lake, Wisconsin in May (**A**), June (**B**), July (**C**), August (**D**), and October (**E**) of 2020.

In July, four sub-stock lengths, 130 stock length, and 11 quality length bullheads with stomach contents were sampled. The diets sampled consisted of yellow perch, bluegill, snails, crayfish, terrestrial insects (Odonata), aquatic insects (Odonata and Chironomidae), aquatic plant material, and detritus (Table 3). Detritus occurred in 50% and snails in 50% of the stomachs from sub-stocked length fish. Detritus occurred in 8%, aquatic plants in 16%, snails in 71%, aquatic insects in 2%, yellow perch in 8%, and bluegill in 1% of the stomachs from stock length fish. Aquatic plants occurred in 36%, snails in 45%, terrestrial insects in 9%, crayfish in 18%, and yellow perch in 9% of the stomachs from quality length fish.

In August, 115 stock length, 17 quality length, and one preferred length bullhead with stomach contents were sampled. The diets sampled consisted of yellow perch, bluegill, black crappie, common shiner, bluntnose minnow, snails, crayfish, leeches, terrestrial insects (Tipulidae), aquatic insects (Ephemeroptera, Odonata, Diptera, Trichoptera, and Chironomidae), aquatic plant material, and detritus (Table 3). Detritus occurred in 3%, aquatic plants in 11%, snails in 70%, aquatic insects in 15%, yellow perch in 3%, bluegill in 2%, cyprinids in 3%, and black crappie in 1% of the stomachs from stock length fish. Detritus occurred in 6%, aquatic plants in 35%, snails in 29%, aquatic insects in 24%, terrestrial insects in 6%, leeches in 12%, crayfish in 12%, and cyprinids in 12% of the stomachs from quality length fish. Yellow perch occurred in the one stomach from the preferred length fish.

In October, four stock length and two quality length bullheads with stomach contents were sampled. The diets sampled consisted of bluegill, a walleye, black bullhead, snails, and one crayfish (Table 3). Snails occurred in 25%, crayfish in 25%, bluegill in 25%, and black bullhead in 25% of the stomachs from stock length fish. Snails occurred in 100%, and walleye in 50% of the stomachs from the quality length fish.

Across all lengths, months and diet items, snails had the highest *IRI,* with trichopterans having the lowest *IRI* (Table 4; Figure 8). Of all prey items, snails had the highest O_i, MN_i, and MW_i throughout the study (Tables 3, 5 and 6; Figures 9 and 10). MW_i of diet items significantly differed over June, July, and August ($p < 0.001$, $df = 2$, $f = 6.82$; Table 4; Figure 7). No differences were found for the MW_i of diet items over June, July, and August for aquatic vegetation ($p = 0.45$), crayfish ($p = 0.58$), leeches ($p = 0.18$), yellow perch ($p = 0.08$), cyprinids ($p = 0.07$), bluegills ($p = 0.55$), black crappie ($p = 0.39$), and unknown diet items ($p = 0.16$; Table 4; Figure 5). Significant differences in the MW_i were observed among months for snails, terrestrial insects, aquatic insects, and detritus (Table 6; Figure 10). Snails accounted for less of the MW_i in June than in July ($p \leq 0.001$) and August ($p < 0.001$), but the MW_i of snails did not differ between July and August ($p = 0.60$; Table 6; Figure 10). Similarly, detritus accounted for significantly less of the MW_i in June compared to July (p <0.001); and August (p <0.001); July and August did not differ ($p = 0.52$; Table 6; Figure 10). The *MWi* of terrestrial insects followed the same trend being significantly less in June ($p = 0.03$; 0.02, respectively) and July and August not being different ($p = 0.98$; Table 6; Figure 10). Aquatic insects were similar and most common in diets from June and August ($p = 0.80$), while July significantly differed from both months ($p = 0.02$; 0.001, respectively; Table 6; Figure 10).

Table 4. Index of relative importance (*IRI*) for seasonal diet composition of black bullheads *Ameiurus melas* collected from May–October 2020 from Howell Lake, Wisconsin.

Diet Item	May	June	July	August	October
	IRI	IRI	IRI	IRI	IRI
Fish					
Bluegill (*Lepomis macrochirus*)			0.01	0.03	5.57
Yellow Perch (*Perca flavescens*)		0.02	1.13	0.25	
Black Crappie (*Pomoxis nigromaculatus*)				0.01	
Black Bullhead (*Ameiurus melas*)					5.57
Walleye (*Sander vitreus*)	0.64				4.01
Common Shiner (*Luxilus cornutus*)		0.02		0.03	
Bluntnose Minnow (*Pimephales notatus*)				0.07	
Eggs	15.55				
Aquatic Invertebrates					
Gastropod (snails)	10.67	6.68	89.49	78.28	37.98
Arthropoda (crayfish)		0.22	0.03	0.04	5.57
Ephemeroptera (larvae)	0.02	0.46		0.00	
Odonota (larvae)	4.10	0.48	0.01	0.00	
Dytiscidae (beetle)		0.07			
Diptera (larvae and pupae)		0.01	0.10	3.19	
Trichoptera (larvae)				0.01	
Hirundea (leeches)	4.85	0.15		0.02	

Table 4. *Cont.*

Diet Item	May	June	July	August	October
	IRI	IRI	IRI	IRI	IRI
Terrestrial Insects					
Odonota (adult)		0.05	0.00		
Tipulidae (adult)		0.04		0.00	
Lepidoptera (adult)		0.02			
Other					
Aquatic Vegetation		3.21	2.77	1.76	
Detritus	3.42	15.95	0.65	0.13	
Unknown		0.02			

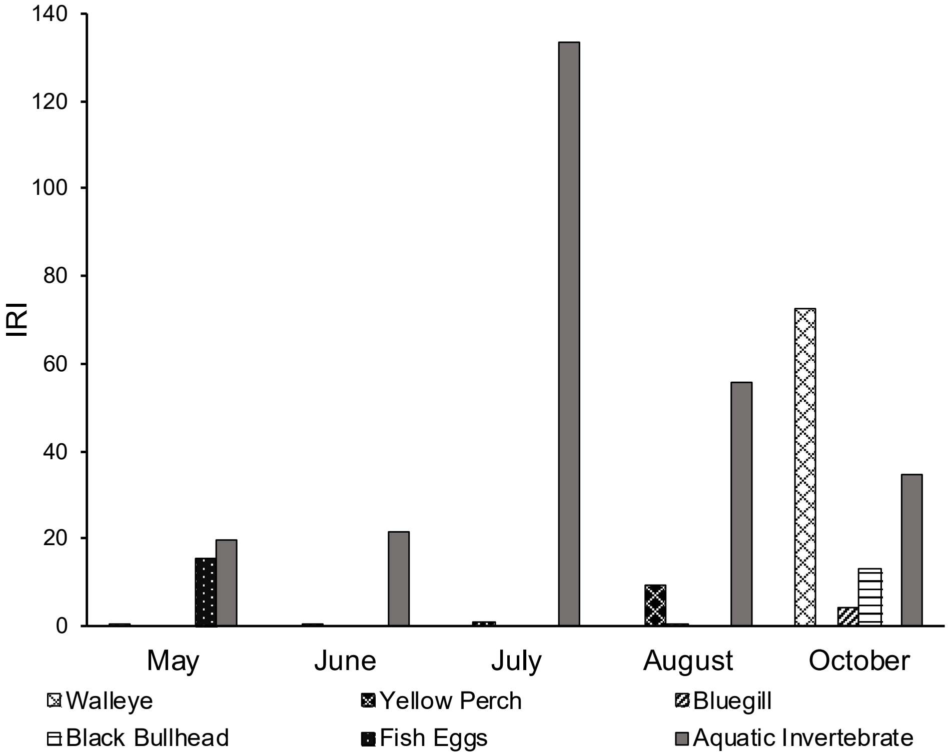

Figure 8. Index of relative importance (*IRI*) of diet items from black bullheads *Ameiurus melas* sampled from Howell Lake, Wisconsin in May, June, July, August, and October 2020.

Table 5. Mean % composition by number (MN_i) for seasonal diet composition of black bullheads *Ameiurus melas* collected from May–October 2020 from Howell Lake, Wisconsin.

Diet Item	May	June	July	August	October
	Mni	Mni	Mni	Mni	Mni
Fish					
Bluegill (*Lepomis macrochirus*)			0.69	1.13	16.67
Yellow Perch (*Perca flavescens*)		0.97	7.47	3.38	
Black Crappie (*Pomoxis nigromaculatus*)				0.38	
Black Bullhead (*Ameiurus melas*)					16.67
Walleye (*Sander vitreus*)	0.25				8.33
Common Shiner (*Luxilus cornutus*)		0.97		0.75	
Bluntnose Minnow (*Pimephales notatus*)				1.45	
Eggs	85.86				

Table 5. *Cont.*

Diet Item	May	June	July	August	October
	Mni	Mni	Mni	Mni	Mni
Aquatic Invertebrates					
Gastropod (snails)	7.00	18.01	66.55	61.92	41.67
Arthropoda (crayfish)		3.11	0.92	1.13	16.67
Ephemeroptera (larvae)	0.25	4.94		0.30	
Odonota (larvae)	4.8	4.85	0.69	1.13	
Dytiscidae (beetle)		1.94			
Diptera (larvae and pupae)		0.97	2.3	12.71	
Trichoptera (larvae)				0.45	
Hirundea (leeches)	1.77	2.91		0.83	
Terrestrial Insects					
Odonota (adult)		1.46	0.23		
Tipulidae (adult)		1.46		0.08	
Lepidoptera (adult)		0.97			
Other					
Aquatic Vegetation					
Detritus					
Unknown		1.13			

Table 6. Mean % composition by weight (MW_i) for seasonal diet composition of black bullheads *Ameiurus melas* collected from May–October 2020 from Howell Lake, Wisconsin.

Diet Item	May	June	July	August	October
	Mwi	Mwi	Mwi	Mwi	Mwi
Fish					
Bluegill (*Lepomis macrochirus*)			0.69	1.09	16.67
Yellow Perch (*Perca flavescens*)		0.97	6.10	3.12	
Black Crappie (*Pomoxis nigromaculatus*)				0.41	
Black Bullhead (*Ameiurus melas*)					16.67
Walleye (*Sander vitreus*)	8.72				15.70
Common Shiner (*Luxilus cornutus*)		0.97		1.33	
Bluntnose Minnow (*Pimephales notatus*)				1.47	
Eggs	22.87				
Aquatic Invertebrates					
Gastropod (snails)	22.90	18.07	65.8	60.58	34.30
Arthropoda (crayfish)		2.57	1.16	1.23	16.67
Ephemeroptera (larvae)	0.05	4.46		0.30	
Odonota (larvae)	14.36	4.85	0.69	1.20	
Dytiscidae (beetle)		1.94			
Diptera (larvae and pupae)		0.32	1.45	12.22	
Trichoptera (larvae)				0.12	
Hirundea (leeches)	15.20	2.14		0.77	
Terrestrial Insects					
Odonota (adult)		1.25	0.20		
Tipulidae (adult)		0.90		0.02	
Lepidoptera (adult)		0.97			
Other					
Aquatic Vegetation		18.32	16.10	12.30	
Detritus	16.00	41.10	7.80	3.42	
Unknown		1.15			

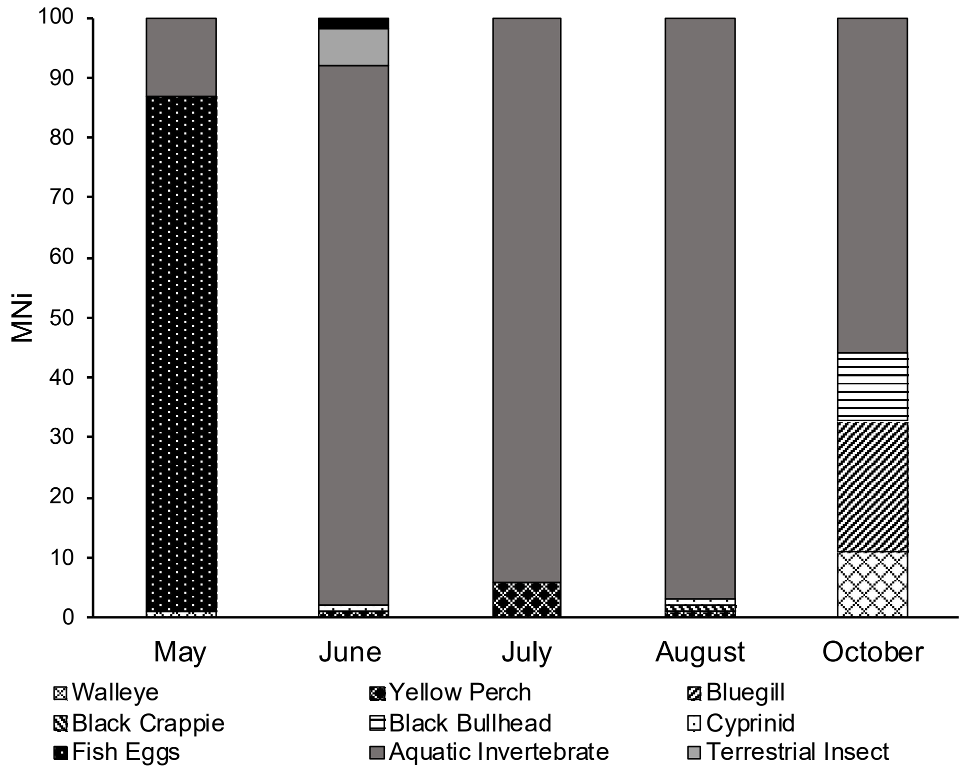

Figure 9. Mean percent composition by weight (MN_i) of diet items from black bullheads *Ameiurus melas* sampled from Howell Lake, Wisconsin in May, June, July, August, and October 2020.

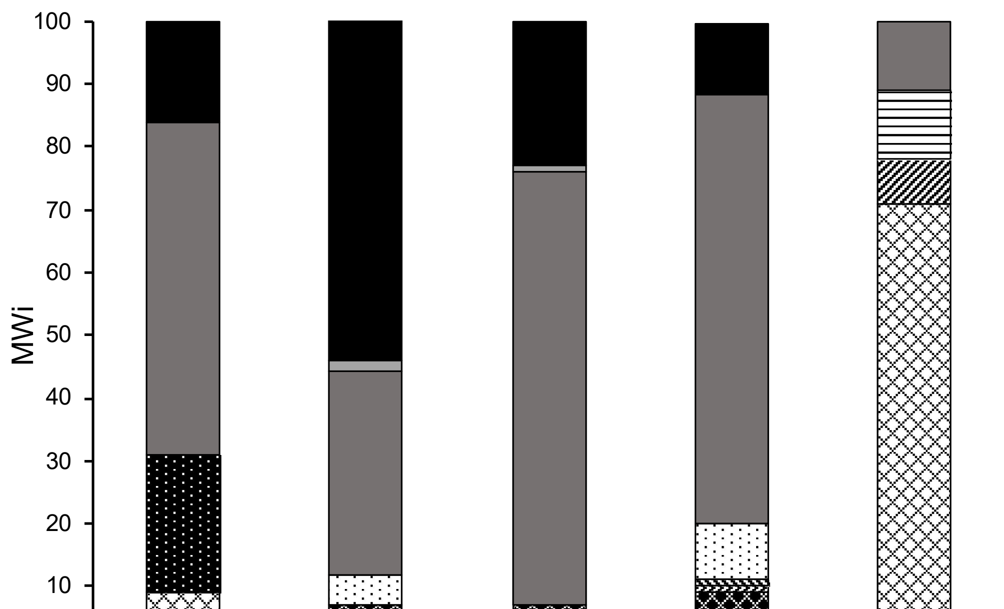

Figure 10. Mean percent composition by weight (MW_i) of diet items from black bullheads *Ameiurus melas* sampled from Howell Lake, Wisconsin in May, June, July, August, and October 2020.

4. Discussion

Black bullheads exhibit relatively fast growth rates, reach an age-at-maturity earlier than many other native north-temperate fish species, and are highly omnivorous. Further, black bullhead can reach high densities in north-temperate lakes. In concert, it appears that black bullheads have the potential to interact extensively throughout the food web. Empirical evidence suggests that high densities of bullheads can lead to undesired effects on popular sportfish, including walleye and yellow perch [11]. Despite the changing environment [27], black bullhead's plastic life history, high degree of fecundity, and extensive food web interaction capabilities will likely allow the species to remain a major component of some north-temperate lake food webs in the future, while more desirable cool-water species (e.g., walleye and yellow perch) decline and(or) become extirpated from some systems. Information realized through our research will allow for better management and mitigation of these 'nuisance species driven' negative effects.

A study of 35 black bullhead populations in South Dakota found highly variable but rapid individual growth rates using back-calculated growth increments and maximum age of eight years, with most fish being younger than age-6 [43]. The Hanchin et al. [43] age distribution generally agreed with that of our study, where the oldest identified age was nine, and most fish were estimated to be < age-5. Previous estimates of black bullhead adult length were varied. Becker [44] suggested an average adult length of 165–229 mm. Several fish in our sample far exceeded this length range, with the largest fish measuring 308 mm. Copp et al. [4] reviewed available literature related to the growth of black bullheads across their native and non-native ranges and found that body lengths and weights varied greatly, though the overall length of bullheads from the native range was greater than observed in the European populations.

Female age at maturity of bullheads in Howell Lake was young and similar to previous observations [16]. Copp et al. [4] mean sex ratio was virtually identical in the non-native and native populations for which data were available and were similar to our estimate near 1:1. Female age at maturity in the native range has been reported to span 2–5 years [13,16,45] and from 1–3.5 years in European non-native populations [4]. The only available detailed information on female maturity in the native range comes from the Mississippi River in Illinois, where bullhead females were reported to mature at 254 mm TL and age-3 [46], and Clear Lake, Iowa, where females matured at 200 mm TL and males at 216 mm TL [47]. Although limited information is available on the fecundity and reproductive potential of black bullhead, Forney [47], Carlander and Sprugel [48], and Dennison and Bulkley [49] estimated the fecundity of black bullheads in Clear Lake, Iowa. Similar to our study, these researchers found variable fecundity of fish of the same length but found that longer fish had higher fecundities. Despite lower average fecundity, stock length fish contributed an estimated 68% of the eggs to the cumulative reproductive potential of the black bullheads removed from Howell Lake in 2020. This is due to stock length black bullheads being much more abundant than quality and preferred length fish. Assuming egg and larval mortalities of 95% each [50], an estimated 75,203 age-1 black bullheads were precluded from recruiting to the Howell Lake fish community. This single whole-lake study provided valuable information on black bullhead fecundity and reproductive potential; however, our conclusions are limited to north-temperate lakes with similar limnological and ecological characteristics.

Black bullhead in Howell Lake preyed on a diverse range of diet items and exhibited an omnivorous and likely opportunistic feeding strategy. Studies have shown that in most cases, bullheads do not exhibit a preference outside of the most abundant prey species and have been shown to prey on insects, snails, clams, crayfish, frogs, plant material, detritus, and fish with varying degrees of piscivory [16,51–55]. Snow et al. [55] suggested that in Lake Carl, Oklahoma, black bullheads showed more piscivory than previous studies, while several others suggested that piscivory was not as large a part of the diets, especially in smaller fish [16,51–54]. In Howell Lake, Chinese mystery snails were found to be the most common prey item in the diets; however, fish were also a common prey item in the stomachs of lack bullheads. Seven fish species were present in the diets, all of which were generally fusiform in body shape at the life stage that they were consumed. Howell Lake has a fish assemblage representative of many northern Wisconsin lakes, which includes several small and abundant minnow species, but the most common prey fish for black bullhead were yellow perch. It is plausible that in certain systems and at certain times of the year, piscivory by black bullheads may negatively influence sport fish populations; however, our initial analyses do not strongly support the notion that black bullheads are suppressing sport fish populations in Howell Lake through direct predation. Black bullheads in Howell Lake may potentially compete with other top predators (walleye, northern pike, largemouth bass, smallmouth bass) to some degree based on the presence of fish in their diets, as yellow perch and bluegills are a common prey item for these piscivores [56–58], but this is likely not to any detectable degree in Howell Lake because of the abundance in forage. Piscivory by bullheads could be problematic if dietary overlap and resource availability is not considered in systems where black bullheads are established, and the goal of the fishery is to promote sportfishes for angling opportunities.

Results from our study show the importance of understanding the role of black bullheads in the ecosystems of north-temperate lakes, particularly when found in high abundances. Furthermore, it introduces the question of how to manage black bullhead populations in situations where they dominate fish community biomass, are highly piscivorous, and function similarly to a top predator in the system. Considerations of diet overlap and fish forage availability are critical when fisheries managers are considering management strategies for other top predators or when contemplating the introduction of a new species into an aquatic system. Further research is needed on a broader scale (multiple systems) to determine the full influences of black bullheads on sportfish populations. Furthering our knowledge and understanding of the demographics and life history of black bullheads across their range will provide managers with valuable information that is at the root of critical management decisions. Although many managers do not specifically manage bullheads directly, bullheads are present in many systems and likely play a role in structuring fish communities [11].

Black bullheads are often considered invasive species and can become overabundant within and outside of their native range. Due to their environmental tolerance (e.g., water quality, thermal) and ecological plasticity, black bullheads have the potential to disrupt native food webs and alternative fish community composition [4,5,10–12]. Our results showed that black bullhead exhibited rapid growth rates, early age at maturity, moderate fecundities, parental care of young, and a diverse omnivorous diet, which increases their invasive potential and prospective effects on native and invaded food webs and fish communities. Ongoing bullhead removal research will provide insights into the mechanistic role of bullheads in food webs to better manage these species as invasives and in situations where they may create fish community imbalances in their native range.

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Institutional Review Board Statement: The animal study protocol was approved by the Institutional Animal Care and Use Committee (IACUC) at the University of Wisconsin-Stevens Point (Protocol: 2020.01.05 "Effects of Bullhead removals on the fish community in Northern Wisconsin lakes").

Informed Consent Statement: Not applicable.

Data Availability Statement: Data are available upon request.

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