

RESEARCH ARTICLE

Angling-induced injuries have a negative impact on suction feeding performance and hydrodynamics in marine shiner perch, *Cymatogaster aggregata*

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ABSTRACT

Fishing is a popular and lucrative sport around the world and, in some cases, may contribute to declining fish stocks. To mediate this problem and maintain fish biomass in aquatic ecosystems, catch-and-release fishing, whereby a fish is caught and immediately released, has been implemented in many countries. It is unclear whether the injuries to the mouth that are caused by the hook have an impact on feeding performance of fishes. Using high-speed video and computational fluid dynamics (CFD), we asked whether injuries around the mouth caused by fishing hooks have a negative impact on suction feeding performance (measured as maximum prey velocity) of the commonly angled marine shiner perch (*Cymatogaster aggregata*). We hypothesized that fish with mouth injuries would exhibit decreased feeding performance compared with controls. Ten shiner perch were caught using scientific angling and 10 were caught using a seine net. Feeding events were then recorded at 500 frames per second using a high-speed camera. Compared with the control group, maximum prey velocity was significantly lower in the injured group ($P < 0.01$). Maximum gape, time to peak gape, maximum jaw protrusion and predator–prey distance were comparable between the control and injured groups, leading us to conclude that the injury-induced hole in the buccal cavity wall reduced the pressure gradient during mouth expansion, thereby reducing the velocity of water entering the fish's mouth. This was confirmed with our CFD modelling. Fishing injuries in nature are likely to depress feeding performance of fish after they have been released, although it is currently unclear whether this has a significant impact on survival.

KEY WORDS: Fishing, Prey capture, Catch-and-release, Mortality, Conservation, CFD

INTRODUCTION

Recreational fishing is popular throughout the world and has significant socioeconomic impacts (Arlinghaus and Cooke, 2008). Given the worldwide popularity of recreational angling, it is not surprising that there are some ecological and conservation risks associated with the large amounts of fish being caught (Arlinghaus

and Cooke, 2008). Declining fish biodiversity and stocks highlight the importance of fishing regulations and catch-and-release programmes (Lewin et al., 2006). Catch-and-release involves recreational anglers catching and then quickly releasing a fish back into the water to help preserve the fish biomass, while still enabling the continuation of fishing practices (Pollock and Pine, 2007). Catch-and-release was initially thought to have a very minimal impact on fish populations given that anglers were not removing fish from the habitat (Bugley and Shepherd, 1991). However, average post-release mortality can be as high as 67% due to the stresses from catch-and-release, raising questions about the efficacy of this fishing method (Bettoli and Osborne, 1998). This mortality is due to many factors involved with fish capture and handling, which includes, but is not limited to, time exposed to the air, the roughness of being handled, time from being hooked to being brought up out of the water, where on the fish it was hooked, the experience of the angler, the depth from which the fish was pulled, and fish size (Cooke et al., 2002; Bartholomew and Bohnsack, 2005). A study on the mortality of fishes after being caught by recreational anglers indicates that fishes have species-specific variability in their mortality, with most mortalities occurring between 4 h and 4 days after being caught (Broadhurst et al., 2005). Most studies generally do not consider the potential impacts of hook injuries around the mouth as contributing to this mortality, and it is generally viewed as the preferred way to catch a fish (Bartholomew and Bohnsack, 2005). Recent studies have examined the impact of hook removal (DeBoom et al., 2010) and the size and style of fish hooks (Robert et al., 2012) on the survival and feeding rate of freshwater fishes. Yet no study has addressed how such injuries may influence suction feeding performance of fishes immediately after they have been released, or the hydrodynamics of suction following an angling-induced injury.

Many species of fishes employ suction feeding, in which the expansion of the buccal cavity creates an area of low pressure, drawing in a volume of water and the prey (Lauder, 1980; Muller, et al., 1985; Day et al., 2005, 2015; Higham et al., 2006a,b). It is likely that this feeding strategy would be most affected by angling-induced injuries, especially those that create a hole to the ambient water, given the importance of an intact buccal cavity for generating suction forces. Indeed, fishing hooks and gear can cause tears and injuries in the skin and membranes surrounding the mouth (Cooke et al., 2003) and, therefore, could reduce the strength of suction. If the injuries from fishing equipment are decreasing the fish's chances of catching prey by decreasing feeding performance, then it might also affect the survivability of the fish until it is able to fully heal. Incidence of complete and successful healing may partially explain why short-term mortality of fishes is generally higher when compared with long-term mortality of released fishes (Pollock and Pine, 2007).

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List of symbols and abbreviations

| | |
|-------------------|--|
| CFD | computational fluid dynamics |
| CSA | cross-sectional area |
| D_{exp} | total duration of head expansion |
| M_{exp} | total magnitude of head expansion distance |
| TTPG | time to peak gape |
| TTPJP | time to peak jaw protrusion |
| V_{node} | velocity of expansion of the nodes of the head surfaces in the CFD model |

Using the marine shiner perch (*Cymatogaster aggregata*), we combined high-speed videography and computational fluid dynamics to determine the role of hook-induced injuries in the performance and hydrodynamics of suction feeding. Shiner perch are ideal for this study as they are easily caught via recreational angling, exhibit specialized suction feeding behavior and morphology (Chu, 1989), and are easily kept in laboratory. Our integrative approach enabled us to test the hypothesis that fishing-induced injuries (holes through the membranes and skin) reduce suction feeding performance (maximum prey velocity) by altering the flow of water into the mouth during mouth expansion.

MATERIALS AND METHODS**Location and animals**

Ten shiner perch (*Cymatogaster aggregata* Gibbons 1854) were caught from a boat via scientific angling in the Bamfield Inlet near the Bamfield Marine Science Centre (BMSC) on Vancouver Island, BC, Canada (48°50'03.5"N, 125°08'12.7"W) in July 2017. An additional 10 individuals were caught via seine net on Wizard Islet in Trevor Channel (48°51'30.3"N, 125°09'32.7"W) in June 2017. The average standard lengths of fish in the control and injured groups were 10.3 cm (range, 9.8–11.5 cm) and 9.1 cm (range, 6.0–11.5 cm), respectively. Body mass ranged from 12.3 to 41.1 g. Fish were caught using worms or bits of mussels as bait, and we used size 8 barbless fishing hooks, with a diameter of 0.75 mm. For the fish that were caught by hook-and-line, the hook was immediately removed and the fish was placed into a 3-gallon holding tank with enrichment and proper shade. Only fish that had mouth injuries on the upper area of the mouth were kept for the experiment, with all others immediately released. Special care was taken to ensure that the specimens being caught experienced minimal stress, and the water was refreshed to maintain appropriate levels of oxygen. Specimens were then transported to a laboratory at the BMSC and were housed in groups of five in 76-liter aquaria with enrichment (plants, shade provided by black netting), sufficient water flow at a stable temperature (9–10°C), and air stones. Individuals that were caught by seine net at Wizard Islet (control group without mouth injuries) were always kept separate from individuals caught by angling. Individual fish were identified by a combination of behaviors, sex, size and different patterning on the sides/fins. The fish were fed once per day by dropping small (3 mm) pieces of tube worm into the tank. Food was withheld for 24 h prior to filming to ensure that the fish were motivated, and to make sure that each fish was satiated to the same degree. At most there were 4 days between capture and the experiments. This was necessary for reducing stress and maximizing motivation. Although not quantified, the injuries were still visible. All sampling and experiments adhered to the approved Animal Use Protocol from the BMSC Animal Care Committee (UP17-SP-BMF-05) in accordance with ethical standards of the Canadian Council for Animal Care.

Experiments

Each of the experiments took place in the housing aquaria (76-liter), which were modified with a white background and a grid (with dots 1 cm apart) for scaling. Three to five individuals were placed into the aquarium and left to acclimate for a minimum of 1 h. If the fish did not appear motivated to eat, additional time was given until they were motivated. At that point, a 3 mm piece of tube worm was dropped into the middle of the tank and the feeding event was recorded in lateral view at 500 frames per second using an Edgertronic high-speed camera (SC1, Sanstreak Corporation, San Jose, CA, USA) (Fig. 1). A minimum of three feeding events was recorded for each individual. In the case where a feeding event was not perpendicular to the camera, additional events were recorded and only the first three suitable strikes were used in analyses. The trial was still considered suitable if the fish deviated only slightly from perpendicular. The results from these trials did not differ from the other trials.

Following the feeding events, the fish was placed into a 76-liter tank with enrichment. This process was completed until all fish were recorded and weighed. After the experiment was completed the fish were released at the point of capture or euthanized with Eugenol (>400 mg l⁻¹) according to BMSC Animal Care standard operating procedures.

Computational fluid dynamics

A computer-aided design model approximating the shape of the head and buccopharyngeal cavity of the shiner surfperch was designed based on MRI data from The Digital Fish Library project (Fig. 2A,B). The 'Blend' functionality of ANSYS SpaceClaim Direct Modeler 18.0 (ANSYS Inc., Canonsburg, PA, USA) was used to fit volumes around three internal and three external ellipses. The axes of these ellipses correspond to the heights and widths of the head and buccopharyngeal cavity measured on the MRI scan sections (see Fig. 2A). A subtraction operation of the buccopharyngeal volume from the head volume in ANSYS DesignModeler 18.0 produced the cavity. An additional subtraction of a cylinder extending laterally created the hole of the piercing by the hook. Next, using the same software module of ANSYS Workbench 18.0, the volume of water that surrounds the head and fills the buccal cavity was created by subtraction of the volume displayed in Fig. 2B from a sphere with a diameter of 0.4 m. The outer boundary of the sphere was then assigned a 'pressure outlet' condition, which implies enforcing a constant pressure at this location. This boundary condition is valid as it is sufficiently far away from the suction feeder.

The kinematics of the phase of cranial expansion during feeding in the shiner surfperch is modelled so that it captures the fundamental components of suction-feeding kinematics in fishes, and achieves realistic suction flow velocities for this species. In absence of quantifications of cranial expansion in the lateral direction (suspensorium and gill cover abduction) and dorsoventral direction (neurocranial elevation and mouth bottom depression), equal motions are prescribed in these two directions in the CFD model. As there is no reason to assume that, at the location of the mouth and puncture, the dominance of anterior-to-posterior flows and occurrence of the typical spatial and temporal gradient of pressure inside the mouth cavity would be significantly affected by the direction of expansion of the head, this assumption seems valid. Two equations describe the kinematics: one for the anterior end and one for the posterior end. Mesh nodes located in between these two ends are moved by a linear combination of both equations in proportion to their position in between. These equations are sine functions controlled by two parameters: (1) M_{exp} , the total

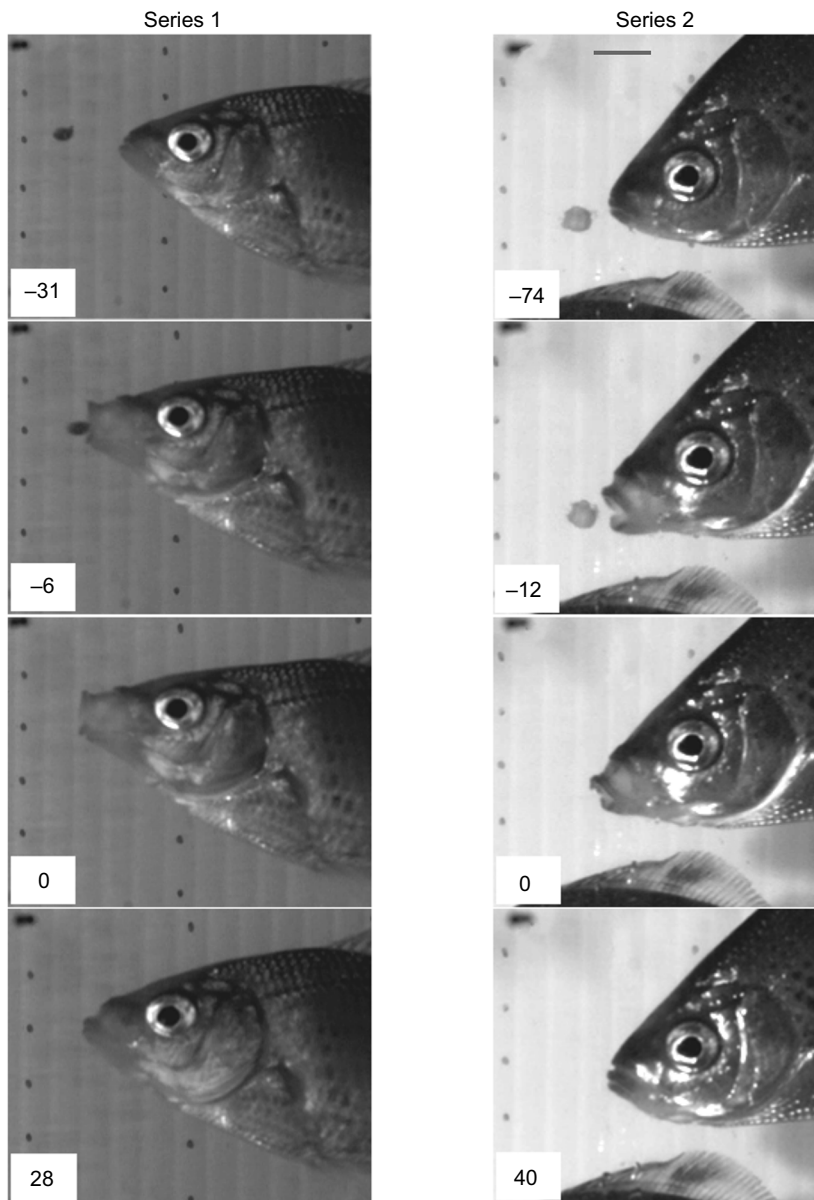


Fig. 1. Representative still images from high-speed videos of prey capture by *Cymatogaster aggregata*. Series 1 is from an individual from the control group and series 2 is from an individual from the injured group. Each of the images (from top to bottom) shows the time (ms) relative to maximum gape. The scale bar in the upper right corner is 1 cm in length.

magnitude of the head expansion distance, and (2) D_{exp} , the total duration of the head expansion. The equations for velocity (V_{node}) have the following form:

$$V_{\text{node}} = \frac{M_{\text{exp}}}{D_{\text{exp}}} \sin\left(\frac{2\pi}{D_{\text{exp}}} + \frac{3}{4}2\pi\right) + \frac{M_{\text{exp}}}{D_{\text{exp}}}. \quad (1)$$

Anterior and posterior expansions start at the same time, but to achieve a high flow velocity at the mouth near the instant of maximum gape, the posterior D_{exp} (50 ms) was set to be twice the value of the anterior D_{exp} (25 ms; corresponding to the observed time to peak gape in the shiner surfperch). In this way, the expansion progresses as an anterior-to-posterior wave, a general characteristic of suction-feeding kinematics of fishes (Sanford and Wainwright, 2002). The anterior M_{exp} was set at 1.2 mm to achieve a mouth diameter of 6 mm, which closely approximates the observed value for the shiner surfperch (data from this study). By monitoring the outcome of the CFD simulations, the posterior M_{exp} was adjusted (final value=6 mm) so that realistic flow velocities at the mouth

(p2 in Fig. 2) are reached: 2.61 m s^{-1} corresponds closely to the observed peak velocities of the prey (2.48 m s^{-1}).

Meshes consisting of between 2.5 and 3.0 million tetrahedra were constructed using ANSYS Meshing 18.0. The mesh was the most refined near the head surfaces, where triangles have edge lengths of 0.05 mm at the surfaces of all holes smaller than 1 mm in diameter, and 0.2 mm elsewhere. The growth rate of the tetrahedra away from the head surfaces was set at 1.1, meaning that tetrahedra are allowed to become 10% larger per layer away from the center. A mesh convergence analysis for the model with a hole of 1 mm diameter showed that pressures at point p2 (see Fig. 2C) after 10 ms in the simulation (the approximate time of peak pressure), while still decreasing from a mesh of 1.4 million to 2.5 million by 6%, did no longer change significantly with further refinement of the mesh to 8 million cells (0.16% change). Also, the change in flow velocity at point p1 at this instant when further refining the 2.5 million cell mesh to 8 million cells was relatively small (about 1% change). Given the considerable computational costs of the latter mesh, and the comparative focus of the study, the 2.5 to 3.0 million cell meshes

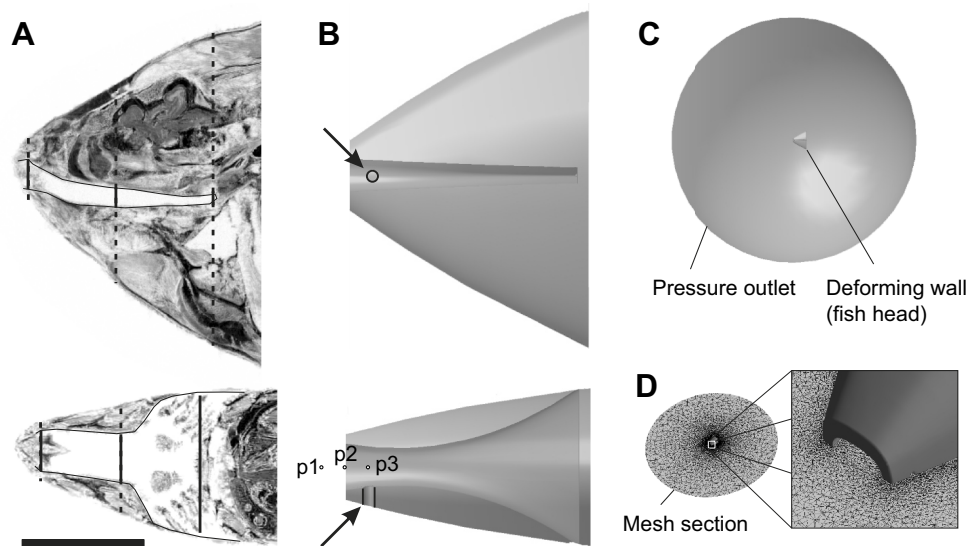


Fig. 2. Geometry of the computational fluid dynamics (CFD) model. (A) Midsagittal section (top) and midfrontal section (bottom) show the outlines of the buccopharyngeal cavity in the shiner surfperch. Heights and widths of the cavity (continuous lines) and the head's external contours (dashed lines) are measured at three positions along the length of the head, and used to construct a computer-aided design surface (shown in B). These Digital Fish Library images were obtained with permission from Lawrence R. Frank, University of California San Diego. (B) Position of the hole is indicated by arrows, as well as the position of three points (p1, p2 and p3) on the central axis of the buccopharyngeal cavity on which flow velocities were monitored. (C) Geometry of the flow domain, with the two boundary condition types. (D) Transect of the mesh, with a detailed view of the mouth on the left. The scale bar in A is 1 cm in length.

were considered to be sufficiently accurate. A convergence analysis of time step size showed negligible effects of refinement from the 0.5 ms (value used in all reported results) to 0.25 ms (differences in velocity at simulation time of 5 ms of less than 0.8%). A transient model of laminar flow was solved using ANSYS Fluent 18.0. Water flow will almost certainly be laminar due to the size of the fish, and the strong acceleration of the water from rest which significantly delays the transition to turbulent flows (Lefebvre and White, 1989; Van Wassenbergh and Aerts, 2009). The recommended (default) solver settings were used, which included solving the pressure–velocity coupling using the SIMPLE scheme, and the following settings for spatial discretization: least-squares cell base method for gradients, second order method for pressures, and second order upwind method for momentum. Water was modelled as a fluid with a constant density of 998.2 kg m^{-3} and a constant viscosity of $0.001003 \text{ kg m}^{-1} \text{ s}^{-1}$.

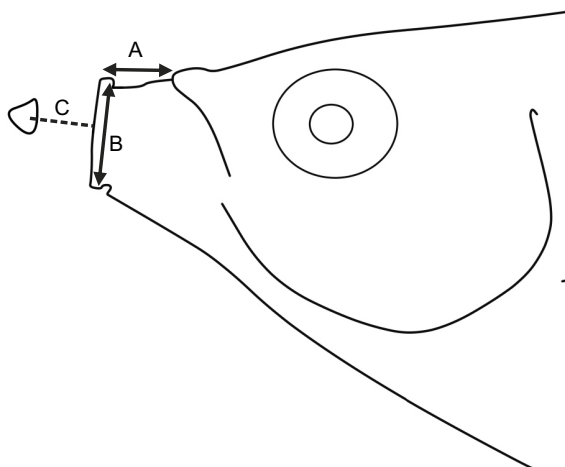


Fig. 3. Outline drawing of a shiner perch showing the three distance measurements. (A) Pre-maxillary jaw protrusion; (B) maximum gape; (C) predator–prey distance.

Data analysis and statistics

Prior to analysis, each video was trimmed and converted from MOV to AVI format using MPEG Streamclip 1.2. The videos were then digitized using ImageJ 1.51k. Variables measured included time to peak gape (TTPG, ms), predator–prey distance (from mouth aperture to the midpoint of the prey) at the time of mouth opening (cm), maximum gape (cm), maximum pre-maxillary jaw protrusion (cm), and the time to peak jaw protrusion (TTPJP, ms) (Fig. 3). Suction feeding performance was measured as maximum instantaneous velocity of the prey item (cm s^{-1}), which was quantified over 2 ms intervals. The prey item was digitized with respect to the earth-bound frame of reference. Thus we are extracting the suction-induced prey velocity. Our measure of suction feeding performance is based on the flow field that is generated when a fish rapidly expands its mouth. The suction-induced flow will entrain the prey item, pulling it towards the fish. Greater suction-induced flows will, therefore, cause the prey to move more rapidly towards the fish. This technique has been used in the past (e.g. Kane and Higham, 2011), and is likely to be valid as long as the prey item is not mobile and if the predator–prey distance does not vary among the groups being compared. Both of these assumptions are true for our study.

A total of 60 trials were analysed, which included three trials per individual. All three trials were averaged, yielding a single value per variable for each of the 20 individuals. Prior to statistical analyses, each variable was regressed against body mass using an ordinary least squares linear regression, and this was done on the combined data from both groups. If the relationship was significant, the residuals were used in further analyses. This method for accounting for variation in body size is commonly used (Hulsey et al., 2007; Revell, 2009). Two-sample *t*-tests were used to compare control and injured groups for all variables described above, with $P=0.05$ as the cut-off for statistical significance.

RESULTS

The only variable that was significantly affected by body mass was the maximum suction-induced velocity of the prey, and we

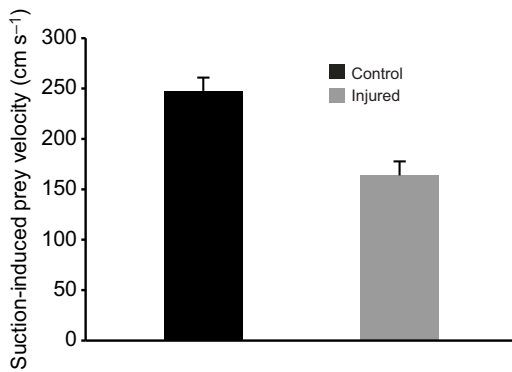


Fig. 4. Differences in maximum prey velocity between control and injured groups. Error bars are s.e.m.

therefore used the residuals for the statistical analysis. In this case, the control group exhibited significantly faster prey velocities ($247.6 \pm 13.2 \text{ cm s}^{-1}$) than the injured group ($163.7 \pm 13.9 \text{ cm s}^{-1}$) (Fig. 4; $t=2.41$, d.f.=18, $P<0.01$). The injured ($0.53 \pm 0.03 \text{ cm}$) and control ($0.54 \pm 0.02 \text{ cm}$) groups had similar predator–prey distance at the time of mouth opening (Fig. 5; $t=-0.394$, d.f.=18, $P=0.70$). In addition, maximum gape was not significantly different between the control group ($0.66 \pm 0.02 \text{ cm}$) and the injured group ($0.68 \pm 0.05 \text{ cm}$) (Fig. 5; $t=-0.349$, d.f.=18, $P=0.73$). Time to maximum gape was not significantly different between the control group ($22 \pm 0.7 \text{ ms}$) and injured group ($26 \pm 2.4 \text{ ms}$) (Fig. 5; $t=-1.635$, d.f.=18, $P=0.14$). Maximum jaw protrusion was 0.38 cm for both the control ($0.38 \pm 0.01 \text{ cm}$) and injured group ($0.38 \pm 0.03 \text{ cm}$) (Fig. 5; $t=0.016$, d.f.=18, $P=0.98$). Similarly, TTPJP was not significantly different between the control ($24.7 \pm 1.2 \text{ ms}$) and the injured ($24.8 \pm 1.6 \text{ ms}$) groups ($t=-0.034$, d.f.=18, $P=0.97$).

Computational fluid dynamics showed that water is drawn through the hole to fill the expanding buccopharyngeal cavity (Fig. 6; Movie 1). The peak flow velocity at the center of the hole was always close (<6% difference) to the peak velocity at the center

of the mouth opening. The volumetric flow rate into the hole, and therefore also the decrease in the speed of the flow entering the mouth opening, can thus be expected to roughly proportional to the cross-sectional surface of the hole. This is illustrated in Fig. 7, in which the cross-sectional area (CSA) of the hole is expressed as a percentage of the mouth opening area, and compared against the decrease in flow speed at the mouth entrance. This graph roughly shows a quadratic increase in the drop in suction speed at the mouth with hole diameter. For the two simulations with the largest hole (1.25 and 1.5 mm diameter), the instantaneous peak decreases in flow speed (12.8 and 18.6%, respectively), fall in between peak and mean percentage of hole-to-mouth CSA. In relation to this hole-to-mouth CSA percentage, the decreases are slightly higher for the smaller holes, where instantaneous maxima of the decrease in flow speed surpass the hole-to-mouth CSAs (Fig. 7). The decrease in flow speed at the mouth for hole that best matches the size of those in the experimental analysis (0.75 mm diameter), was 3.7 and 6.2% for time-averaged and peak instantaneous flow speeds, respectively (also see Movie 1). The quadratic relationship between hole diameter and decrease in flow speed at the mouth no longer applies to the smallest holes (0.25 and 0.5 mm), which cause approximately equal decreases in flow speed at the mouth entrance (1.9 and 2.0% for time-averaged flow velocities, respectively).

DISCUSSION

For the first time, we show that angling-induced injuries have a negative impact on suction feeding performance and hydrodynamics in fishes. As predicted, *C. aggregata* with mouth injuries exhibited a reduction in maximum suction-induced prey velocity in comparison with the control group. Given that no other differences between the groups were observed, we posit that the difference between these two groups arises from the presence of the fishing injuries in the mouth. Computational fluid dynamics confirmed a drop of performance due to the hole caused by the hook, although this did not completely account for the observed decrease in performance. Although we do not currently know

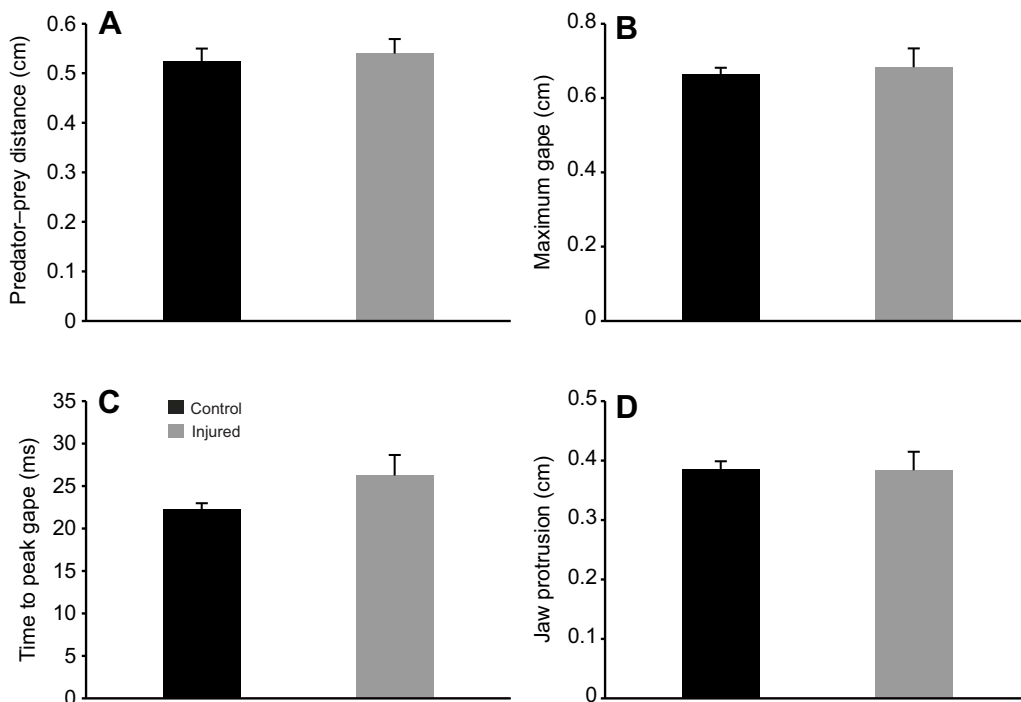


Fig. 5. Feeding kinematics in the control and injured shiner perch. (A) Predator–prey distance, (B) maximum gape, (C) time to peak gape and (D) jaw protrusion in the control group (black) and injured group (gray). Error bars are s.e.m.

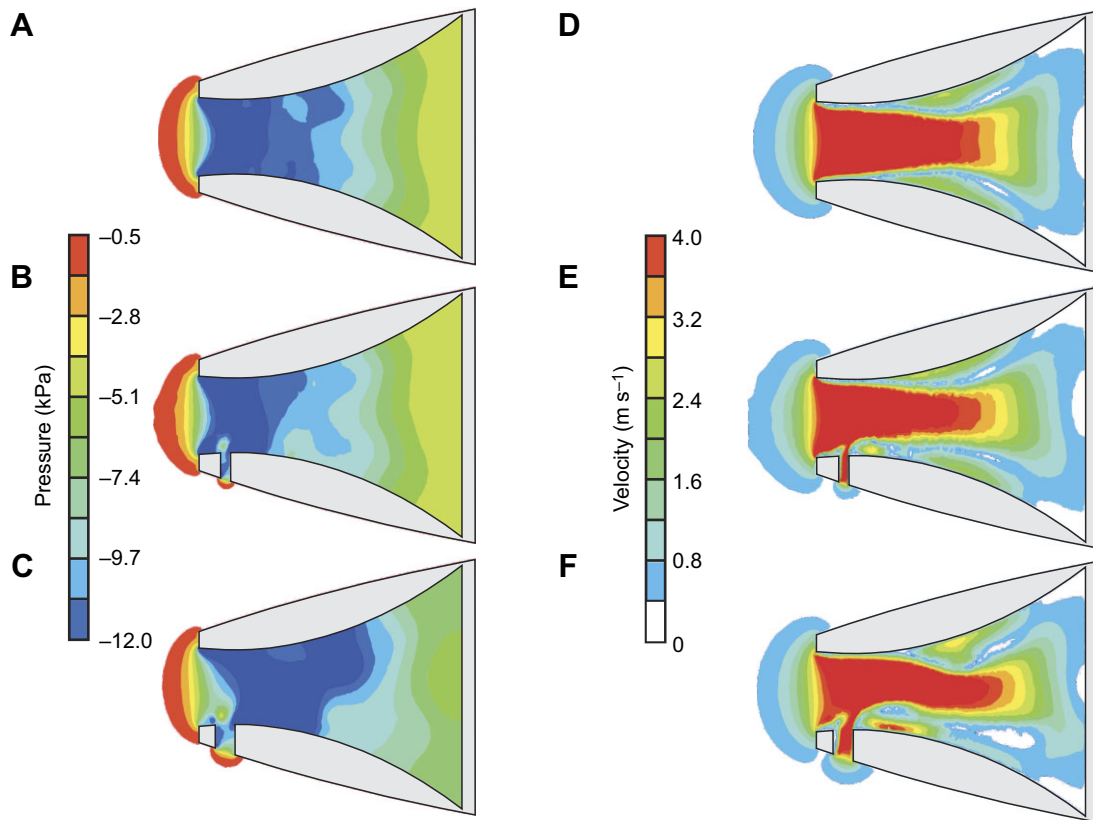


Fig. 6. Flow patterns calculated by CFD. Pressures (A–C) and 3D flow velocity magnitudes (D–F) are shown at mid-expansion (time=12.5 ms) in the mid-frontal plane. Results are shown for three of the seven models: (A,D) without hole; (B,E) with a hole of 0.75 mm diameter; (C,F) with a hole of 1.5 mm diameter. Note that the presence of a hole introduces a limited amount of asymmetry in the pressure and flow patterns, and that the widest high-velocity inflow zone (darkest red in D–F) is present without the hole (D).

whether this would have an impact on fitness in nature, we suggest that fishing-induced injuries may have an impact on the ability to capture prey and grow while the mouth is healing.

The mechanism of reduced prey velocity is likely to be a result of a lower pressure gradient developed during mouth expansion (Higham et al., 2006a). Motivation did not differ between the treatment groups, given that time to peak gape and maximum gape were not affected significantly. However, the injured fish exhibited an average TTPG that was longer, but not significantly different, from the control individuals. Using the data from Higham et al. (2006a), the difference between 22 and 26 ms TTPG, the values

observed for the control and injured fish, respectively, would result in a decrease in maximum fluid speed entering the mouth of approximately 13 cm s^{-1} . This is not in the proximity of the difference in suction-induced prey velocity observed in our study (84 cm s^{-1} ; Fig. 4), suggesting that TTPG was not the determining factor. It is unlikely that motivation differed between our groups, as maximum gape is often observed to decrease with reduced motivation (e.g. largemouth bass in Sass and Motta, 2002). This variable was not affected in our study. Body size differences did not account for the differences in prey velocity as we used the residuals in our analyses. Based on previous work (Holzman et al., 2008), our

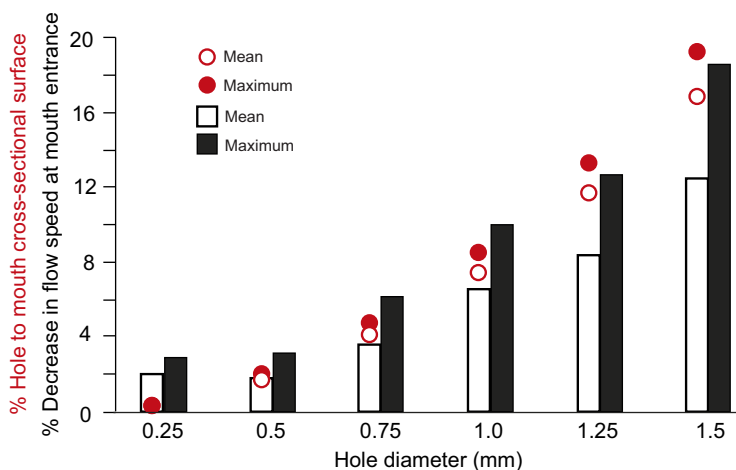


Fig. 7. Relative decrease in flow velocity in front of the mouth varies with hole size as calculated by the CFD models. The reference model is the one without hole (Fig. 6A,D). Flow velocities are means of the values at points p1, p2 and p3 (see Fig. 2). The reported values of relative decrease are either averaged over the entire expansion phase (white bars) or instantaneous maxima (black bars). To present a reference in size, the cross-sectional surface area of the hole relative to the mouth-opening surface area is plotted in red (filled circles represent instantaneous maxima, open circles are time averaged).

difference in standard length between the groups (1.2 cm) would not cause a noticeable difference in suction flow speed relative to the differences observed between our groups. In addition, maximum gape did not differ between our groups, a variable that would be expected to differ if body size differences were having an impact on the results.

In healthy fish, the membranes surrounding the buccal cavity are sealed, enabling the development of negative pressure inside the cavity relative to the surrounding fluid (Higham et al., 2006a; Day et al., 2007). Our CFD approach revealed a drop in pressure and fluid velocity with the presence of a hole, and this decrease is roughly proportional to the size of the hole. This decrease, coupled with the slight increase in TTPG, still falls short of explaining all of the decrease in suction performance observed in the high-speed video trials. One possibility is that the prey item deviated slightly from the virtual transect extending from the center of the mouth opening. Our video only captured a lateral view, so it is not possible to quantify any mediolateral offset of the prey relative to the fish. There is no reason to expect that injured fish would be less accurate when striking at prey, but more data are needed to confirm this. Future experiments involving the implantation of pressure transducers (Nemeth, 1997; Higham et al., 2006a; Sanford and Wainwright, 2002), and the use of particle image velocimetry (PIV), would build upon the CFD data to confirm the drop in pressure and fluid velocity.

The location where a fish can be hooked with the least effect on short-term mortality is in and around the membranous parts of the mouth, presumably because it causes less damage and is easier to remove if the hook is barbless (Cooke et al., 2003). It is expected that barbed hooks would cause greater injury due to the barb making it harder to remove, thereby increasing the overall handling time (Alós et al., 2008). The barb, combined with the shaft of the hook, would increase the effective diameter of the hole, further reducing suction performance. Furthermore, a study found that there was no substantial mortality of black sea bass after they were caught and held in cages, and mortalities only occurred when fish were hooked either incorrectly or accidentally (Bugley and Shepherd, 1991). Thus, fishes that are hooked correctly do not usually die from the injuries themselves, and any longer-term mortality probably stems from stress, infection or inability to capture prey.

Given that many fishes exhibit long-term survival following release, it is clear that the reduction in suction performance is either not ubiquitous, not always a factor in survival, or does not occur in all species that are caught by angling. Regardless, this sudden shift in feeding performance may result in missed feeding opportunities, especially for suction feeders that employ very accurate and quick attacks. Surfperches, including *C. aggregata*, usually eat non-evasive prey and stick close to benthic/kelp terrain (Laur and Ebeling, 1983). However, accuracy might be especially important for fishes that attack highly evasive prey, like shrimps or other small fish, which are very difficult to catch (Higham, 2007; Kane and Higham, 2014). For example, bluegill sunfish (*Lepomis macrochirus*) strike with greater accuracy compared with largemouth bass (*Micropterus salmoides*) due to the very limited distance of a suction feeding event and relatively small mouth (Higham et al., 2006b). It is more important for suction feeders to maintain accuracy and a high pressure gradient to enable successful prey capture than it would be for fishes that employ a ram strategy, which involves larger mouths and fast approach speeds to capture the prey quickly before it can escape (Norton, 1991; Kane and Higham, 2015). A vast majority (~83%) of sportfish caught in North America are ram feeders (trout, northern pike, walleye). However, a minimum of 29% of sportfish (perch, bass) caught in

Canada during 2010 use, or partially use, suction feeding as a main mode of prey capture (Fisheries and Oceans Canada, 2012). In the United States, however, around 53% of anglers went fishing for sportfish that use suction (panfish, crappie, black bass) (US Fish and Wildlife Service, 2011). It is currently unclear whether fishing-induced injuries would have an impact on a fish that employs a ram strategy.

Although there is a short-term impact of angling due to the injury to the buccal cavity, further study is needed to determine the healing rates of various fishes after they are caught by fishing hooks. This is important as we predict that suction feeding performance is restored following healing as the hole would no longer be present. It is likely that marine and freshwater fish differ in their healing rate due to the differences in infection rates and healing times for injuries cleaned with fresh versus saline solution (Trevillion, 2008). This could prove to have interesting effects, such as changing practices for catching and releasing fishes and having different areas dedicated to recreational fishing, and especially highlighting how we should treat these two systems with separate conservation tactics, but also pay attention to inter-connectivity of these areas that should require other, more complicated conservation tactics (Beger et al., 2010).

The effects of recreational fishing on both physiological and behavioural traits of an individual, even for a very brief period, are poorly understood. Yet these impacts could have extreme consequences on long-term survival. For example, do angling-induced injuries change the predatory behavior of a fish? Would there be any differences in how the fish handles and captures prey when fishing injuries are present? Our integrative study suggests that *C. aggregata* with fishing injuries do not approach or handle their food differently from the control group without injuries. However, they may choose to consume different types of prey in nature, which would 'carry' them through the healing time until they could resume feeding on their normal prey items. Field studies are necessary to address this possibility.

Conclusions

Catch-and-release fishing is an effective conservation approach to help keep the biomass of fish at a stable level or even increase it (Anderson and Nehring, 1984), but the injury caused by the hook causes a reduction in suction feeding performance. Future research should address how catch-and-release fishing and various fishing pressures can influence the feeding behaviors of a variety of fish species employing a variety of prey capture strategies.

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Competing interests

The authors declare no competing or financial interests.

Author contributions

Conceptualization: M.T., S.M.R., T.E.H.; Methodology: M.T., S.V.W., S.M.R., S.G.S., T.E.H.; Software: M.T., S.V.W., T.E.H.; Formal analysis: S.V.W., T.E.H.; Investigation: M.T., S.V.W., S.G.S., T.E.H.; Resources: T.E.H.; Data curation: T.E.H.; Writing - original draft: M.T., S.V.W., T.E.H.; Writing - review & editing: S.M.R., S.G.S., T.E.H.; Visualization: S.V.W., T.E.H.; Supervision: S.M.R., S.G.S., T.E.H.; Project administration: T.E.H.

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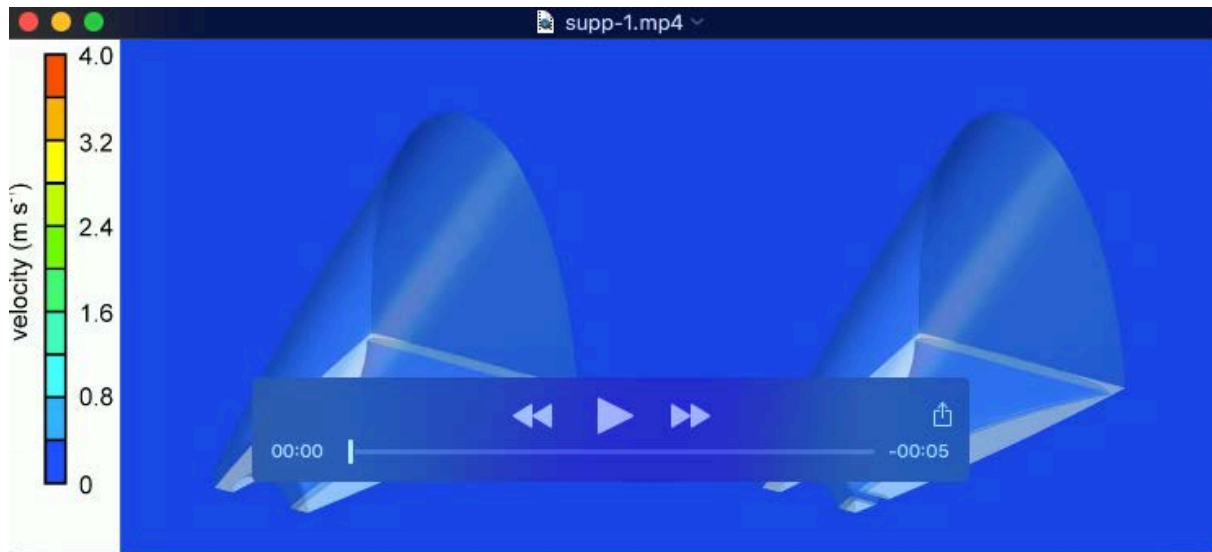
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Supplementary information

Supplementary information available online at
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Movie S1. This shows our CFD model for the control (left) and the trials with a 0.75mm hole (right). Colors represent the flow velocities through time.