RESEARCH ARTICLE

Longer development provides first-feeding fish time to escape hydrodynamic constraints

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Abstract

What is the functional effect of prolonged development? By controlling for size, we quantify first-feeding performance and hydrodynamics of zebrafish and guppy off-spring (5 ± 0.5 mm in length), which differ fivefold in developmental time and twofold in ontogenetic state. By manipulating water viscosity, we control the hydrodynamic regime, measured as Reynolds number. We predicted that if feeding performance were strictly the result of hydrodynamics, and not development, feeding performance would scale with Reynolds number. We find that guppy offspring successfully feed at much greater distances to prey (1.0 vs. 0.2 mm) and with higher capture success (90 vs. 20%) compared with zebrafish larvae, and that feeding performance was not a result of Reynolds number alone. Flow visualization shows that zebrafish larvae produce a bow wave ∼0.2 mm in length, and that the flow field produced during suction does not extend beyond this bow wave. Due to well-developed oral jaw protrusion, the similar-sized suction field generated by guppy offspring extends beyond the horizon of their bow wave, leading to successful prey capture from greater distances. These findings suggest that prolonged development and increased ontogenetic state provides first-feeding fish time to escape the pervasive hydrodynamic constraints (bow wave) of being small.

KEYWORDS
guppy, ontogeny, particle image velocimetry, suction feeding, zebrafish

1 | INTRODUCTION

Juvenile vertebrates are constrained in function by small size and immature tissues (Carrier, 1996). Among first-feeding larval fishes, small size has been identified as the major constraint affecting the hydrodynamics of suction feeding (China & Holtzman, 2014). Due to their small size (<5 mm), many first-feeding fishes experience a viscous hydrodynamic environment (low Reynolds number) that largely restricts their movements and leads to poor feeding performance and high mortality rates (Bremigan & Stein, 1994; Fuiman & Webb, 1988; Hernandez, 2000; Hjort, 1914; Houde & Schekter, 1980; Miller, Crowder, Rice, & Marschall, 1988; Rosenthal & Hempel, 1969). Compounding the negative effects of small size is the observation that larval fishes are immature in the degree to which their tissues have

developed (Cubbage & Mabee, 1996). Many first-feeding larval fishes are forced to obtain exogenous food resources at <5 days postfertilization (dpf; Pauly & Pullin, 1988), which means the underlying morphology responsible for swimming and feeding must function successfully at an immature stage. Here, we present results from experiments that control for the effects of small size in an effort to determine the relative effects of developmental immaturity on suction feeding performance in first-feeding fishes. We use two model organism freshwater fishes (zebrafish and guppy) that each produce small offspring (5 ± 0.5 mm standard length), but that undergo a fivefold difference in developmental time prior to first-feeding (Figure 1).

The utility in comparing zebrafish to guppies extends outside the simple observation that they are both canonical model organisms in genetics, development, medicine, ecology, and evolution. These two

FIGURE 1 Two model species of fishes exhibiting similar size of adult and offspring, but which possess considerably different modes of reproduction. Oviparous zebrafish spawn large clutches and offspring begin feeding only 5 days postfertilization (dpf), whereas ovoviviparous guppy produce smaller broods that gestate for at least 25 days prior to birth (which equates to first-feeding at 25 dpf). Due to their similarly small size, the offspring of these two species are each predicted to feed at Reynolds numbers in the viscous regime, but what effect on feeding performance has the fivefold difference in developmental time? (Scale bars = 1 mm)

species make a valuable comparison because they are two of the most morphologically different available species for examination of the effects of growth and reproduction on form and function of similarly-size offspring. The zebrafish (*Danio rerio*) is a freshwater, broadcast spawning, oviparous minnow (Family Cyprinidae) inhabiting the Himalayan riparian environment (Ruhl, McRobert, & Currie, 2009; Sih, 1994). Female zebrafish produce several dozen eggs per reproductive effort, which hatch and the larvae begin first-feeding after ~5 dpf and at ~4.5 mm standard length (SL; Figure 1; Pauly & Pullin, 1988; Hernandez, 2000; Pekkan et al., 2016). In contrast, the Trinidadian guppy (*Poecilia reticulata*) is an ovoviviparous livebearer (Family Poeciliidae) inhabiting the freshwater streams flowing out of the southernmost Lesser Antilles island (Figure 1; Magurran, 2005; Zandonà, Auer, Kilham, & Reznick, 2015). Exposure to high levels of predation has led to the evolution of numerous, yet small (~5.5 mm SL) offspring (Endler, 1995; Reznick, 1982; Reznick & Endler, 1982; Torres-Dowdall et al., 2012). Yet, even the smallest guppy offspring do not begin first-feeding prior to 25 dpf – a fivefold increase in developmental time prior to first-feeding over zebrafish larvae. Here, we compare first-feeding performance between these two species, quantifying craniofacial kinematics and development, ontogenetic state (Fuiman, 1994), and experimentally manipulating the hydrodynamic environment in an attempt to determine the relative effects of size and maturity on the performance of first-feeding fishes.

Foraging at small size in water means operating at intermediate to low Reynolds numbers (Re), where viscous forces dominate over inertial ones (Muller & Videler, 1996; Vogel, 1996). At this end of the hydrodynamic spectrum, the fluid resists flow and makes it more difficult for small larval fish to obtain food particles through suction

feeding, as compared with their adult counterparts (China & Holtzman, 2014; Hernandez, 2000; Yaniv, Elad, & Holzman, 2014). By experimentally increasing the dynamic viscosity of the water by adding a physiologically inert hydrogel (dextran), China and Holtzman (2014) simulated the viscous regime of newly hatched seabream larvae (4.4 mm SL) in offspring that were several weeks old (10 mm SL). The results showed that the hydrodynamics of small size constrained feeding performance: larger fish feeding at neonate-equivalent Re (~30) have similarly poor feeding performance as first-feeding larvae. Feeding rate was limited by the action (kinematics) of the jaw and the ability to produce enough force to overcome viscous effects at low Re. Thus, the authors hypothesize hydrodynamic starvation due to small size and the challenging viscous feeding environment as the underlying cause of first-feeding larval mortality.

However, to what extent does development play a role in constraining or allowing suction feeding performance and the generation of a flow field? At only 5 dpf, zebrafish larvae have been shown to be capable of producing respiratory flows into the mouth when embedded in agarose gel (Pekkan et al., 2016). Here, we expand on these efforts by quantifying free-swimming suction feeding in larval zebrafish, in addition to measuring feeding performance and morphological development. In comparison, the smallest guppy offspring (5.5 mm SL) are close to the size of the smallest first-feeding larval fishes (4.4 mm SL; Hall & Wake, 1999; Miller & Kendall, 2009), including zebrafish larvae, but guppy neonates have developed for at least 25 dpf prior to first-feeding. No work to date has quantified the hydrodynamics of suction feeding in newborn guppies, but there is substantial evidence from substrate feeding that performance correlates strongly and positively with developmental maturation (Dial,

Hernandez, & Brainerd, 2017; Dial, Reznick, & Brainerd, 2017). The goals of this study are (a) to identify if these two fish species experience poor feeding performance at first-feeding; (b) identify morphological, kinematic or hydrodynamic traits that correlate with feeding performance; and (c) to understand what effect, if any, the fivefold difference in developmental time has on suction feeding performance at small size.

We propose two hypotheses relating suction feeding performance to either (a) viscosity treatment (size) or (b) ontogenetic state. We will test these effects by comparing feeding performance (strike frequency and success) and flow generation into the mouth between the two species across a range of viscosity treatments. We predict a significant relationship between feeding performance and Reynolds number if size is the main driver of feeding performance. If feeding performance is a product of effects other than Reynolds number (such as craniofacial development), the prediction is that the experimental treatments will produce a reduced or non-significant relationship between feeding performance and Re. Feeding rates, jaw kinematics, and suction performance will be measured to determine feeding performance and Reynolds number across a wide range of viscosity treatments, and particle image velocimetry (PIV) will be used to quantify hydrodynamics during suction generation.

2 | MATERIALS AND METHODS

2.1 | Animals

Standard wildtype laboratory zebrafish larvae were obtained at 5 days postfertilization (dpf) from the Zebrafish facility within the Biological Laboratories on Harvard University campus. These fish were transported to the Harvard lab in standard petri dishes. All research reported here followed strict ethical guidelines and complied with the US federal government. Procedures were approved by the Institutional Animal Care and Use Committee at Brown University (protocol: 1211035) and at Harvard University (protocol: 20–03-2 to G. V. Lauder).

In order to obtain first-feeding newborn guppy offspring, adult female guppies (*Poecilia reticulata* Peters, 1859) were collected throughout Trinidad's Northern Range Mountains from five distinct populations (Caroni HP, Aripo HP, Aripo LP, Yarra HP, and Yarra LP). These females (*n* = 25 per population) plus 5 males per population were transported in 2 L bottles to a field laboratory where they were treated with furan (antifungal), methylene blue (antiparasite) and stress coat for 1 week prior to exportation to US. Export permit was issued by Trinidad's Ministry of Fisheries and the US Fish and Wildlife Service issued an import permit upon arrival into the US (Declaration confirmation number: 2016MI1850731). All procedures were approved by the Brown University Institutional Animal Care and Use Committee (Protocol #: 1211035 to E. L. Brainerd). All experiments were performed in accordance with the relevant guidelines and regulations.

Data were obtained from the two species as follows: under Brown (#1211035) guppy strike and capture rate and kinematic analyses were collected; under Harvard (#20–03-2) both guppy and zebrafish flow visualization data were collected, as well as zebrafish strike and capture rate and kinematic analysis data.

2.2 | Husbandry

Stock populations of Trinidadian guppies were housed in 37,85 L glass aquaria, isolated by population so males and females could mix. Gestating females were isolated within 11,35 L tanks that were partitioned into 5 chambers (leaving 2,27 L of filtered and temperature regulated water per female). Upon parturition, female guppies were removed and placed back into the communal tanks. Age starting at birth (day 0) was tracked for individual offspring. All fish were fed twice daily on a diet consisting of live *Artemia* nauplii in the morning and algae flakes in the evening.

Stock populations of zebrafish were maintained in petri dishes up until 2 weeks of age (14 dpf), at which point they were transferred into 2 L glass aquaria. The larvae were maintained on a diet of paramecium, fed twice daily.

2.3 | Filming

Individual zebrafish larvae (*n* = 18) and guppy neonates (*n* = 26) were isolated within a small (3.57×10^{-6} m³) custom-built plastic tank (using optically clear plastic from Edmund Optics Inc. Barrington, NJ), with inner dimensions: 0.00703 m × 0.02022 m × 0.02512 m (depth × width × height). Fish were acclimated for 2 min prior to filming. Video sequences were captured using a Photron FASTCAM MiniAX (Photron USA, Inc., San Diego, CA) fitted with an Infinity Photo-Optical Company lens (Boulder, CO). The filming area was illuminated using fiber-optic illumination (ThorLabs OSL2, Newton, NJ). Following the period of acclimation, ~25 individual prey items were delivered to the 3.57 ml volume feeding chamber. In an effort to match relative prey and predator size, we used *Paramecium* (100–300 μm length) for filming zebrafish, and *Artemia* nauplii (400–500 μm length) for filming guppies. All hydrodynamic manipulations made to the experimental treatments equally affected both the fish and their prey (i.e., the effect of viscosity manipulation was linear).

Three sets of video recordings were made to gather three separate sets of data: (a) strike and capture rate data were obtained from video at 250 fps, which recorded continuously for 48 seconds, over which feeding performance was measured; (b) data for kinematic analyses were filmed at high-speed (1,000 frames per second; fps) to measure feeding kinematics; and (c) flow visualization data were obtained with video recordings at 1000 fps with suspended neutrally buoyant particles to obtain PIV, which we used to determine flow fields during in vivo and unrestrained prey capture.

Following each feeding trial, fish were euthanized by an overdose of tricane methanosulfonate (Tricane-S, Western Chemical, Inc., Ferndale, WA) buffered in sodium bicarbonate (Fisher Scientific, Fair Lawn, NJ). Specimens were fixed in 4% buffered paraformaldehyde (Sigma, St. Louis, MO) overnight and transferred to 70% ethanol for long-term storage.

2.4 | Dextran solutions

In order to control for slight size differences and to experimentally compare the suction feeding performance of first-feeding zebrafish and guppies, we manipulated water viscosity by adding known concentrations of an inert polysaccharide (dextran; Danos & Lauder, 2012; Dial, 2016). By increasing water viscosity, we can simulate feeding at smaller-than-natural size by forcing a larger fish to feed at similar Reynolds numbers as a smaller fish. Using aquarium water (previously treated with stress coat) we made solutions of Dextran-40 (Sigma Aldrich, St. Louis, MO) from 0% (water) to 4% weight by volume. To determine the effect of dextran on the viscosity of the aquaria water, we measured viscosity of each treatment using a calibrated Cannon-Ubbelode viscometer (#9721-K53; Cannon Instrument Co., State College, PA). Using a temperature-controlled water bath set to 40°C, we determined the kinematic viscosity (m^2/s) of each dextran solution (see below for more info on kinematic viscosity as it relates to Reynolds number). Dextran was used to manipulate water viscosity both the feeding rate experiments (strike and capture rate) and the kinematic analysis experiments.

2.5 | Reynolds number manipulation

The Reynolds number is a dimensionless number that describes the relative dominance of inertial to viscous forces experienced by an organism in its fluid environment, and is calculated as follows:

$$Re = \frac{lu}{v} \qquad (1)$$

where l is length (in m), u is velocity (in m/s) and is kinematic viscosity (in m^2/s). As is commonly used in the larval fish feeding literature (Krishnan, Nafi, Gurka, & Holzman, 2020; Sommerfeld & Holzman, 2019) and in our previous research on prey capture in guppies (Dial, 2016), we use swimming velocity to calculate Reynolds number.

While suction feeding, a guppy at 5.5 mm SL with mouth opening rates similar to zebrafish and gilthead seabream (China & Holtzman, 2014; Hernandez, 2000), is predicted to produce Reynolds number (Re) = 30 or less. Although this estimate is likely to be within the range of the Re of miniaturized fish suction feeding, we used high-speed video recordings to calculate Re definitively based on body velocity during feeding. We estimated that a 2% dextran solution will increase the viscosity of water for a 5.5 mm offspring to simulate the hydrodynamic environment of a 4.4 mm offspring, but we use dextran manipulations up to 3% in zebrafish and 4% in guppies (the maximum concentrations from which we obtained data from each species) in our methods. Zebrafish would not feed in the 4% dextran solution.

2.6 | Strike and capture rates and kinematic analysis

We used three metrics (calculated from three separate experiments) to quantify feeding performance among groups: (a) feeding rate was determined by counting the number of prey items consumed within 48 s of feeding at prey densities of 10 individual brine shrimp or paramecium per milliliter; (b) distance to prey at frame prior to the first visual evidence of mouth opening, and (c) flow field generation, each determined from high-speed recordings of individual feeding strikes. These metrics were used to distinguish performance among experimental groups.

Feeding performance was measured over a 48-s interval at 250 fps by determining the total number of strikes and total successful feeding events made during reduced speed playback. An additional, high-speed video at 1000 fps was recorded from the same individual during one strike and used to obtain feeding kinematics and to calculate Reynolds number. These videos were digitized in Matlab R2016a, using DLTdv5 software (Hedrick, 2008) to assign points to the eye, quadrate-angular jaw joint, distal tip of dentary, caudal peduncle, and prey. Movements were calibrated to a scale accurate to 0.01 mm, which was placed in view and used for calibration during each recording. Jaw protrusion, prey displacement, peak gape diameter, and standard length were calculated using the digitized points. Oral jaw protrusion was measured as the difference of the distance from the distal tip of the premaxilla to anterior orbit at peak gape minus that same distance at start of mouth opening. Distance to prey was calculated as the distance from the center of the prey to the distal tip of the dentary at frame just prior to mouth opening. Reynolds number was calculated using velocity of the swimming fish and standard length to calculate the Reynolds number of swimming (Re_{swim}), for each viscosity treatment.

Additionally, we quantified and analyzed Reynolds number of the jaw (Re_{jaw}) during peak suction using gape and prey velocity for several individual strikes ($n = 9$). The values were no different from those measured using Re_{swim} ($p = .986$; t-test; means: $Re_{jaw} = 70.48$ vs. $Re_{swim} = 70.46$).

2.7 | Flow visualization

In order to visualize fluid flows generated by the approaching predator and the effects of mouth opening on the prey, we used 1,000 fps video recordings to record the motion of particles introduced into the experimental arena. We used fiber optic illuminators as a light source to reflect light off 1–2 μm *Nannochloropsis* algae (Reed Mariculture,

Campbell, CA) introduced into the feeding arena following a modified version of the brightfield protocol by Gemmell, Jiang, and Buskey (2014). Particle seeding density was ~150 million algae cells per milliliter within the filming chamber of 3.57 ml volume. Videos captured the motion of these small nonmotile algae as zebrafish and guppies approached their prey, and the subsequent movement of water into the mouth. The distance microscope lens was positioned 3–4 cm from the filming chamber and was configured with a fully open aperture, which provided a narrow depth of field within which only a sheer plane of particles (0.5 mm) are in focus and tracked by the PIV software.

Videos were analyzed using standard particle imaging software (DaVis 8.3, LaVision Inc, Göttingen Germany) as in our previous research (Flammang & Lauder, 2016; Lauder, 2015; Lauder & Madden, 2008; Lehn, Thornycroft, Lauder, & Leftwich, 2017) to generate a matrix of velocity vectors for each pair of frames throughout the feeding strike. Interrogation windows varied from 16 by 16 pixels to 48 by 48 pixels (with 50% overlap and two iterative passes) depending on predator location and camera position. This initial calculation of the velocity vector field was followed with postprocessing in DaVis 8.3 software by deleting outlier vectors using a median filter and then smoothing once with a 3 x3 filter window and denoising with a 5×5 window. We did not perform any image pre-processing. These analyses generated vector fields that were used to calculate peak velocity of flow into the mouth and the size of the bow wave, measured as distance rostrally to point where flow decays to <10% velocity of fish prior to mouth opening. Use of the term "bow wave" herein does not refer to surface features produced by a swimming fish (all fish were fully submerged), and in some ways this is a misleading term but one that is standard in the literature of larval fish feeding (Gemmell, Adhikari, & Longmire, 2014; Holzman & Wainwright, 2009; Stewart, Nair, Jiang, & McHenry, 2014). We use the term "bow wave" to refer to the size and mass of entrained water carried forward with a swimming fish, visible in the supplemental video (Video S1) as particle motion in front of the head moving with the larval fish prior to prey capture.

2.8 | Anatomy

Bone and cartilage were differentially stained and the body was cleared to enable us to characterize and quantify differences in skeletal morphology associated with offspring size. Stains and measures of maturity were performed following the methods outlined in Dial, Hernandez, and Brainerd (2017). Specimens were visualized using a Nikon dissecting microscope system (Nikon SMZ800 dissecting scope and Nikon DXM1200C digital camera). Guppy ossification sequence was determined using the specimens generated from this study (n = 66). Zebrafish ossification sequence was determined from Cubbage and Mabee (1996), and only a subset of zebrafish larvae from this study (n = 10) were stained to validate the ossification sequence and provide images shown herein.

Ontogenetic state (Fuiman, 1994; Fuiman & Higgs, 1997) was determined in an effort to quantitatively compare relative degree of size and maturation (development) among the individuals and species tested. Ontogenetic state (O_L) was determined using the following equation:

$$O_L = \frac{\log(L)}{\log(L_{juv})}$$

where L = standard length (in mm) and L_{juv} = standard length (in mm) at which the species attains reference stage, in this case referring to adult morphology (quantified as complete ossification; Figure 2). Thus, an O_L score of 100 indicates a fish that has attained the adult morphological condition. By using this method of determining ontogenetic state, the two species examined herein are compared in relative terms, as opposed to simply comparing based on size or developmental state alone.

2.9 | Statistical analysis

In the experimental treatments, Reynolds number was calculated to control for size and fluid regime, thereby allowing degree of maturation to be the main independent variable across treatments. Each of the three data sets described previously were treated statistically independent. Sigmoidal growth data were log-transformed before fitting linear regression models.

The best model to explain variation in capture success was chosen using Akaike Information Criterion (AIC) model selection. AIC eliminates each parameter of small effect in order to provide the smallest possible model that sufficiently explains the response variable (Akaike, 1974). Response variables of capture success from feeding rate and kinematic data sets were analyzed using corrected Akaike Information Criterion (AICc) model selection, which is appropriate if n/k < 40 (where n is sample size and k is number of parameters; Hlavac, 2018). Statistical analyses were performed using JMP v.11 (SAS Institute, Cary, NC), IGOR Pro (WaveMetrics, Lake Oswego, OR) and R (v3.4.3, R Foundation for Statistical Computing, 2016).

3 | RESULTS

3.1 | Maturation as a function of offspring size

Zebrafish (*Danio rerio*) offspring included in this study ranged in size from 4.5 mm at first-feeding to 10 mm as nearly-metamorphic juveniles at 18 days post first-feeding. Zebrafish fully metamorphosed at 15 mm SL at ~30 days post first-feeding. Sigmoidal regression analysis showed a positive and significant correlation between maturation and standard length (R^2 = 0.92, p < .0001; Figure 2). At first-feeding, zebrafish larvae are ~10% ossified, with the oral jaw apparatus maturing early in development (Figure 2). Degree of ossification continued to increase throughout the postnatal period among all zebrafish offspring, beginning to plateau at ~90% at ~9.0 mm SL (Figure 2) Fully
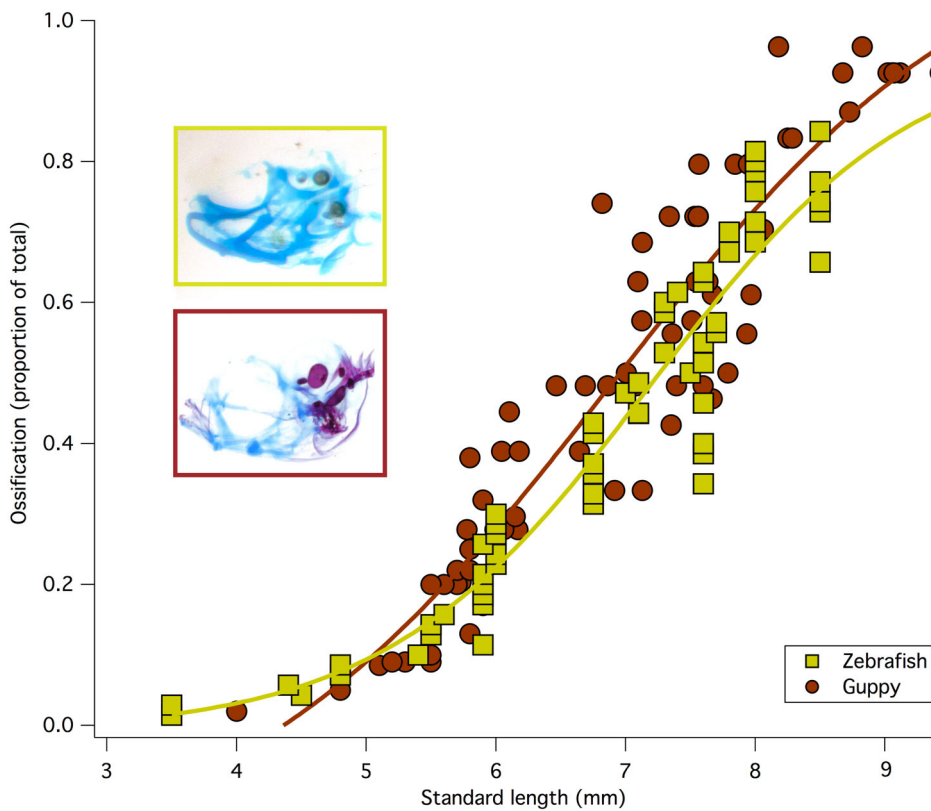
FIGURE 2 Maturation of the skeleton occurs at a similar size and pace in zebrafish (n = 69) and guppies (n = 66). Each species is half (50%) ossified at ~7 mm SL and first-feeding occurs at <10% total ossification. The maturation onsets and rates of ossification are not significantly different from one another (p = .88; see Results). Inset images show representative craniofacial ossification at first-feeding of zebrafish (4.5 mm SL) and guppy (5.5 mm SL), with bone stained red and cartilage blue

TABLE 1 Corrected AIC results from separate analyses of kinematics and feeding performance

	Null deviance	Residual deviance	df	AICc	deltaAICc	AICc weight
Feeding performance	10.89872					
Capture ~ fish + strike + dextran		0.32435	75	−199.1	2.14	0.255
Capture ~ fish + strike		0.32493	76	−201.3		0.745
Kinematics	9.3261					
Capture ~ fish + length + dextran + viscosity + re + distance + protrusion		3.5497	38	35.7	3.11	0.022
Capture ~ fish + length + viscosity + re + distance + protrusion		3.5498	39	32.6	2.06	0.103
Capture ~ fish + length + viscosity + distance + protrusion		3.6168	40	30.5	1.43	0.288
Capture ~ length + viscosity + distance + protrusion		3.7273	41	29.1		0.588

Note: Under each analysis is the several models fit to the data. The lowest model under each analysis, with the smallest AICc score, indicates a best fit.
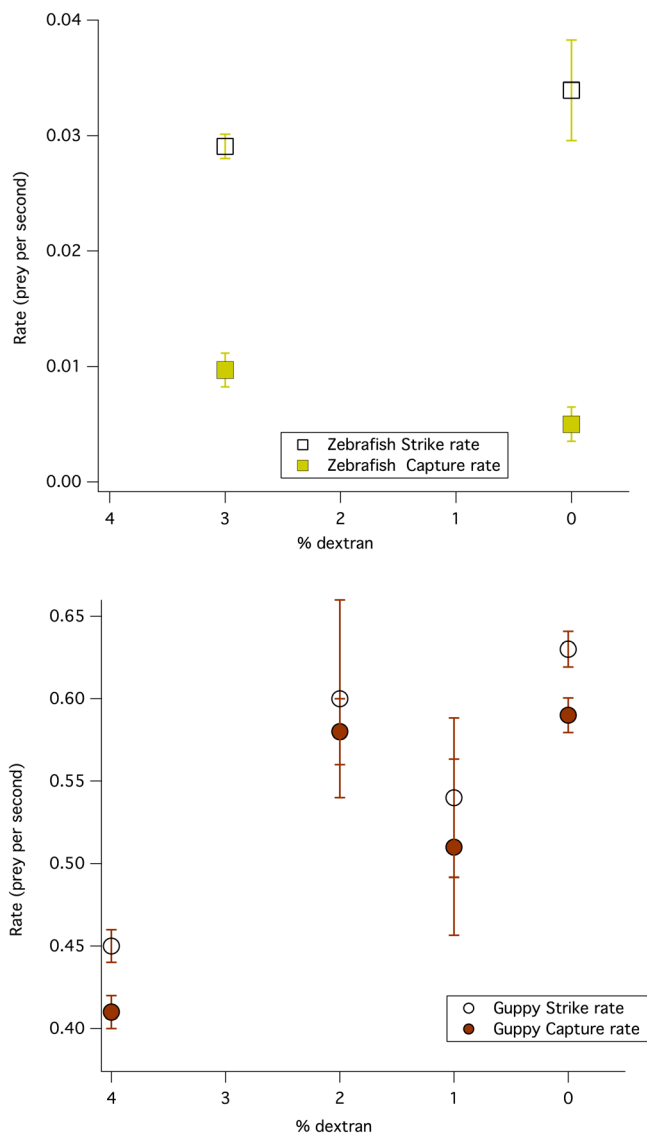
ossified zebrafish offspring are witnessed at ~15 mm SL (Cubbage & Mabee, 1996), which is larger than the largest offspring examined within this study.

Size-specific degree of ossification was found to be comparable between zebrafish and guppy (*Poecilia reticulata*). Guppy offspring size ranged from 5.5 mm neonates to 10 mm postnatal juveniles at 16 days after first-feeding (birth). Over this range, offspring maturity varied as a function of offspring size (Figure 2), as previous studies have found (Dial, Hernandez, & Brainerd, 2017; Dial, Reznick, & Brainerd, 2016; Dial, Reznick, & Brainerd, 2017). Regression analysis

showed a positive and significant correlation between maturation and standard length (R^2 = 0.84, p < .0001). Guppy neonates experienced a fourfold increase in degree of maturity from 5.5–10 mm SL. At first-feeing, the smallest guppy offspring were 20% ossified compared with fully-ossified and mature juveniles (Figure 2).

In an attempt to quantify the relative influence of size and maturity between the two species, Ontogenetic State (O_L) was calculated based on the relative size of the experimental fish, in reference to the size at which full ossification (maturation) is achieved for that species (Fuiman, 1994; Fuiman & Higgs, 1997). The Ontogenetic State index

considers both size and development, in a unitless term, which allows for more appropriate comparison between the two species, and among individuals within a species. The range of O_L values observed for zebrafish individuals examined herein was 45.7 at first-feeding to 83.6 at the largest size class used within this study. O_L values for guppies ranged from 75.8 at first-feeding (birth) to 98.6 at the largest size class observed herein. The disparity of O_L values at first-feeding between zebrafish and guppies reflects the status of both size and development of each species at this stage. To effectively compare performance between the two species, we employ dextran treatments to manipulate the viscosity of the water to examine the effects of hydrodynamic regime on feeding performance.

3.2 | Strike and capture rates

Results from a corrected Akaike Information Criterion (AICc) model on feeding rates indicated that capture success is best predicted by species (zebrafish or guppy) and strike rate (Table 1). Guppy offspring fed with higher capture success than did zebrafish larvae, but in both species, individuals feeding with higher strike frequencies also had higher capture rates.

Zebrafish strike frequency showed no difference across dextran treatments and Reynolds number (Re) (Figures 3a and 4a). If feeding
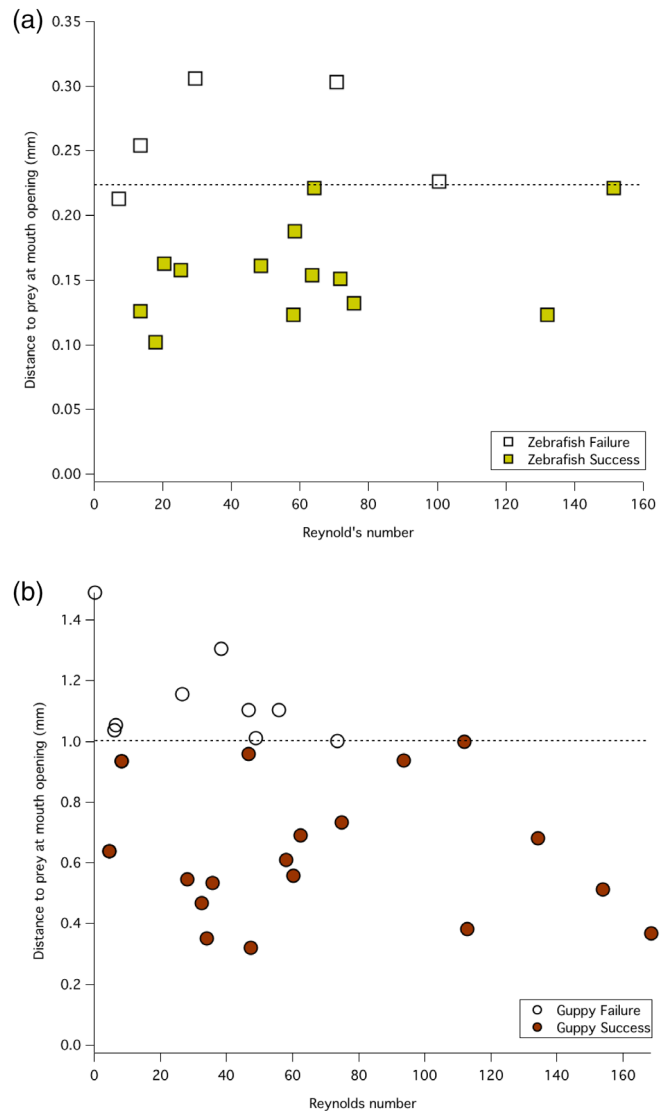

FIGURE 3 Strike and capture rates vary as a function of viscosity (% dextran) for guppies, but not zebrafish. Behaviorally, guppies exhibit higher strike rates than zebrafish, by nearly 10-fold. Furthermore, guppies maintain high strike and capture rates, achieving a high (>90%) success rate, whereas zebrafish capture rates are significantly lower than their strike rates, at 25% success rate. Averages ± *SE* reported for zebrafish (*n* = 18) and guppies (*n* = 26)

FIGURE 4 Across a range of Reynolds number, offspring of both species experience an upper limit in the distance to which they can successfully capture prey, but this upper limit is 5× greater in guppies compared with zebrafish. (a) Successful zebrafish captures occurred when fish began the suction strike at ~0.2 mm distance to the prey (dashed line). (b) A similar upper limit was observed in guppies, but at ~1.0 mm distance (dashed line). This expanded range of successful feeding might help explain the observed difference in feeding rates (Figure 2). Note the difference in scale along vertical axis between A and B. Individuals reported for zebrafish (*n* = 18) and guppies (*n* = 26)

performance were primarily dependent upon Re then, regardless of viscosity treatment, we should observe an increase in feeding performance concomitant with an increase in Re. Control and experimental groups showed ~1.8 strikes per minute. Capture rate was slightly lower in control group at 0.3 captures per minute, compared with 3% dextran treatment, which was 0.6 captures per minute. Success rate was ~25% (14% in 0% dextran, 36% in 3% dextran; Figure 3a).

Guppy strike rate was >10x higher than zebrafish, at ~40 strikes per minute in water and ~ 28 strikes per minute in 4% dextran (Figure 3b). Capture rate varied from 24–35 captures per minute across a range of Re. Success rate was over 90% across all viscosity treatments. Guppies therefore consumed over 50× the number of prey items in a given feeding trial compared with zebrafish. These results indicate that Re alone is not a good predictor of feeding performance between the first-feeding offspring of the two species.

3.3 | Kinematic analysis

AICc results of the kinematic data showed that capture success largely depends on fish length, viscosity, distance, and premaxillary protrusion (Table 1). Inclusion of the upstream variables: species type, dextran, and Reynolds number do not improve model fit (Table 1). Capture success increases with increasing fish size and protrusion, and with decreasing viscosity and distance to prey. For a given size, fish in unmanipulated water, capture depends on close proximity to prey and an increased ability to protrude the oral jaws.

3.4 | Distance to prey

The marked difference in prey capture performance between the two species correlates with initial strike distance to prey. Zebrafish initiated mouth opening between 0.1–0.3 mm from prey (Figure 4a). Successful captures occurred at <0.22 mm to prey, across a wide range of Re. Guppies fed between 0.2–1.4 mm from prey, with successful strikes occurring at <1 mm, across a similar range of Re (Re = 5–160), which spans the viscous and intermediate regimes (Figure 4b). At any given Re, guppy offspring are able to successfully feed at nearly 5× the distance to prey compared with zebrafish. This indicates that zebrafish are constrained to feeding at very close distances for successful captures, compared with guppies, which may explain the observed difference in feeding rates between the two species (Figure 3).

3.5 | Protrusion

Using high-speed video, we measured the distance of premaxillary protrusion anteriorly during prey capture. Guppy and zebrafish offspring differ in their ability to protrude the oral jaws (Figure 5), and this difference correlates with the variation observed in feeding success (AICc results, Table 1). On average, guppy offspring produce over twice the protrusion that is observed among zebrafish offspring. This additional protrusion correlates with feeding success among the offspring. At distances to prey where the zebrafish offspring begin to fail (~0.3 mm), guppy feeding success is 100% and protrusion is double that of zebrafish. Guppy offspring begin to fail at prey capture at
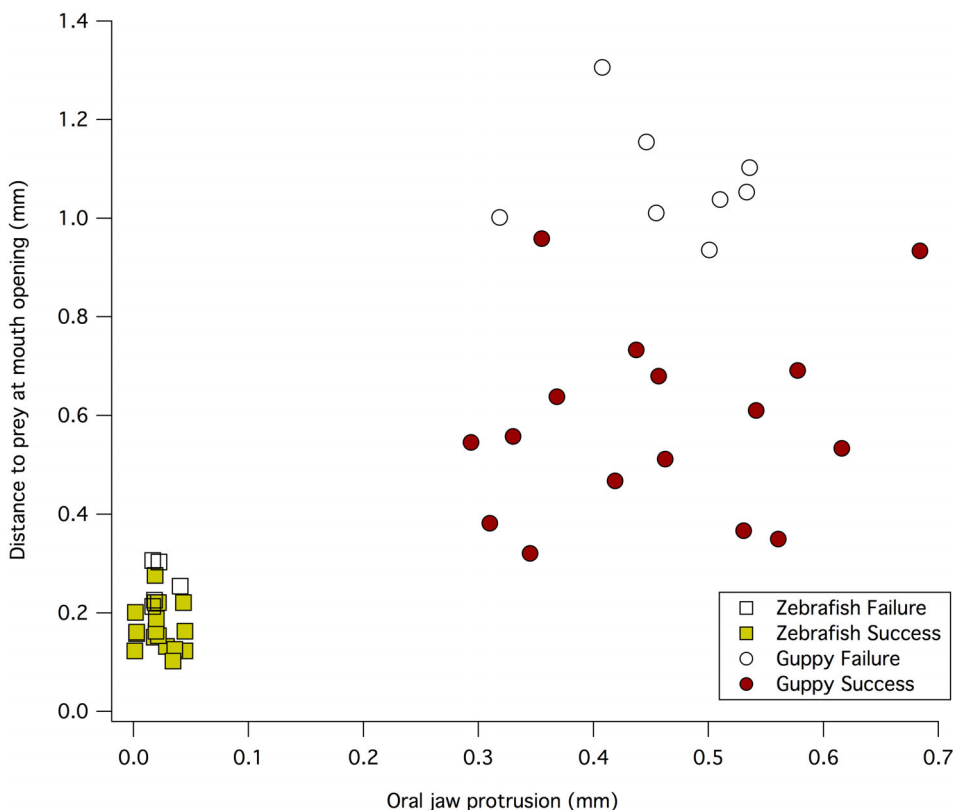
FIGURE 5 Successful feeding strikes occur at increasing distances to prey with increasing levels of jaw protrusion. We find that guppy offspring protrude their oral jaws a greater distance during suction feeding than zebrafish larvae, and thus are able to retain high capture success even at large distances to prey. Note that at ~0.3 mm distance to prey, zebrafish larvae fail to capture prey, whereas guppy offspring successfully feed at this and much greater distances, owing to a substantially greater degree of jaw protrusion. Individuals reported for zebrafish (*n* = 18) and guppies (*n* = 26)

much greater distances, likely the result of an inability to further protrude the jaws and produce adequate suction.

3.6 | Flow visualization and bow wave

PIV reveals that both zebrafish (n = 5) and guppy (n = 5) offspring produce a bow wave ahead of the approaching fish (Figures 6–8). This wave extends 0.19 ± 0.04 mm in front of the zebrafish (Figure 7). Zebrafish initiate successful strikes at 0.18 ± 0.06 mm distance to prey (Figure 4a), and PIV indicates that the prey item upon suction initiation is often within the leading edge of the bow wave (Figure 6a, 7). At the moment the fish initiates suction, the bow wave is temporarily disturbed, and the prey moves toward the expanding mouth (Figure 6b). It appears that the momentum of the approaching fish carries it through the position of the prey (a form of ram feeding), as the prey is engulfed

(Figure 6c). We note that the generation of suction is performed by a depression of the hyoid and elevation of the head (a form of pivot feeding)—both of which together expand the buccal cavity, thereby producing suction adequate to temporarily remove the bow wave.

In stark contrast to the zebrafish feeding mechanics, an approaching guppy offspring initiates the feeding strike prior to the encounter between bow wave and prey item (Figure 6d). The bow wave extends 0.17 ± 0.05 mm in front of the guppy, but the size of the flow field generated during suction (0.54 ± 0.21 mm) extends beyond the leading edge of the bow wave. Guppy suction is powerful enough to generate flow at distances of 5× that of zebrafish at the same Re (Figure 6e). During many strikes the guppy carried momentum toward the prey (Figure 6f), but protrusion of the oral jaws and the strong flow stream generated by an expanding head allow guppy offspring to more effectively capture evasive prey, and from much greater distances.
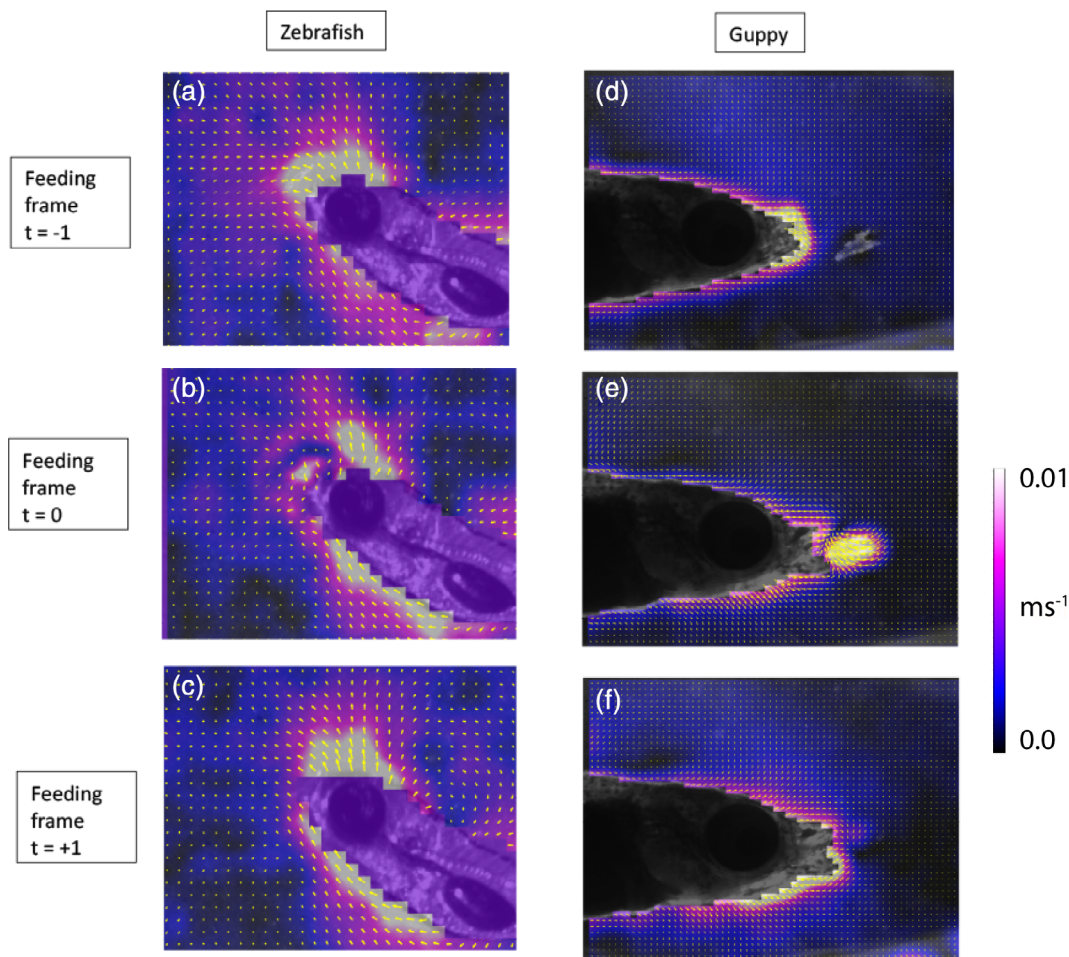
FIGURE 6 Typical ram-suction mechanics of zebrafish (a–c) and guppy (d–f) from lateral view. Flow visualization shows that a bow wave leads the approaching zebrafish prior to mouth opening, which continues to push the prey item ahead of the approaching mouth by ∼1/2 head length (a). During successful zebrafish suction feeding (b), the bow wave temporarily ceases and the fish captures the prey. The bow wave returns (c) following the termination of the suction strike, closing of the mouth, and as momentum of the fish carries it over the previous position of the prey item. Guppy strikes begin before the prey enters the bow wave (d), and mouth protrusion produces suction at a much greater distance (e). Bow wave returns after mouth closing (f). 0.5 ms between frames
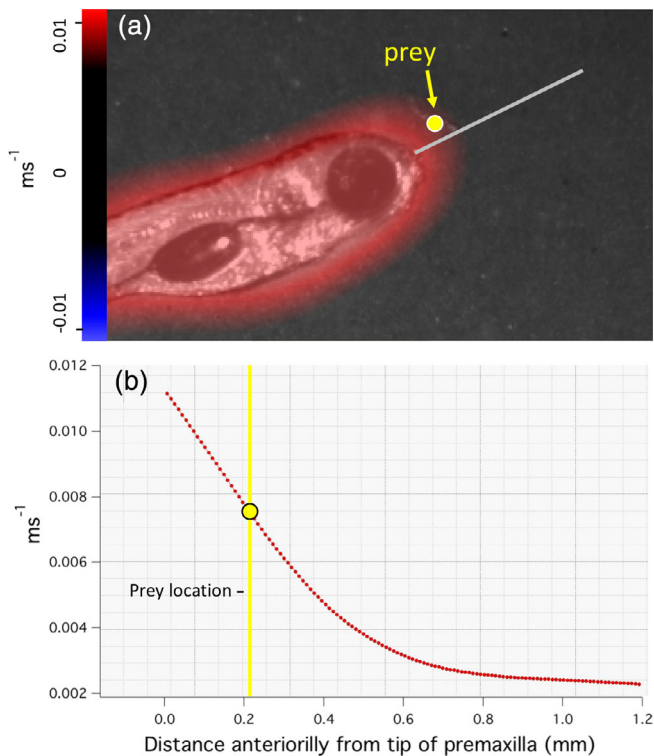
FIGURE 7 First-feeding zebrafish produce a substantial bow wave as they approach their prey. (a) Still image from high-speed video of a zebrafish larva approaching a prey item with water velocity determined from PIV hydrodynamic analysis (scale bar on y-axis shows flow to the right in red and to the left in blue). Water velocity within 90% of fish speed extends ∼0.2 mm ahead of the fish, continuously pushing the prey (yellow arrow) away from the zebrafish's mouth. (b) Water velocity as a function of distance anteriorly from tip of premaxilla (gray line in a), shows the extent of the bow wave as it diminishes with distance away from the approaching predator

4 | DISCUSSION

4.1 | Escaping the bow wave

In an experimental comparison between first-feeding zebrafish and guppy offspring, we find that suction feeding performance is highly dependent on proximity to the prey item. In both zebrafish and guppies, the approaching fish generates a bow wave, as a result of the entrained or added water mass that accompanies forward body motion, that may be up to a mouth diameter in front of the head (Video S1). In zebrafish, the bow wave appears to limit the distance to which a fish can approach near-neutrally buoyant suspended prey, forcing predators to rely on suction and forward body motion (ram) for successful prey capture (Figure 6a–c). In many suction feeding fish, flows decay to <1% within the distance of one mouth diameter (Day, Higham, Cheer, & Wainwright, 2005; Day, Higham, & Wainwright, 2007; Higham, Day, & Wainwright, 2006; Holzman, Collar, Day, Bishop, & Wainwright, 2008; Staab, Holzman, Hernandez, &

Wainwright, 2012). From our PIV data, we observe that zebrafish produce suction flows that extend only to the front edge of the bow wave, and not beyond (Figure 6b)—indicating that successful prey captures only occur if and when the fish is able to approach the prey at, or even within, the front limit of the bow wave.

In contrast to zebrafish larvae, guppy offspring are capable of generating a suction field that extends beyond the leading horizon of the bow wave (Figure 6e). It is perhaps due to this ability to produce suction beyond the bow wave that guppy feeding performance is observed to be so much higher (Figures 3 and 4). At 90% capture success, guppy offspring represent the upper limit among those first-feeding fishes that have been investigated, many of which show 50–70% success rate at first-feeding (Houde & Schekter, 1980), and some species, such as herring, show <10% capture success (Rosenthal & Hempel, 1969). Prior work lacks quantification of bow wave size and flow field size generated during suction feeding in unrestrained larval fishes, and our data show that it is the relative sizes of these two parameters which most effectively explains variation in feeding success between the two species studied herein.

Mechanisms for overcoming the effects of a bow wave have been observed through both behavioral and mechanical alterations to the feeding strike. In an effort to reduce the size of the bow wave, adult zebrafish will begin suction generation at twice the normal approach distance when feeding on evasive prey (Gemmell, Adhikari, & Longmire, 2014). By beginning the suction phase early, the mechanosensory capabilities of copepods are not triggered by the hydrodynamic disturbance of a large bow wave. The flow field of adult zebrafish must be relatively large compared with the size of the bow wave produced in order to both remove bow wave fluid and pull in prey from beyond it. Here, a modification in the timing of suction initiation provides a behavioral mechanism to overcome the conspicuous nature of a bow wave, though prior research has also shown that certain jaw mechanics can increase the size of the flow field produced during suction (Holzman et al., 2008).

4.2 | Jaw protrusion and head elevation

Jaw protrusion enhances the force exerted on prey during suction feeding. Increases in force of up to 35% have been shown, allowing fish to initiate their strike from greater distances, while still providing the necessary force to capture evasive prey (Holzman et al., 2008). Adult poeciliids are specialized for jaw protrusion, an adaptation thought to be particularly useful during substrate feeding (Hernandez, Ferry-Graham, & Gibb, 2008). Even among first-feeding guppy offspring, jaw protrusion is associated with increased feeding capacity (Dial, Hernandez, & Brainerd, 2017). First-feeding guppy offspring also use jaw protrusion during their suction strikes (Figure 6e), and such kinematics distinguish the feeding mechanics of first-feeding guppies and zebrafish.

Although no jaw protrusion was evident in larval zebrafish, a substantial degree of head elevation was observed. Dorsal rotation of the head provides a substantial amount of power for the suction strike (Camp, Roberts, & Brainerd, 2015; Lauder, 1982). Atlantic salmon

(a)

(b)
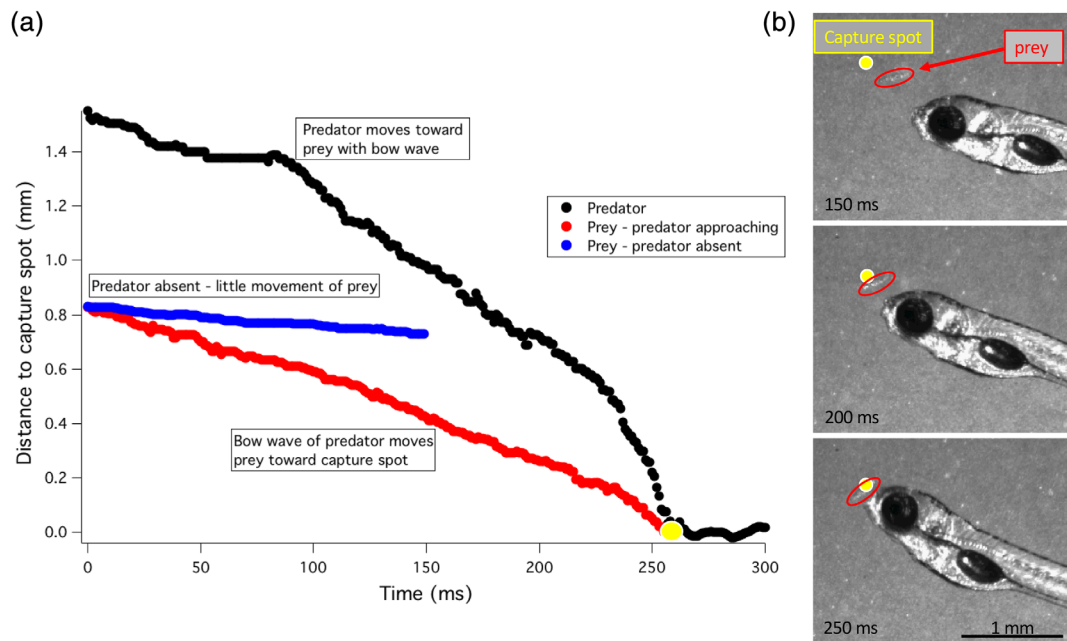
FIGURE 8 Does the bow wave influence the prey? (a) Traces of the zebrafish predator (black dots) and the paramecium prey (red) in relation to distance to the capture spot (yellow dot, in global reference). The blue trace shows normal displacement of prey when predator is absent. (b) Still images from high-speed video at three time points showing displacement of the prey toward the capture spot as the predator approaches. The approaching predator displaces the prey item by 0.8 mm in total, in contrast to the "predator absent" prey, which moves <0.1 mm on its own volition. See Video S1 for this feeding sequence

(Salmo salar) alevins also show a substantial degree of cranial elevation during suction feeding (Coughlin, 1991). This observation is similar to the pivot feeding observed in sygnathids (de Lussanet & Muller, 2007; Van Wassenbergh et al., 2009) and might be an adaptation that larval fishes use to produce the required suction necessary to draw water into the buccal cavity at relatively low Reynolds numbers. Indeed, head elevation is thought to be the ancestral behavior during suction feeding and is retained through the diversification of fishes (Lauder, 1980).

4.3 | Developmental effects

Here, we show that feeding performance is dramatically different between two fish species despite experiencing overlapping hydrodynamic regimes, suggesting that size alone does not predict suction feeding performance of zebrafish and guppy offspring. Our performance experiments controlled for slight differences in offspring size by equalizing the Reynolds number through viscosity manipulations and our prediction was that observed differences in performance would be correlated with differences in underlying ossification. But, we observe that ossification patterns are similar between the two species studied here and coincide closely with size of fish (Figure 2). Using ossification as a metric for maturity, we calculated Ontogentic State (O_L) as a means of effectively comparing the size and maturation of these two distinct species. O_L of first-feeding zebrafish larvae = 45.7, while the smallest guppy offspring are born and begin

feeding at O_L = 75.8. Although the offspring of these two species begin first-feeding at similar sizes, the difference in ontogenetic state is quite striking and most likely the result of different developmental programs and periods.

The major difference observed in suction feeding performance between zebrafish and guppy offspring is the degree to which the kinematics of jaw protrusion have developed at the time of first-feeding (Figure 5). Our data suggest that jaw protrusion is much greater in first-feeding guppies compared with zebrafish larvae (Figure 5), and this observation is not a product of bony ossification, but rather of well-developed feeding linkages in the jaws (Hernandez et al., 2008). The jaw protrusion mechanism has been shown to increase throughout ontogeny in both guppies (Dial, Hernandez, & Brainerd, 2017) and zebrafish (Staab & Hernandez, 2010). It has been shown that guppy offspring are born with the ability to protrude their jaws, and that this ability increases throughout early ontogeny (Dial, Hernandez, & Brainerd, 2017). In contrast, zebrafish begin first-feeding without the ability to protrude their jaws, and it is only until after metamorphosis that they develop the jaw protrusion mechanism (Staab & Hernandez, 2010). That the ability to protrude the jaw increases with ontogeny, indicates that suction generation at first-feeding is a product of developmental time. It is therefore most likely due to the longer time spent developing the feeding apparatus and hence differences in the developmental program between guppies and zebrafish, that guppies exhibit markedly higher suction feeding performance over zebrafish larvae. These findings suggest that developmental maturation is as an important trait for effective feeding in a fluid environment as is size.

So why then do we not witness more prevalent selection for larger and more mature offspring? Overwhelmingly, broadcast spawners include species that produce small eggs and larvae (Pauly & Pullin, 1988). This is because selection in general, but particularly in broadcast spawning fishes, favors high fecundity (Einum & Fleming, 2000) with the tradeoff that offspring are both diminutive and immature. These multitudinous offspring enjoy high dispersal with minimal parental care. In the live bearing guppy, however, offspring are produced in much fewer numbers (10% the number of zebrafish eggs are produced by an individual female guppy) and are required to be housed *in utero* for the extent of their incubation (Magurran, 2005). The cost of incubation is perhaps not recouped in the slight additional survivorship pelagic larvae might enjoy from a longer incubation period, and thus is not selected for among the broadcast spawners.

Generally, it is adaptive to produce as many offspring as will survive to the next size class (Brockelman, 1975; Lloyd, 1987; Roff, 1992; Smith & Fretwell, 1974; Stearns, 1992). In populations experiencing low predation (LP), competition for food is the predominant selective pressure, and female guppies produce larger offspring in fewer numbers (Endler, 1995; Reznick, 1982; Reznick & Endler, 1982). In LP populations, the adaptive benefit of sacrificing number for size is that larger offspring are better able to compete for limited resources (Bashey, 2008; Dial, Hernandez, & Brainerd, 2017). In environments favoring high fecundity, the size of guppy offspring is driven down by tradeoffs of yolk allocation (Reznick & Yang, 1993), but not indefinitely. Offspring size in the highest predation environments has converged on ∼5.5 mm among independent lineages (Reznick & Bryga, 1996), which is nearly as small as the smallest first-feeding larval fishes found in plankton.

4.4 | Concluding remarks

The juvenile stage is particularly vulnerable in fishes, owing to small size, immature tissues, behavioral inexperience at capturing prey, and high fluid viscosity with a consequent increase in energetic costs. Most first-feeding fishes exist at the lower limit of size and development and therefore experience extremely low rates of survivorship. Here we observe that at the lower limit of size among first-feeding fishes, the physics of being very small are not able to explain all of the variation observed in feeding performance. Trinidadian guppy offspring, that are similar in size to zebrafish larvae, perform orders of magnitude higher in feeding performance, and we propose that this is due to the relatively advanced ontogenetic state (O_L) at first-feeding in the live-bearing fish. The effects of the added developmental time are not reflected directly in guppy skeletal maturation, but rather, in the kinematics of their suction feeding. Extreme jaw protrusion, a product of protracted developmental time in both species, sets the guppy neonate apart from the zebrafish larvae at first-feeding. We argue that it is the increase in time spent developing these linkage mechanisms of their feeding apparatus that confer a suction feeding advantage to guppy neonates and allows them to evade hydrodynamic constraints of small size.

CONFLICT OF INTEREST

The authors declare no competing financial interests.

AUTHOR CONTRIBUTIONS

Terry Dial: Conceptualization; data curation; formal analysis; funding acquisition; investigation; methodology; resources; validation; visualization; writing-original draft; writing-review and editing. **George Lauder:** Conceptualization; funding acquisition; investigation; methodology; resources; supervision; validation; visualization; writing-original draft; writing-review and editing.

DATA AVAILABILITY STATEMENT

Morphological, kinematic and performance data for zebrafish and guppies have been deposited in the Dryad Digital Repository (doi: https://doi.org/10.5061/dryad.j3tx95x9x), along with the raw videos used for PIV.

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