

Research Article

Characterization and management implications of silver carp (*Hypophthalmichthys molitrix*) jumping behavior in response to motorized watercraft

Brooke J. Vetter^{1,*}, Andrew F. Casper² and Allen F. Mensinger¹

¹Biology Department, University of Minnesota Duluth, 1035 Kirby Drive, Duluth, MN 55812, USA

²Illinois River Biological Station, Illinois Natural History Survey, University of Illinois, 704 N. Schrader, Havana, IL 62644, USA

*Corresponding author

E-mail: vett0114@d.umn.edu

Received: 22 July 2016 / Accepted: 29 November 2016 / Published online: 9 February 2017

Handling editor: Katherine Dafforn

Abstract

Silver carp (*Hypophthalmichthys molitrix*), an invasive planktivorous fish species in North America, pose a threat to aquatic ecosystems throughout the Mississippi River Drainage. These fish are well known for their airborne leaps in response to passing watercraft, but the trigger for, and functional significance of jumping remains unknown. The behavior of wild silver carp responding to moving (16, 24, 32, and 40 km/hr) 6 m aluminum boats equipped with 4-stroke outboard motors (100 or 150 hp) was quantified. Experiments were conducted at three sites on the Illinois River near Havana, IL and most boat transits (57.9%) stimulated five or more fish to jump. The frequency of jumping (fish/min) was independent of speed and motor type and the vast majority of fish (> 90.0%) jumped after the boat had passed their position but avoided the area directly astern (< 4.0 m). Furthermore, 79.8% of fish vectored away from the moving watercraft. The results suggest that jumping direction is not random and fish can localize the stimulus source. The “delayed” jumping until after the boat had transited the area indicates that the trigger may be turbulence and/or higher sound pressure levels. This is the first study to model silver carp jumping in response to motorized watercraft and can aid fisheries managers in predicting the direction and location of airborne fish to develop effective herding and capture methods.

Key words: invasive species, management, bioacoustics

Introduction

Silver carp (*Hypophthalmichthys molitrix* Valenciennes, 1844) are an invasive fish species that escaped from captivity in the southern part of the United States in the 1980's and have since moved northward, colonizing much of the Mississippi River Drainage (Kolar et al. 2005; Kolar et al. 2007). In areas where carp are abundant, these planktivorous fish have drastically altered the composition of the lowest trophic levels (Kolar et al. 2005; Sass et al. 2014). Furthermore, they compete with native filter feeders such as such as bigmouth buffalo (*Ictiobus cyprinellus* Valenciennes, 1844; Irons et al. 2007) and gizzard shad (*Dorosoma cepedianum* Lesueur, 1818; Sampson et al. 2009). Silver carp are abundant in the northern

reaches of the Illinois River where they threaten to expand into the Laurentian Great Lakes, which would expose the entire system to ecological disruption (Sass et al. 2010; Moy et al. 2011; Murphy and Jackson 2013).

An additional reason these fish have gained notoriety is their jumping behavior. Both juvenile and adult silver carp jump in response to moving watercraft, with reports of airborne fish injuring boaters (Kolar et al. 2007). Jumping in freshwater fish has been associated with upstream migration, circumventing barriers, or escaping predators (Aronson 1971; Bayliss 1982; Bierman 2013). Smallscale archer fish (*Toxotes microlepis* Günther, 1860; Shih and Techet 2010) can jump up to 2.5 body lengths out of the water to catch prey and salmonid species, such

as sockeye salmon (*Oncorhynchus nerka* Walbaum, 1792; Lauritzen et al. 2010) and brook trout (*Salvelinus fontinalis* Mitchell, 1814; Kondratieff and Myrick 2006), will leap several body lengths while negotiating boulders or waterfalls during spawning migrations. Many fish, including the African butterfly fish (*Pantodon buchholzi* Peters, 1877; Saidel et al. 2004) and the hatchet fish (*Carnegiella strigata* Günther, 1864; Wiest 1995), leap as an avoidance response when startled by predators. However, the silver carp's jumping behavior is unusual for cyprinids. Jumping may help larval and juvenile carp evade predation, but mature animals have few, if any, natural predators in North America. Although silver carp jumping has been well documented in the popular literature and numerous social media outlets, the trigger and functional significance of this behavior remains unclear.

This study evaluated wild silver carp responding to different outboard motors and speeds to characterize and better understand the jumping behavior. Jumping is both energetically costly and can have deleterious consequences for carp, such as self-stranding (into boats or on shore) or hard impacts with boat hulls or woody debris that often cause injury. From a management view, it could be the carp's "Achilles' fin" if the behavior can be controlled or directed. For instance, if there is a predictable pattern to jumping, nets could be designed to target jumping fish. A better understanding of this behavior could prove useful to fisheries managers working to control the current silver carp populations and prevent further range expansion.

Methods

Behavioral observations

Three 200 m sections of the Illinois River near Havana, IL were delineated with buoys and served as the testing sites (Figure 1A). Sites 1 and 2 were located 200 m apart in a narrow (180 m width) side channel of the river, which was separated from the navigation channel by a large island. Site 3 was situated in the main channel of the river (370 m width) approximately 1 km upstream from Site 2. Water depth ranged from 6–9 m throughout the sites.

The jumping behavior of wild silver carp was assessed using a 6 m aluminum boat, equipped with either a 100 or 150 hp Yamaha (Kennesaw, GA) 4-stroke outboard motor, and operated at four different speeds (16, 24, 32, or 40 km/hr). Four GoPro Hero3 (San Mateo, CA) cameras (recording quality: 1080 pixels; 30 frames/second) were attached to the bow, stern, port, and starboard sides providing

360° coverage around the boat, to record fish jumping behavior. A 2 m PVC pipe demarcated into 0.25 m sections was mounted below each camera for distance reference (Figure 1B, C).

A trial consisted of the boat, with either the 100 or 150 hp outboard motor, transiting the three sites at one of the four speeds (16, 24, 32, or 40 km/hr). For every trial, the boat started downstream of Site 1, attained the randomly selected speed before entering the first site, and maintained the speed through all sites. Immediately after exiting Site 3, the boat turned 180° to port, moved downstream paralleling the western side of Site 3 (Figure 1A), and continued west of the island that separated the main channel from Sites 1 and 2, to a waiting point downstream of Site 1. After at least a one hour recovery period, the sequence was repeated at a different speed. One session consisted of either four morning or afternoon trials, with the order of speeds randomized for each session and the motor type alternated between each session. All tests were conducted on August 8th and 9th, 2013 and October 7th, 2013.

Underwater sound generated by the boat motor was recorded using two hydrophones (HTI-96-MIN, High Tech Inc., Long Beach, MS) connected to a Zoom H4n Handy Recorder (Ronkonkoma, NY). The hydrophones were placed on the western edge of the sites, either between Sites 1 and 2 or at the halfway point (100 m) of Site 3 (Figure 1A), and were situated in the middle of the water column (3–4 m deep) about 10 m from the transit area. Sound pressure levels (SPL) for both outboard motor types were calculated by measuring the root mean square (rms) voltage and converting to SPL in dB re 1 μ Pa (Avisoft-SASLab Pro version 5.2.07). The frequency components and power spectrum of the sound emitted by both the 100 and 150 hp motor were analyzed using Audacity (version 2.0.5).

Data analysis

Number of Jumping Fish: The GoPro video files (mp4 format) from all four cameras were analyzed using frame-by-frame analysis (30 frames per second) in Adobe Photoshop CS6 (version 13; San Jose, CA). Boat transit time through each site varied with speed, therefore jumping frequency (number of jumping fish/second) was used for analysis.

Jumping Angles: The jump's origin was defined as the point where the fish head broke through the water surface and its position and movement vector relative to the center point of the boat (bow = 0°; starboard = 90°; stern = 180°; port = 270°) (Figure 1C, Angle α), were determined. The jumping vector was defined as the angle of the fish's trajectory from jump

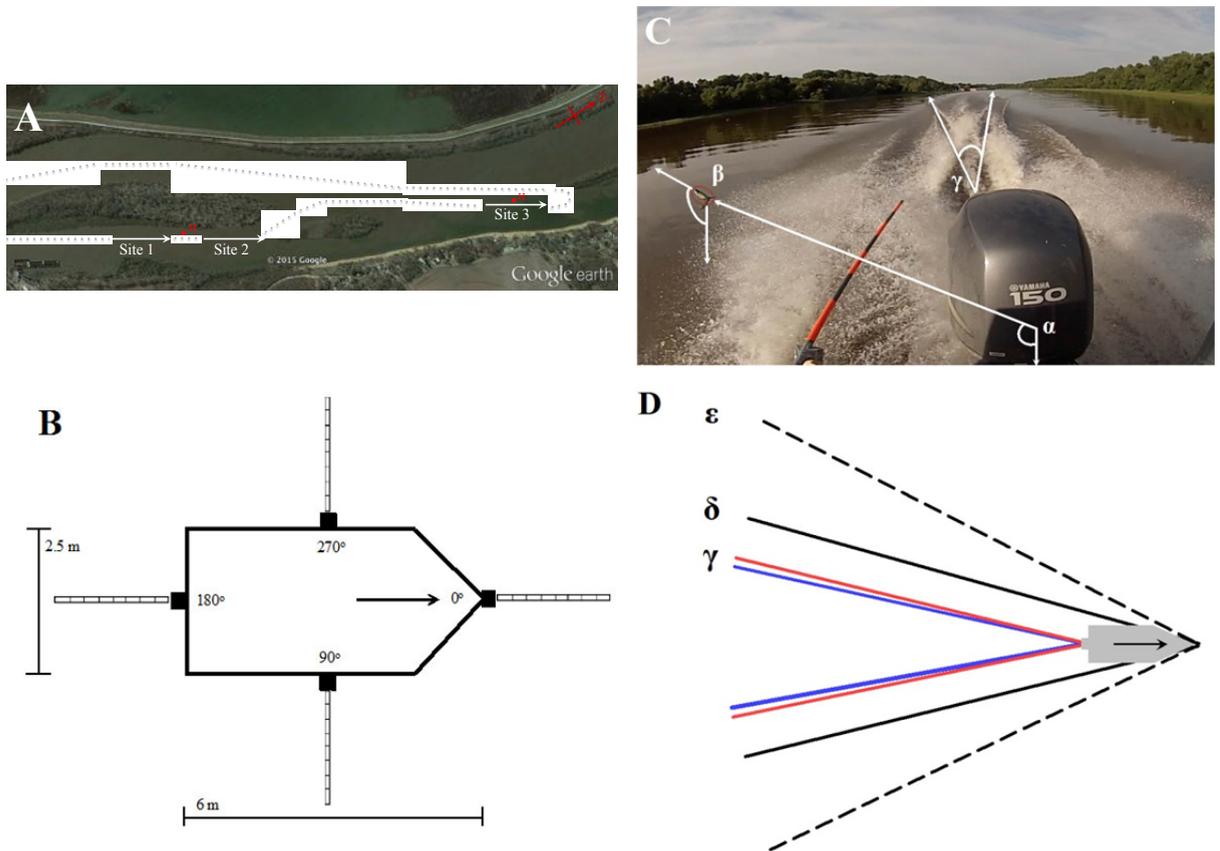


Figure 1. **A)** Aerial view of the three testing sites near Havana, IL on the Illinois River. Each site is marked with an arrow indicating the direction of boat travel. The dashed line represents the boat path through all three testing sites. Red dots marked with an “H” indicate the location of hydrophones. **B)** Schematic showing the position of the cameras (black boxes) and 2 m PVC pipes used to estimate distance. The boat length and widths are indicated; also the direction of movement and bow = 0° (360°); starboard = 90°; stern = 180°; and port = 270°. Figure is not to scale. **C)** Screen shot from the stern camera taken while using Adobe Photoshop CS6, version 13. The 2 m PVC rod used to estimate distance jumped from boat is visible. The red circle indicates a jumping carp from which the jump initiation angle (α) and jumping vector (β) were measured. The angle of the wake (γ) is also specified. **D)** The entire boat wake, including the average boundary lines of the Kelvin wake (δ), and the waves generated from the Kelvin wake (ϵ) (Partially adapted from Reed and Milgram 2002).

initiation to reentry (Figure 1C, Angle β) in relation to the center point of the boat at the time of jump initiation. Jumps also were categorized as either “towards” or “away” from the boat. For example, bow camera trajectories $> 90^\circ$ and $< 270^\circ$ were considered towards the boat.

Jumping distance from the boat was determined by calculating the number of pixels for each 0.25 m segment of the 2 m PVC pipe, plotting a linear regression, and extrapolating these measurements for jumps originating beyond the marker. To account for parallax, the pixel measurements were taken using a straight line originating at the bottom of the frame. This measurement technique was verified using objects placed at known distances from the camera but positioned at different angles.

Boat Wake: This study assessed fish jumping in relation to the components that constitute the boat’s full wake, including the centerline wake, Kelvin wake, and Kelvin wake-associated surface waves that serve as the boat wake border (Reed and Milgram 2002). The centerline wake, which includes the propeller downwash and viscous wake, lies within the Kelvin wake and is created by the outboard motor. The centerline wake was determined from the stern camera for each of the motor/speed combinations. The angle was measured with the middle of the outboard motor serving as the center point (Figure 1C, D; Angle γ). The extent of the Kelvin wake, which forms a 39° angle starting at the boat bow (Reed and Milgram 2002), was verified using the stern, port, and starboard cameras (Figure 1D;

Angle δ). Finally, footage from the stern camera showed the presence of waves that are typically generated by the Kelvin wake (Figure 1D; Angle ϵ) and span approximately 15° on either side of the Kelvin wake's boundaries (Reed and Milgram 2002).

Statistical analyses

Sites 1 and 2 were not considered to be independent, as they were located only 200 m apart, and therefore, the number of jumping fish in these sites was pooled. Statistical tests comparing the number of jumping fish at each site, jumping frequency, and jump distance failed the Shapiro-Wilk test of normality ($P < 0.05$), and therefore non-parametric statistics (Mann-Whitney Rank Sum Test or Kruskal-Wallis ANOVA with a post-hoc Tukey Test) were used. The effect of motor and speed on jumping frequency was examined for fish jumping only in Sites 1 and 2, as more fish were observed jumping in these areas than in Site 3. For each motor, jumping frequency and distances were compared between the 16, 24, 32, and 40 km/hr speeds (Kruskal-Wallis ANOVAs) and then by motor type. The median and quartiles (25th and 75th) were reported using the following formats (median; 1st Q, 3rd Q) or median (1st Q, 3rd Q). All analyses were conducted using SigmaPlot for Windows (version 12.5; SYSTAT Software; San Jose, CA). The jump origin and vector were analyzed using Oriana (version 4; Kovach Computing Systems; Wales, UK) for motor type and speed. Rao's Spacing Test was used to determine if the angular data (jump initiation angles and vectors) was randomly distributed around the boat.

Jumping direction (towards vs. away from the boat) was normally distributed among the eight motor/speed combinations, therefore a t-test was performed and the jump totals are represented as mean \pm SE. The centerline wake angle measurements were also parametric allowing a one-way ANOVA to compare the four speeds for both motor types (all means reported as mean \pm SE).

Results

The maximum sound pressure levels were similar between the two motors and ranged from 130.0–136.0 dB re $1\mu\text{Pa}$ for the 100 hp motor and 131.8–137.2 dB re $1\mu\text{Pa}$ for the 150 hp motor. The power spectrum between the two boats was similar, with the 100 hp peaking at 1.5 kHz and the 150 peaking at 2.0 kHz (Figure 2).

The number of fish jumping at each site during each transit ($N = 66$) ranged from 0 to 75 and during 57.9% of the transits, at least five fish jumped. In

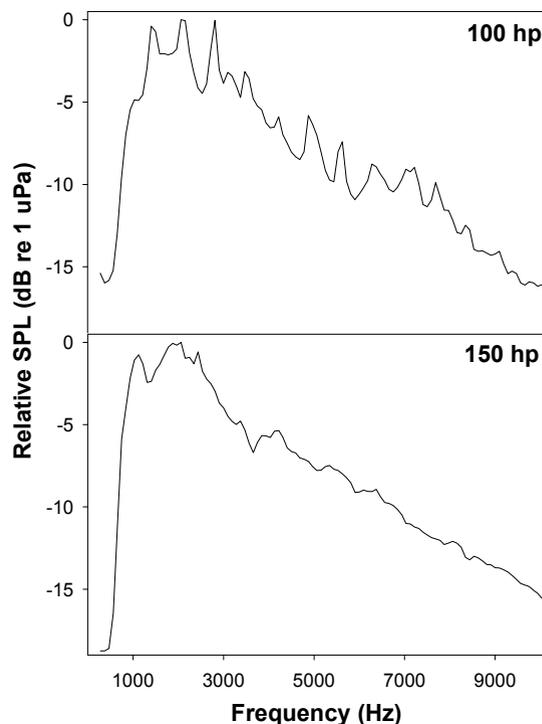


Figure 2. The power spectrum in relative dB of the 100 and 150 hp outboard motors is plotted versus frequency (Hz).

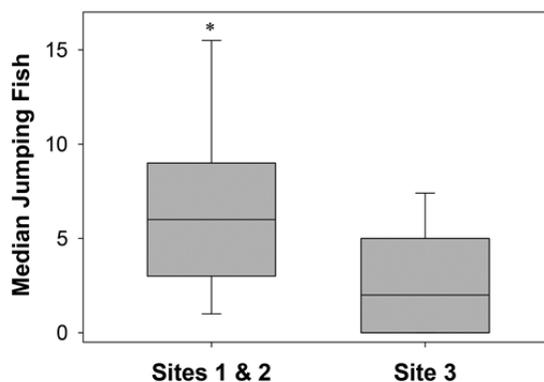


Figure 3. Median jumping silver carp in pooled Sites 1 and 2 versus Site 3. Each box represents the 25th (bottom of box) and 75th (top of box) quartiles with the median marked by the line within the box. Whiskers (error bars) above and below the box indicate the 10th and 90th percentiles. * indicates significantly different group (Mann-Whitney $P < 0.001$).

Sites 1 and 2, the boats stimulated jumping from silver carp during 95% of the transits ($N = 44$). Furthermore, significantly more fish jumped in Sites 1 and 2 (6.0; 3.0, 9.0) than in Site 3 (2.0; 0.0, 5.0) (Mann-Whitney $P < 0.001$) (Figure 3).

Table 1. Summary of the percentage of all airborne fish that jumped in the centerline wake, the Kelvin wake (excluding the centerline wake area), the waves generated by the Kelvin wake, and the full boat wake, which is bordered by the waves generated from the Kelvin wake. N represents the total number of jumping fish for each motor and speed combination.

Motor (hp) @ Speed (km/hr)	N	Centerline Wake (%)	Kelvin Wake (%)	Kelvin Waves (%)	Full Wake (%)
100 @ 16	41	22.0	2.4	19.5	43.9
100 @ 24	32	3.1	6.3	12.5	21.9
100 @ 32	17	0	5.9	17.6	23.5
100 @ 40	27	3.7	22.3	18.4	44.4
150 @ 16	63	12.9	13.1	9.5	35.5
150 @ 24	52	30.8	17.3	9.6	57.7
150 @ 32	70	8.6	5.7	30.0	44.3
150 @ 40	96	6.3	9.3	20.9	36.5

The median jumping frequency varied from 0.11 fish/second (0.05, 0.22; 16 km/hr) to 0.31 fish/second (0.10, 0.46; 40 km/hr) for the 100 hp motor and 0.13 fish/second (0.11, 0.51; 32 km/hr) to 0.39 fish/second (0.13, 1.6; 40 km/hr) for the 150 hp motor (Figure 4). There was no significant difference in jumping frequency between the four speeds for either the 100 hp or the 150 hp (Kruskal-Wallis ANOVA $P = 0.407$) motors, allowing the jumping frequency to be pooled for each motor. The median jumping frequencies for the 100 and 150 hp motors were 0.17 fish/second (0.07, 0.32) and 0.31 fish/min (0.13, 0.56), respectively, and were also not significantly different (Mann-Whitney $P = 0.064$).

The arc created by the centerline wake (viscous wake and propeller downwash) ranged from $26.4^\circ \pm 2.4^\circ$ to $19.9^\circ \pm 3.1^\circ$ (100 hp) and $31.1^\circ \pm 2.0^\circ$ to $20.8^\circ \pm 3.0^\circ$ (150 hp). However, there was no significant difference in the wake angle between the speeds for either the 100 hp (ANOVA $P = 0.358$) or 150 hp motors (ANOVA $P = 0.257$) allowing the data to be pooled and resulting in no significant difference in wake angle between the motor types (100 hp: $22.4^\circ \pm 3.8^\circ$; 150 hp: $25.2^\circ \pm 5.0^\circ$; $P = 0.152$). The Kelvin wake, which is often independent of boat speed and size, was verified to project astern in a 39° arc (160.5° – 199.5°) and the Kelvin waves were observed radiating out approximately 15° on either side of the Kelvin wake (Reed and Milgram 2002).

Fish were observed jumping in the centerline wake for all motor and speed combinations except for the 100 hp motor trials at 32 km/hr. The percentages of fish jumping in the centerline wake ranged from 3.1% (100 hp at 24 km/hr) to 30.8% (150 hp at 24 km/hr) (Table 1). Of all the airborne fish, 2.4% (100 hp at 16 km/hr) to 22.3% (100 hp at 40 km/hr) jumped within the Kelvin wake area beyond the centerline wake (100 hp motor: $\sim 160.5^\circ$ – 168.7° and 191.3° – 199.5° ; 150 hp motor: $\sim 160.5^\circ$ – 167.2° and 192.8° – 199.5°) (Table 1). Finally, 9.5% (150 hp at

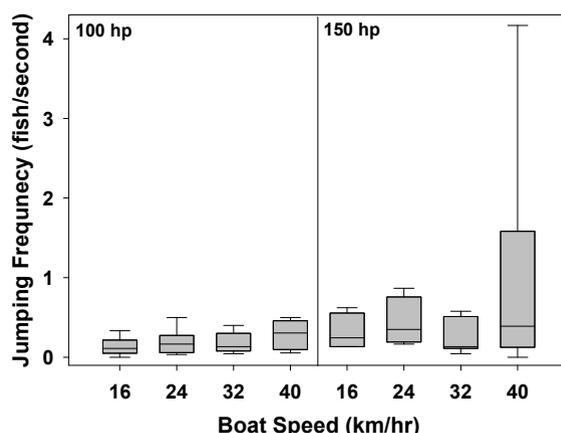


Figure 4. Median frequency of jumping carp responding to each of the eight motor speed combinations. The boxes represent the 25th (bottom) and 75th (top) quartiles and the line within the box indicates the median value, with the 10th and 90th percentiles shown as whiskers. There was no significant difference in jumping frequency among the motor type and speed variables (Kruskal-Wallis ANOVA $P = 0.407$).

16 km/hr) to 30.0% (150 hp at 32 km/hr) jumped in the waves created by the Kelvin wake ($\sim 145.5^\circ$ – 160.5° and 199.5° – 214.5°). The edge of these waves formed the outermost border of the wake ($\sim 145.5^\circ$ – 214.5°) and 21.9% (100 hp at 24 km/hr) to 57.7% (150 hp at 24 km/hr) jumped in the full boat wake (which includes the centerline wake, Kelvin wake, and Kelvin waves) (Table 1).

For the 100 hp motor, 90.6% of the fish initiated their jumps in the region astern, after the boat had passed ($> 90^\circ$ and $< 270^\circ$). The fish also primarily vectored their jumps away (84.8%) from the boat (Table 2, Figure 5). Jump origin was not randomly distributed (Rao's $P < 0.01$) and was initiated primarily in a 90° arc behind the boat, with the stern serving as the center, and median jump origin locations ranged from 135.9° (129.2° , 166.3°) at 24 km/hr to

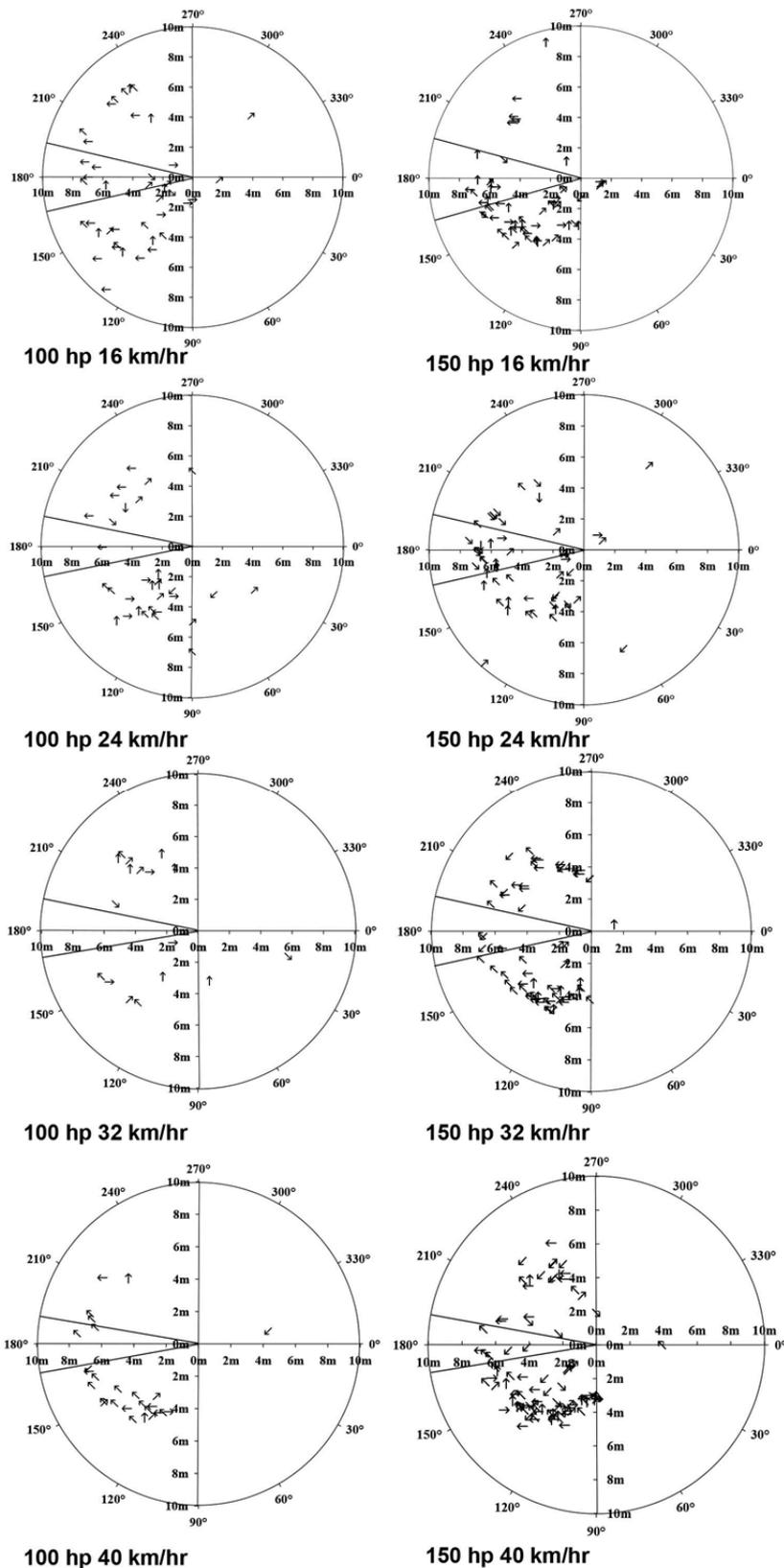


Figure 5. Polar plots for all eight treatments. Each arrow represents one fish and marks the estimated distance from and jump initiation angle in relation to the boat and its direction of movement (0°). To assess the jumping vector, each fish was categorized in one of eight arcs ($0^\circ\text{--}45^\circ$, $46^\circ\text{--}90^\circ$, $91^\circ\text{--}115^\circ$, $116^\circ\text{--}135^\circ$, $136^\circ\text{--}180^\circ$, $181^\circ\text{--}270^\circ$, $271^\circ\text{--}315^\circ$, and $316^\circ\text{--}360^\circ$) and plotted with a corresponding arrow. The arrows point in the direction of each fish's trajectory (jumping vector). The solid lines represent the boat's wake.

Table 2. Summary of the angle data for all eight stimuli. N represents the number of fish analyzed for both the jump initiation angle and jumping vector (Median; 1st Q, 3rd Q) (Rao's P < 0.01). * indicates the only non-significant group.

Motor (hp) @ Speed (km/hr)	N	Jumping Initiation Angle Median° (1 st Q°, 3 rd Q°)	Jumping Vector Median° (1 st Q°, 3 rd Q°)
100 @16	41	156.7 (149.9, 180.0)	149.1 (119.3, 168.0)
100 @ 24	32	135.9 (129.2, 166.3)	121.8 (92.8, 167.4)*
100 @ 32	17	222.3 (158.1, 220.7)	102.2 (66.3, 118.3)
100 @ 40	27	145.0 (136.6, 165.1)	153.1 (142.2, 176.9)
150 @ 16	63	143.9 (138.7, 161.2)	129.6 (105.1, 141.6)
150 @ 24	52	168.6 (150.8, 176.1)	90.1 (45.2, 124.7)
150 @ 32	70	152.9 (150.0, 176.5)	186.0 (165.6, 193.1)
150 @ 40	96	140.9 (139.7, 159.5)	138.3 (116.3, 159.0)

222.3° (158.1°, 220.7°) at 32 km/hr. The jumping vectors were also not randomly distributed (Rao's P < 0.01) and median angles ranged from 102.2° (32 km/hr: 66.3°, 118.3°) to 153.1° (40 km/hr: 142.2°, 176.9°) (Table 2).

Similar to the 100 hp motor, fish responding to the 150 hp motor primarily jumped away (77.0%) from and behind (95.0%) the moving boat. The jump origins for the 150 hp motor favored the starboard/stern quadrant (Rao's P < 0.01), with median origination angles ranging from 140.9° (40 km/hr: 139.7°, 159.5°) to 168.6° (24 km/hr: 150.8°, 176.1°) (Table 2). Furthermore, the jumping vectors were non random (Rao's P < 0.01), varying from 90.1° (24 km/hr: 45.2°, 124.7°) to 186.0° (32 km/hr: 165.6°, 193.1°) (Table 2).

Jumping patterns for each motor type and speed are summarized in Figures 5 and 6. The pattern for both motor types shows a semicircle array astern with the motor as the center point and is more pronounced for the 150 hp motor (Figure 5). Fish avoided the area directly astern (< 4.0 m) within the motor wake (Figures 5, 6).

Figure 7 summarizes the jump origination by quantifying the number of jumps in 20° arcs centered around the boat, with each arc subdivided into 2.0 m lengths. There is a clear exclusion zone from 0.0–4.0 m between 140°–220° in the area directly astern (Figure 7). The majority of jumping occurred between 4.0–8.0 m in the 100°–180° arcs, within and just outside the Kelvin wake and in the distant portion of the centerline wake (> 4.0 m astern). The fish avoided the area directly astern (0–4.0 m) independent of motor and speed (Figures 5, 6, 7).

The median distance of the jump origin from the boat (100 hp) varied from 5.2 m (24 km/hr: 3.8 m, 6.1 m) to 6.4 m (16 km/hr: 3.1 m, 7.3 m), with no significant difference between the speeds (Kruskal-Wallis ANOVA P = 0.117). Similarly, there was no significant difference in distance for fish reacting to the 150 hp motor (Kruskal-Wallis ANOVA P = 0.274),

with distances ranging from 4.9 m (40 km/hr: 3.9 m, 5.8 m) to 5.7 m (24 km/hr: 3.7 m, 6.5 m). Therefore, the distances were pooled by motor type. The fish jumped slightly further (5.6 m; 4.7 m, 6.8 m) from the boat during the trials with the 100 hp motor versus the 150 hp motor (5.1 m; 3.9 m, 5.9 m) (Mann-Whitney P < 0.001) (Figure 8A). The highest percentages of jumping fish occurred at distances 5, 6, and 7 m from the boat for both the 100 hp (19.2%, 22.1%, and 19.2%,) and 150 hp (20.4%, 31.1%, and 20.4%) motors (Figure 8B).

All jumping vectors were categorized as moving either towards or away from the boat. 79.8% of all observed jumps were angled away from the boat and significantly (P < 0.001) more fish (42.0 ± 6.3) fish jumped away from the boat (10.6 ± 3.4) when each motor type and speed was compared (Figure 9).

Discussion

This study is the first to quantitatively examine silver carp jumping behavior in response to motorized watercraft. The frequency of jumping was independent of boat speed and the two motor types examined. However, the results indicate that jumping is non-random as the fish primarily jumped behind and away from the boat but rarely in the area directly astern (< 4.0 m). Furthermore, there is a pattern in fish response to moving (> 15 km/hr) boats as both motor types elicited a semi circle arrangement of jumping behind the boat.

Although the exact jumping trigger remains unclear, the results indicate that the majority of fish moved away from the stimulus source. Unfortunately, only above water behavior was observed in the turbid water, with nearby turbidity readings between 22 and 97 FTU on the testing days (USGS 2016). Therefore, it is uncertain if jumping was initiated as a c-start, which is an evasive reflex in fish that occurs rapidly (< 100 ms) (Eaton et al. 1977; Fetcho et al. 1991), or slower neuromuscular pathways. The

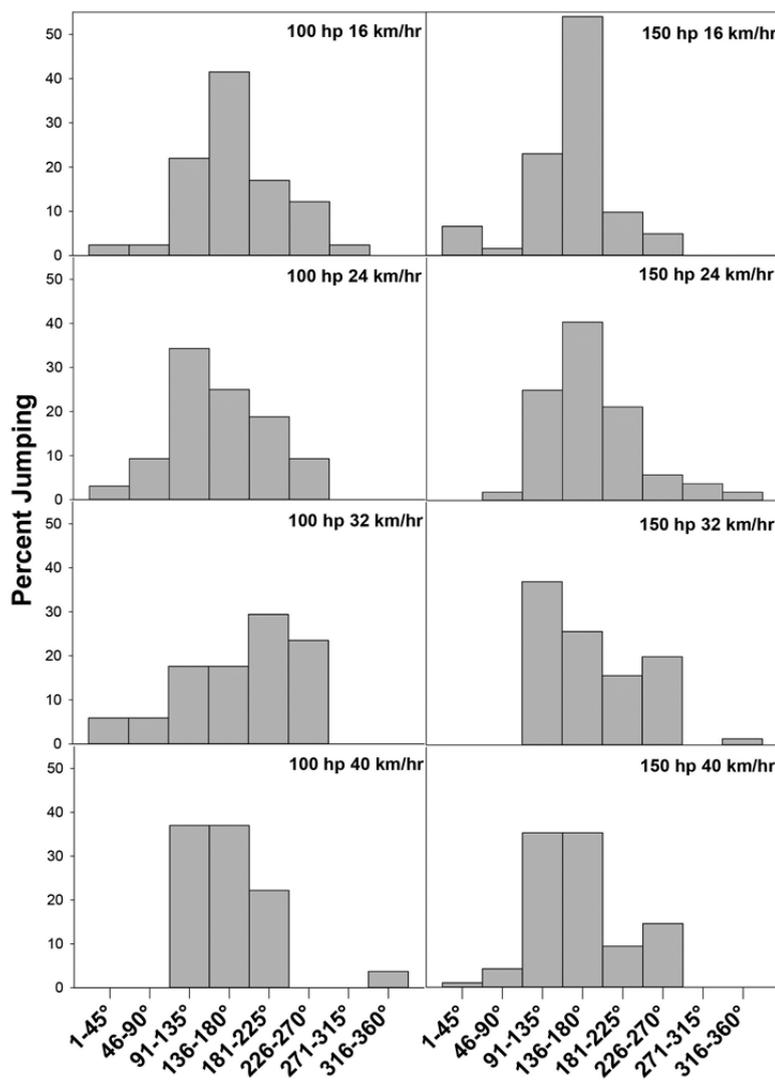


Figure 6. Histograms assessing the percentage of fish that initiated jumping in one of eight angular arcs (0°–45°, 46°–90°, 91°–115°, 116°–135°, 136°–180°, 181°–270°, 271°–315°, and 316°–360°) in relation to the boat.

results presented reflect the behavioral response of carp at the point when the fish broke the water surface, but the fish's location in relation to the boat when it first responded underwater is unknown. Both the fish's depth and the type of response (e.g. c-start) could have resulted in a time lag between when the fish reacted to the oncoming boat and when it broke the water surface. For instance, a fish that was near the surface of the water and reacting with a c-start response would break the water's surface quicker than a fish that was either deeper or had a slower reaction time. Observing jumping in clear water could provide insight into the biomechanics of jumping, however anecdotal evidence suggests that this behavior is reduced in these environments. Alternatively, sonar imaging could evaluate the depths at which fish respond and move to the surface to jump.

It is unlikely that vision was a factor in detecting the boat. In the turbid water, fish and submerged objects were only visible to human observers within a few centimeters of the surface. Although the silver carp's visual sensitivity remains to be determined, light adsorption and scattering in turbid environment degrade visual range relatively quickly for aquatic animals (Lythgoe 1979; Benfield and Minello 1996).

It is likely that the jumping fish were responding to mechanosensory cues from hydrodynamic water changes. The majority of fish initiated their jumps after the boat stern passed their position and therefore, the jumping location was compared with the hydrodynamic disturbance created by the boat to determine if any particular component influenced jumping. The boat wake consists of the Kelvin wake (originating at the bow), the waves created by the

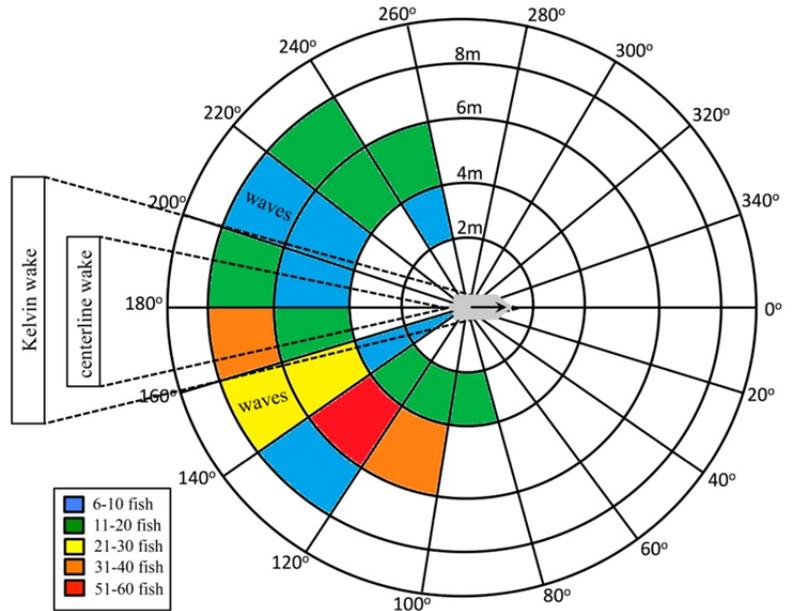


Figure 7. Summary of all jump initiation locations. The area around the boat was divided into 2 m segments in 20° arcs, giving 90 total sections. The colors represent the number of jumping fish in each section, see legend inset. White segments represent areas where 5 or less fish jumped. There were no sections in which the total number of jumping fish was between 41–50.

Kelvin wake, and the centerline wake (which includes the propeller downwash and the viscous wake) (Reed and Milgram 2002). The Kelvin wake begins at the bow and forms a 39° angle, extending past the stern of the boat. Additionally, a series of surface waves generated by the boat wake extends approximately 15° beyond and on either side of the Kelvin wake. Both motors generated a semi-circle jumping pattern around the full wake and the highest densities of jumping fish were observed within the centerline wake (100 hp: 168.7°–191.3°; 150 hp: 167.2°–192.8°), the Kelvin wake (which spanned approximately 160.5°–199.5°), and the waves that radiated out from the Kelvin wake (~145.5°–214.5°). Additionally, the propeller downwash may have deterred fish from jumping directly behind the boat. Jumping origin was independent of motor size and speed, suggesting that under certain conditions the jumping pattern can be predicted.

While the results from this study strongly suggest that jumping is largely associated with turbulence generated by the wake, the contribution of sound to behavior cannot be discounted. At least part of the sound (0.06–10 kHz) emitted by the outboard motors used in this experiment is within the hearing range of the silver carp, as Lovell et al. (2006) reported frequency sensitivity up to 3 kHz in this species. Furthermore, the lateral line, which is sensitive to low frequency water movement, has recently been determined to assist in sound detection. For instance, goldfish (*Carassius auratus* Linnaeus, 1758), another

carp species, responded to sounds up to 200 Hz with their lateral line (Higgs and Radford 2013). Additionally, the particle motion component of the sound field may also influence behavior and its contribution still needs to be determined. Therefore, the fish in this study that jumped in the boat wake may have perceived and responded to sound and/or vibrations from the motor with both their lateral line and inner ear.

However, the jumping pattern observed strongly suggests that the sound of the approaching boat is insufficient to trigger jumping. The sound of the outboard motor was detected by the hydrophone well before the boat passed its location and an examination of sound pressure levels (130–137 dB re 1 µPa) indicates that, depending on boat speed and motor type, the silver carp should be able to detect the sound generated by the outboard motor well in advance of the boat approaching their position. This suggests that the pressure levels or particle motion may have to reach certain thresholds, which are only surpassed when the boat is near the fish, to trigger the jumping. Therefore, the sound thresholds that could modify silver carp behavior still need to be determined. Finally, jumping could be elicited by a combination of sound and water turbulence. Further examination of wild silver carp behavior in response to sound is imperative to better define the relationship between sound and jumping.

In Sites 1 and 2, which had more jumping fish than Site 3, there was a bias for jumping on the starboard (eastern) rather than the port (western) side

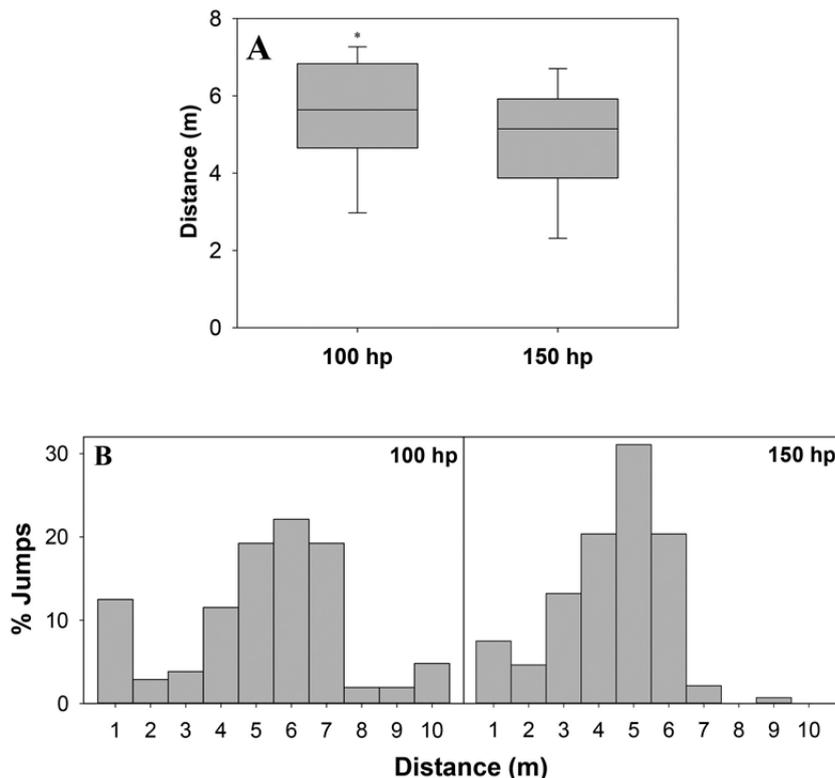


Figure 8. **A)** Median distance from the boat in which fish initiated jumping for the 100 and 150 hp motors. Each box represents the 24th and 75th quartiles with the median marked by the line within the box. The 10th and 90th percentiles are indicated by the whiskers (error bars). * indicates significantly different groups (Shapiro-Wilk $P < 0.001$) **B)** Histograms representing the percentage number of jumps that occurred at 1 m increments from the boat.

of the boat. An extensive shallow flat on the west side of the river, in which Sites 1 and 2 were located, forced the boat to favor the east side of the channel. This asymmetrical depth profile could have created a non-random distribution of fish underwater, as the fish may have preferred the deeper eastern side of the river, explaining the greater numbers that jumped between 100°–180°. Since Sites 1 and 2 were in close proximity, the results from these sites were pooled, as the boat could have influenced the fish in Site 2 as it passed through Site 1. However, it is unlikely that downstream boat movement impacted the fish in Site 3, as this location was 1 km upstream and separated from the first two sites by an island. Rather, the decreased jumping in Site 3 was probably related to the greater river width at this site. Therefore, there may have been less fish present in this region or the sound stimulus could have been attenuated. A sonar system to evaluate fish behavior underwater would aid in a better understanding of the differences between jumping at the sites.

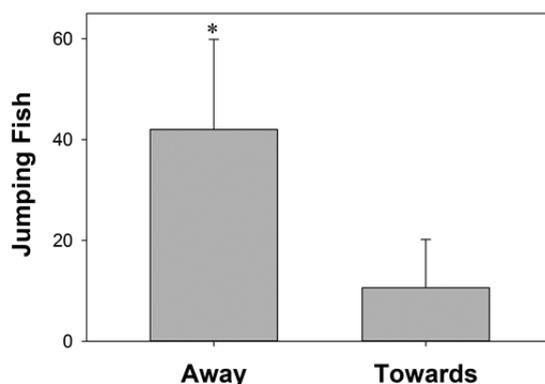


Figure 9. Average number of fish that jumped “away” from versus “towards” the boat. Averages were calculated based on pooling the total number of jumping fish in response to each outboard motor type at one of the four speeds (100 hp @ 16 km/hr, 100 hp @ 24 km/hr, 100 hp @ 32 km/hr, and 100 hp @ 40 km/hr, 150 hp @ 16 km/hr, 150 hp @ 24 km/hr, 150 hp @ 32 km/hr, and 150 hp @ 40 km/hr), * indicates significantly different groups (t-test $P < 0.001$). Error bars represent \pm SE.

The two motor types and four speeds of travel were chosen based on anecdotal input from the researchers at the Illinois River Biological Station that different motors and speeds were most effective in stimulating jumping. Therefore, the study evaluated jumping in response to two motor types (100 and 150 hp) and four speeds (16–40 km/hr). However, the results indicated that there was no significant difference in jumping frequency for any of the motor or speed combinations. This could be related to redundancy in site testing or limited trials. Additional replicates and a greater number of sites could better evaluate jumping. Alternatively, as the hydrophone data suggests that the sound pressure levels and spectrum were similar across trials, wild silver carp may not differentially respond to the two boats used in the study.

Water clarity limited the current study to examining only carp jumping behavior, however the results presented can be applied to fisheries management strategies. Commercial fishermen currently drive fish towards nets by banging on their boat hulls and revving partially submerged outboard propellers, which suggests refinement of these techniques could allow a greater number of fish to be captured and removed. By modeling the jumping, managers will be able to optimize capture or killing methods using boom nets, solid screens, or towed collecting vessels. The results from this study, which indicate that carp responding to moving (16–40 km/hr) watercraft primarily jump behind the boat, suggest that two laterally extending nets mounted on the back of a boat may be successful in capturing or killing airborne fish. Alternatively, another method could involve using 2–3 boats spaced across a river channel to drive fish toward a block net for capture and removal. Further research is also needed to determine the jumping trigger, as this could be another useful tool in managing silver carp. Isolating the exact trigger for jumping, combined with the ability to consistently induce the behavior, could also be used to census areas for number of fish and refine herding technologies, as the airborne fish reveal their position and vector.

The results presented provide the first evidence that silver carp jumping can be modeled, as the fish demonstrated a distinct and consistent behavioral pattern. This study suggests that jumping is non-random and that the fish primarily moved away from the moving boats. A better understanding of silver carp jumping behavior can help officials determine the best methods for capturing fish.

Acknowledgements

We would like to thank the staff and interns at the Illinois River Biological Station (IRBS) in Havana, IL and their sponsors, Sport-fish Restoration Fund project F-101-R, Illinois DNR Great Lakes Restoration Initiative Asian Carp Removal Program, and Upper Mississippi River Restoration Long-term Resource Monitoring Element, for providing resources (including boat time and buoys) and input on the experimental design. We would also like to thank Graham Hanson for assisting with fieldwork. Funding was provided by University of Minnesota Duluth, the Minnesota Environment and Natural Resources Trust Fund, and the Illinois Natural History Survey. Finally, the authors wish to thank the reviewers for the time and effort put in to providing feedback on this manuscript.

References

- Aronson LR (1971) Further studies on orientation and jumping behavior in the gobiid fish, *Bathygobius soporator*. *Annals of the New York Academy of Sciences* 188: 378–392, <https://doi.org/10.1111/j.1749-6632.1971.tb13110.x>
- Bayliss JR (1982) Unusual escape response by two cyprinodontiform fishes, and a bluegill predator's counter-strategy. *Copeia* 1982: 455–457, <https://doi.org/10.2307/1444631>
- Benfield MC, Minello TJ (1996) Relative effects of turbidity and light intensity on reactive distance and feeding of an estuarine fish. *Environmental Biology of Fishes* 46: 211–216, <https://doi.org/10.1007/BF00005223>
- Bierman HS (2013) Aerial Jumping in the Trinidadian Guppy (*Poecilia reticulata*). *PLoS ONE* 8: e61617, <https://doi.org/10.1371/journal.pone.0061617>
- Eaton RC, Bombardieri RA, Meyer DL (1977) The Mauthner-initiated startle response in teleost fish. *Journal of Experimental Biology* 66: 65–81
- Fetcho JR (1991) Spinal network of the Mauthner cell. *Brain, Behavior and Evolution* 37: 298–316, <https://doi.org/10.1159/000114367>
- Higgs DM, Radford CA (2013) The contribution of the lateral line to “hearing” in fish. *Journal of Experimental Biology* 216: 1484–1490, <https://doi.org/10.1242/jeb.078816>
- Irons KS, Sass GG, McClelland MA, Stafford JD (2007) Reduced condition factor of two native fish species coincident with invasion of non-native Asian carps in the Illinois River, USA—Is this evidence for competition and reduced fitness? *Journal of Fish Biology* 71: 258–273, <https://doi.org/10.1111/j.1095-8649.2007.01670.x>
- Kolar KS, Chapman DC, Courtenay WR, Housel CM, Williams JD, Jennings DP (2005) Asian carps of the genus *Hypophthalmichthys* (Pisces, Cyprinidae)—a biological synopsis and environmental risk assessment. U.S. Fish and Wildlife Service, 183 pp
- Kolar KS, Chapman DC, Courtenay WR, Housel CM, Williams JD, Jennings DP (2007) Bigheaded carps: a biological synopsis and environmental risk assessment. American Fisheries Society Special Publication 33. Bethesda, MD, 204 pp
- Kondratieff M, Myrick C (2006) How High Can Brook Trout Jump? A Laboratory Evaluation of Brook Trout Jumping Performance. *Transactions of the American Fisheries Society* 135: 361–370, <https://doi.org/10.1577/T04-210.1>
- Lauritzen DV, Hertel FS, Jordan LK, Gordon MS (2010) Salmon jumping: behavior, kinematics and optimal conditions, with possible implications for fish passageway design. *Bioinspiration and Biomimetics* 5, <https://doi.org/10.1088/1748-3182/5/3/035006>
- Lythgoe JN (1979) *The Ecology of Vision*. Oxford University Press, New York, 244 pp
- Lovell JM, Findlay MM, Nedwell JR, Pegg MA (2006) The hearing abilities of the silver carp (*Hypophthalmichthys molitrix*) and bighead carp (*Hypophthalmichthys nobilis*). *Comparative Biochemistry and Physiology A* 143: 286–291, <https://doi.org/10.1016/j.cbpa.2005.11.015>

- Moy PB, Polls I, Dettmers JM (2011) The Chicago sanitary and ship canal aquatic nuisance species dispersal barrier. In: Chapman DC, Hoff MH (eds), *Invasive Asian carps in North America*, American Fisheries Society Special Publication 74. Bethesda, MD, pp 1–10
- Murphy EA, Jackson PR (2013) Hydraulic and water-quality data collection for the investigation of Great Lakes tributaries for Asian carp spawning and egg-transport suitability: U.S. Geological Survey Scientific Investigations Report 2013–5106, <http://pubs.usgs.gov/sir/2013/5106/>
- Reed AM, Milgram JH (2002) Ship wakes and their radar images. *Annual Review of Fluid Mechanics* 34: 469–502, <https://doi.org/10.1146/annurev.fluid.34.090101.190252>
- Saidel WM, Strain GF, Fornari SK (2004) Characterization of the Aerial Escape Response of the African Butterfly Fish, *Pantodon buchholzi* Peters. *Environmental Biology of Fishes* 71: 63–72, <https://doi.org/10.1023/B:EBFI.0000043153.38418.cd>
- Sampson SJ, Chick JH, Pegg MA (2009) Diet overlap among two Asian carp and three native fishes in backwater lakes on the Illinois and Mississippi Rivers. *Biological Invasions* 11: 483–496, <https://doi.org/10.1007/s10530-008-9265-7>
- Sass GG, Cook TR, Irons KS, McClelland MA, Michaels NN, O'Hara ETM, Stroub MR (2010) A mark-recapture population estimate for invasive silver carp (*Hypophthalmichthys molitrix*) in the La Grange Reach, Illinois River. *Biological Invasions* 12: 433–436, <https://doi.org/10.1007/s10530-009-9462-z>
- Sass GG, Hinz C, Erikson AC, McClelland NN, McClelland MA, Epifanio JM (2014) Invasive bighead and silver carp effects on zooplankton communities in the Illinois River, Illinois, USA. *Journal of Great Lakes Research* 40: 911–921, <https://doi.org/10.1016/j.jglr.2014.08.010>
- Shih AM, Techet AH (2010) Characterization of the Jumping Behavior of Archer Fish, *Toxotes microlepis*. 6th World Congress of Biomechanics (WCB 2010). August 1–6, 2010 Singapore, pp 48–51, https://doi.org/10.1007/978-3-642-14515-5_13
- USGS (2016) Historical Water Quality Data through the National Water Information System for Station 05586300 (Illinois River at Florence, IL) (accessed March 11, 2016)
- Wiest FC (1995) The specialized locomotory apparatus of the freshwater family Gasteropelecidae. *Journal of Zoology* 236: 571–592, <https://doi.org/10.1111/j.1469-7998.1995.tb02733.x>