# How to surprise a copepod: Strike kinematics reduce hydrodynamic disturbance and increase stealth of suction-feeding fish

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### Abstract

To capture prey with suction, fish must get sufficiently close to their prey to allow the suction flow to overwhelm the prey and draw it into the mouth. Both swimming towards the prey and suction flow create a hydrodynamic disturbance, which can elicit an escape response by the prey. Using particle image velocimetry, we measured flow speeds and derived fluid deformation rates at the location of the prey as bluegill sunfish fed. In front of the mouth, flows had a composite time-dependent nature. First, the bow wave pushed water away from the fish, but when the mouth opened and suction commenced, flow reversed and water deformation rates increased rapidly. Our inferences indicate that, at the prey, the approaching bluegill is detected primarily based on its suction-induced disturbance, rather than its bow wave–induced disturbance. A comparison of suction-induced disturbance than expected based on their flow speeds and mouth size alone. Jaw protrusion and the rapid opening of the mouth during the strike both help to minimize the signal available to the prey. We propose that the temporally quick strikes and high jaw protrusion that are seen in many zooplanktivorous teleosts represent adaptations that minimize the time available to prey for executing an escape response.

In aquatic communities, predation on zooplankton by fish is a major trophic pathway (Kerfoot 1987; O'Brien 1987; Aksnes et al. 2004), and the nature of these predatorprey interactions is greatly influenced by the dense and viscous surrounding medium (Kiørboe et al. 1999; Visser 2001; Wainwright and Day 2007). Fish typically use suction feeding to capture zooplankton, and so they must get close enough to the prey so that the suction flows they generate can exert large enough hydrodynamic forces to pull the prey into their mouth (Holzman et al. 2007; Wainwright and Day 2007). However, aquatic predators push water as they move towards the prey, creating a hydrodynamic disturbance in front of them (Vogel 1994; Kiørboe et al. 1999; Visser 2001). Many aquatic organisms, including copepods, Cladocera, cephalopods, insect larvae, polychaetes, larvae and adult fishes, jellyfish, and other groups of aquatic metazoans can sense these hydrodynamic disturbances to detect predators (Fields and Yen 1997; reviewed by Visser 2001; Van Trump and McHenry 2008). Hydrodynamic disturbances are sensed when specialized sensory setae (e.g., in crustaceans, polychaetes) or sensory cells (fish, mollusks) respond to displacement, fluid velocity, or acceleration caused by the differential motion of the individual sensor and the body to which it is attached (Yen et al. 1992; Visser 2001; Van Trump and McHenry 2008). The relative motion of the sensors leads to nerve depolarization, which triggers the escape motor pattern.

Following their approach to the prey, fish rapidly open their mouth to generate an external flow of water that pulls the prey into the mouth. Experimental evidence (Ferry-Graham et al. 2003; Day et al. 2005; Holzman et al. 2008*a*) and modeling studies (Muller et al. 1982; de Jong et al. 1987; Van Wassenbergh and Aerts 2009) reveal that these

flows are exceptionally short-lived, lasting only 10-50 ms, and are restricted to an area very close to the mouth. Suction flows generate a region with strong spatial gradients in flow speed and high temporal instability. Although these steep gradients and extreme accelerations can potentially inform the prey of the attacking fish, the nature of these signals and how prey use them to avoid the striking fish is still unclear. Despite the pronounced reliance of fish on suction feeding to capture small prev, studies and modeling of fish-zooplankton interactions have attributed the hydrodynamic disturbance generated by fish predators to the bow wave produced by swimming (Viitasalo et al. 1998; Kiørboe and Visser 1999; Visser 2001). Previous research approaches to identify the hydrodynamic signals perceived by flow-sensing organisms used artificially generated fluid disturbances such as siphon flows (Fields and Yen 1997; Viitasalo et al. 1998; Kiørboe et al. 1999), moving and oscillating bodies (Buskey et al. 2002; Heuch et al. 2007), and flow chambers (Haury et al. 1980; Kiørboe et al. 1999; McHenry et al. in press). Although being instrumental in defining the sensory capabilities of small aquatic organisms, the signal produced by these artificial sources of hydrodynamic disturbances is likely an oversimplification of the highly dynamic hydrodynamic signal produced by suction-feeding fishes (Day et al. 2005). Moreover, from the perspective of the fish there may be a trade-off inherent in the effect of suction flows on the prey: fast flows will exert higher forces on the prey, but will also create a stronger disturbance that might lead to an earlier escape response.

Our goal in this study was to characterize the hydrodynamic disturbance generated by the striking fish and ask whether and how fish attempt to reduce this disturbance. Specifically, we ask how rates of water deformation and flow (flow speed and strain rate) change in space and time during feeding strikes, and how the observed disturbance differs from that produced by other biological flow sources.

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Using particle image velocimetry (PIV), we measured the flow patterns generated in front of the mouth of feeding bluegill sunfish and derived fluid deformation rates. We compared the observed spatiotemporal patterns to those of the bow wave, constant, and time-dependent potential flows, and asked how responses of various prey should differ between these cases. We were particularly interested in identifying behaviors that allow the suction feeder to minimize the detectable signal it produces, or the time that the prey has to respond to the strike.

#### Methods

Bluegill (*Lepomis macrochirus*) were caught locally in Yolo County, near Davis, California, and housed in 100-liter aquaria at 22°C. Bluegill are the most planktivorous of all centrarchid species, feeding predominantly on cladocerans in North American lakes (Collar et al. 2009). Our fish were fed daily with pieces of squid (*Loligo* spp.) and live ghost shrimps (*Palaemonetes* spp.). Following several days of acclimation to the experimental aquaria, the fish were trained to feed in the laser sheet (*see* below) for at least a week before experiments began. Our study included six adult and subadult individuals (standard length between 95 and 155 mm). The experiments described below complied with the Institutional Animal Care and Use Committee guidelines for the use and care of animals in research at the University of California.

*Experimental protocol*—At the onset of each feeding trial, the fish was kept in a holding area that was separated from the feeding arena by a sliding door. When the door was opened, the fish was permitted to move across the aquarium and capture the prey. The position and width of the door ensured that the fish approached the prey horizontally, at a right angle to a video camera. The prey, segments of ghost shrimp and squid, were attached to a thin metal wire and held within the laser sheet. Prey size was adjusted to the fish's mouth size, ranging from 3 to 6 mm in length, ca. 20–100 mm<sup>3</sup> in volume.

Digital PIV (dPIV)—dPIV was used to quantify water motion in front of the fish and near the prev during feeding strikes. The details of the dPIV method, as well as the experimental protocol, are described elsewhere (Raffel et al. 1998; Day et al. 2005). Briefly, an Innova I-90 5W Argon-Ion continuous-wave laser (Coherent) was used with a set of lenses and mirrors to produce a vertical laser sheet in the experimental aquarium. The laser sheet, about 5 cm in width and 1 mm in thickness, was oriented upwards and then reflected down using a mirror at the surface of the aquarium to reduce the effect of the feeding fish's shadow (see fig. 1 in Day et al. 2005). To visualize flow, the water was seeded with nearly neutrally buoyant (specific gravity of 1.05), 12-µm, silver-coated, hollow glass beads (Potter Industries). Feeding strikes were filmed in lateral view using a high-speed digital video camera (500 frames s<sup>-1</sup>, NAC Memrecam Ci) equipped with a 55-mm lens (TEC-55 f/2.8, Computer Optics). The field of view was adjusted to capture the fish's head during its approach to the prey. Additionally, a camcorder recording at 30 frames  $s^{-1}$ 

(Sony) captured anterior views of the striking fish, which were used to verify the orientation and location of the fish within the laser sheet. Sequential images taken during feeding strikes, treated as image pairs, were analyzed using a cross-correlation algorithm in MatPIV (http://www.math. uio.no/-jks/matpiv), a free toolbox for PIV analysis in MATLAB (MathWorks). Image pairs were analyzed using a windows-shifting technique, starting with  $64 \times 64$ -pixel interrogation areas and ending with  $16 \times 16$ -pixel areas (with 50% overlap) after six passes. The cross-correlation algorithm returned a two-dimensional grid of  $70 \times 53$  vertical and horizontal velocities and signal-to-noise ratio (SNR) for each image pair analyzed. We omitted flow measurements with SNR lower than 2.

Velocity fields generated from dPIV images were used to calculate strain rate, a measure of the deformation of a fluid element as it moves. In a two-dimensional dPIV setup where the planar laser sheet is in the x-z plane, strain rate (s<sup>-1</sup>) components that can be calculated are

$$e_{xx} = \left(\frac{du_x}{dx}\right), \quad e_{zz} = \left(\frac{du_z}{dz}\right),$$
$$e_{xz} = e_{zx} = \frac{1}{2}\left(\frac{du_x}{dz} + \frac{du_z}{dx}\right) \tag{1}$$

where  $u_x$  and  $u_z$  are the x and z velocity components, respectively. Strain rate components were calculated from velocity vectors at each point in our grid using a finite central difference scheme (Moin 2001). Because each of the individual components of the tensor ( $e_{xx}$ ,  $e_{zz}$ ,  $e_{xz}$ ) changes with the coordinate system, we used these components to calculate the principal strain, a quantity representing the largest magnitude of normal and shear strain that is independent of the coordinate system (Crandall et al. 1999). In our analysis below, we report the principal shear strain rate (hereafter strain rate), which we consider adequate to represent the information available to a prey animal with no known orientation. Our in-plane measurements capture only four of the nine components of the tensor matrix, and the realized strain rate can be higher, but not lower.

Spatiotemporal pattern of flow in the fish's frame of *reference*—We assessed the spatial and temporal patterns of bow wave-induced and suction-induced flow at the fish's frame of reference. To investigate those patterns, we recorded the flow speed and strain rates over three parallel transects placed at a right angle to the mouth. The first transect was placed at the center of the mouth and the origins of the other two were set one interrogation area above and below the central transect (Day et al. 2005). In each frame, the length of each transect was adjusted to five times the gape diameter or a minimum length of 12 mm (the longer of the two). Flow speeds and strain rate were averaged for the three transects. We considered these transects to be relevant and representative of the hydrodynamic disturbance perceived by the prey, as bluegill approached the prey in our experiments head-on.

Hydrodynamic theory predicts that the bow wave in front of a sphere moving in a fluid will be proportional to the distance to the object cubed, the object's volume, and the object's speed, as well as to the angle relative to the swimming velocity (Visser 2001). To ask whether observed slopes conform to those expectations, we measured flow speed and strain rates before suction commenced (gape diameter  $\ll 10\%$  peak gape) along the aforementioned profile, from nine arbitrarily selected transects for each fish (total n = 56). We then fitted each transect with an exponential decay model representing the relationship between flow speed and distance from the mouth (using the MATLAB fit tool) and calculated the average best-fit exponent and the correlation coefficient for each transect. A similar analysis was made to assess the spatial pattern of suction flows. Here, we could only extract profiles for five of our fish because in the strikes of the sixth individual, the prey was located too close to the edge of the image. For each of the available five fish, we analyzed profiles from 12 randomly selected strikes (total n = 60 profiles). In each strike, we extracted flow speeds and strain rates along the transects at an arbitrary time point through the gape cycle, usually when the mouth was opened >50% of peak diameter. Because gape size and peak flow speeds varied between individuals and strikes, we scaled the fluid speed at each point along the transect to that at a distance of one-half gape away from the mouth and scaled distance by gape size (Day et al. 2005). Similarly, we scaled strain rate by flow speed at onehalf gape distance.

The temporal patterns of the hydrodynamic disturbance in front of the mouth were investigated by measuring flow speeds and strain rates on the aforementioned three transects during suction production. We extracted flow speeds and strain rates for each frame, starting  $\sim 10$  frames before the mouth was opened and continuing until the mouth closed or the fish was out of the field of view.

Spatiotemporal pattern of flow in the prey's frame of *reference*—In addition to measuring suction flows in front of the mouth, we measured the hydrodynamic disturbance at the location of the prey, where the temporal pattern of the flow is the result of interactions between the forwardmoving body, the opening mouth, and the accelerating fluid (see Results). To determine sampling points in each frame, we digitized the x and y coordinates of the anterior-most points on the fish's upper and lower jaws and the prey's edge (closest to the fish), using MATLAB package DLTdataviewer2 (http://www.unc.edu/%7Ethedrick/software1.html). We used these landmarks to calculate the distance and angle between the center of the mouth and the prey in each frame. We then recorded flow speed and strain rate very close to the prey (two interrogation areas downstream) to represent the flows sensed during the strike. Flow velocities and shear strain rates were averaged across five interrogation areas on transects laid perpendicular to the imaginary mouth-prey axis. Each record started when the fish initiated its strike at the trap door ( $\sim$ 5 cm away from the prey). From that point, it took  $\sim 0.5$  s (250 frames) before the prey was engulfed. Flows and strain rate at the prey were below detectable levels throughout most of this time frame and increased to detectable levels only when the fish was very close to the prey. Hereafter we report flows and strain rates for the last 30-150 ms of the strikes (see Results).

To estimate the disturbance available to the prey from the bow wave alone, we compared the disturbance at the prey with disturbance at a point closer to the trap door, on the fish's path to the prey (hereafter "bow wave" point). Flows at this point are the result of the bow wave only, because suction has not yet been produced. The effect of bow wave-mediated disturbance cannot be isolated at the prey sampling point, where water is moved by the interaction between bow wave and suction flows, but can be estimated from our measurements at the bow wave point if ram speeds are similar. Tracking of flows and strain rate was made for the same temporal scales for the bow wave and prey points (starting ~100 ms before the fish's arrival), with the fish at least 6 mm from the sampling points.

For each sequence we calculated body ram (swimming speed) by tracking a landmark on the fish's body. Only strikes in which ram speed was constant through the strike were taken for analysis. For each of the six fish we analyzed nine strikes.

Comparison with potential flows—prey's frame of reference—During suction-feeding strikes, the mouth opens rapidly while suction flows are being produced. To assess the effects of mouth kinetics on the signal available for the prey, suction-induced deformation rates at the prey's frame of reference were compared to deformation rates produced by fixed-aperture siphon flows (potential flows). These flows represent commonly used artificial disturbance generators (Fields and Yen 1997; Viitasalo et al. 1998; Kiørboe et al. 1999) and the disturbance generated by active suspension feeders (Vogel 1994). We used two types of potential flows: constant potential flow, where siphon aperture and flow speed are fixed with respect to time, and time-dependent potential flow, where siphon is fixed but flow speed accelerates and decelerates during the strike.

The hydrodynamic disturbance for constant potential flow was calculated for each strike and independently parameterized with gape size fixed at the maximal diameter observed in the strike and flow speed fixed at the peak speed observed for the strike. We used consensus profiles for speed and strain rates (*see* Results) to project the hydrodynamic disturbance at the location of the prey. These flow profiles also fit the profiles derived analytically for potential flow modeled as a circular vortex and parallel streams (Muller et al. 1982; Day et al. 2005). Simulated prey was treated as a particle of water advancing towards the mouth with its movement driven by the constant suction flow, starting at a distance of one gape diameter.

For time-dependent potential flow we parameterized each strike with gape size fixed at the maximal diameter observed in the strike. Flow speed had a time-dependent pattern based on the observed gape cycle with peak flow occurring at 95% of time to peak gape (TTPG) and flow initiating at 20%. Consensus profiles for speed and strain rates (*see* Results) were used to project the hydrodynamic disturbance at the location of the prey. Simulated prey was treated as a particle of water advancing towards the mouth with its movement driven by suction flow, starting at the observed strike initiation distance (*see* Results; usually shorter than one gape diameter). *Estimating prey response*—For each of these four disturbance sources, we calculated the response distance and time for response thresholds ranging from 0.2 to  $4 \text{ s}^{-1}$ , representing the natural range of behavioral response threshold in copepods and rotifers (Kiørboe et al. 1999; Green et al. 2003). Response distance was defined as the distance from the disturbance source at the point in time when strain rate reached the threshold. Response time was defined as the time it took a parcel of water to travel to the mouth from the time the threshold was met.

*Statistical analysis*—Because fish in our experiments were measured multiple times, the strikes of each fish were not independent. Therefore, for the bulk of our analysis we used a mixed-model approach (Pinheiro and Bates 2000). In essence, these models enable a regression- and ANOVA-like analysis, while accounting for the dependent errors due to repeated measurements on individuals.

The decay of bow wave-induced flow speeds as a function of the distance from the swimming fish was analyzed using a mixed-effect model that included the distance from the fish cubed, fish size, and ram speed as independent variables, flow speed as the dependent variable, and fish as a random factor. A similar analysis was run to assess the decay of strain rate as a function of the distance from the mouth.

Suction-induced speed and strain rate profiles where characterized using a mixed-effect model with scaled flow speed (or strain rate) as the dependent variable, scaled distance as the independent variable, and fish as a random factor. We explored various decay functions for flow speed and strain rate, including linear, polynomial, exponential, and logarithmic models. The best model was selected based on likelihood ratio and Akaike's information criterion (AIC) score or  $R^2$ . Comparisons of response distance and time were made using a mixed-effect model with response time (or distance) as the dependent variable and the threshold level and flow source (bow wave, suction flow, constant and time-dependent potential flow) as dependent variables. Fish and strike sequential number were used as random factors.

To ensure that the above statistical models accounted for the correlation structure among the dependent samples, we built for each of the analyses a series of mixed-effect models with increasing complexity and then selected the best model based on AIC score and a likelihood ratio test (Pinheiro and Bates 2000; Johnson and Omland 2004). The basic model included fish as a random factor, whereas more complex models included a correlation structure in observation order, autocorrelated error, and an error correlated with the independent variable. However, in all analyses these models did not provide additional explanatory power, and only results from the basic models are discussed here. In the regression analysis, we also calculated the coefficient of determination  $R^2$  based on the log-likelihood results of the model using the equation

$$R^{2} = 1 - \exp\left[-\frac{2}{n}(\log L_{m} - \log L_{0})\right]$$
(2)

where *n* is the number of observations,  $\log L_m$  is the loglikelihood of the model of interest, and  $\log L_0$  is that of an intercept-only model (Magee 1990). Statistical analyses were done using the free software R Statistics (R Development Core Team 2009), after verifying normal distribution of residuals for mixed-effect models.

#### Results

Bow wave properties—Ram speed for the fish in our experiments ranged from 2 to 60 mm  $s^{-1}$ , with an average of 11 mm s<sup>-1</sup>. Considering a standard length of  $\sim 0.12$  m, the Reynolds number of the swimming fish was  $\sim 1200$ . The magnitude of bow wave-generated flows in front of the swimming fish decayed as a function of the distance cubed from the fish (Fig. 1), with an average correlation coefficient ( $R^2$ ) of 0.77  $\pm$  0.09 (n = 56 profiles). A mixed-effect model that included swimming speed, fish size, and the distance from the fish as independent variables, and flow speed measured on the transects as dependent variable, indicated significant effects of swimming speed and body size (mixed-effect model;  $F_{1,53} = 271.8$ , p < 0.001, and  $F_{1,53} =$ 37.9, p < 0.001, respectively). Prey displacement due to bow wave flows (calculated by integrating flows at the prey from prev detection until suction commenced) was negligible, with mean displacement of  $0.85 \pm SE = 0.1 \text{ mm}$  (median = 0.64 mm).

Bow wave-induced strain rates followed a similar pattern, with an average correlation coefficient ( $R^2$ ) of  $0.60 \pm 0.11$  (n = 56 profiles; Fig. 1) between strain rate and distance cubed. By and large, bow wave-induced strain rates were 5–20 s<sup>-1</sup> at 1–2 mm from the body and <0.5 s<sup>-1</sup> at a distance >5 mm from the body (Figs. 1, 2). A mixed-effect model with strain rate as dependent variable indicated significant effects of swimming speed and body size (mixed-effect model;  $F_{1,53} = 53.8$ , p < 0.001, and  $F_{1,53} = 7.72$ , p < 0.005, respectively).

Spatial and temporal pattern of flow in the fish's frame of reference—Before suction started, the flow in front of the mouth moved away from the fish, decaying as a function of the distance from the body (Fig. 1, cold colors in Fig. 2A). With the opening of the mouth (at an average distance of  $8.13 \pm SE = 0.54$  mm from the prey), the flow direction in front of the mouth was reversed as water started flowing into the mouth (warm colors in Fig. 2A). Flow speeds near the mouth increased with increasing gape (Fig. 2A). Both the magnitude and the spatial reach of water deformation rates increased with increasing gape size (warm colors in Fig. 2B).

Regardless of gape size, the flow generated by the suction-feeding fish was restricted to the proximity of the mouth, and the magnitude of fluid speed dropped sharply as a function of the distance from the mouth center. On average the speed at one-half gape distance away from the mouth was  $\sim 22\%$  of that at the center of the mouth, and the speed at one gape distance from the mouth was 4% of that at the mouth. This pattern was consistent regardless of gape size and body length; velocity profiles at the centerline, representing the scaled speed (relative to the



Fig. 1. Bow wave-induced flow speeds and strain rates in front of a swimming fish. Before suction commenced, bow wave-induced flows (black lines) and strain rates (grey lines) decreased as a function of the distance from the body, where flow speed was proportional to the swimming speed. Nine strikes were analyzed for each of six fish. Shown are representative profiles for each fish, noted by line patterns.

speed at one-half gape distance from the mouth) as a function of scaled distance from the mouth center (expressed in gape diameters) were similar through the gape cycle and between different individuals (Fig. 3). The deviations of individual profiles from the mean profile averaged over all individuals were small (average residual = 9.25% of the speed at one-half gape  $\pm 11.4\%$ ).

The scaling of suction-induced strain rates was similar in nature. Regardless of gape size, high strain rates were restricted to the proximity of the mouth, and the magnitude of strain rate dropped sharply as a function of the distance from the mouth center. Strain rate profiles were scaled by expressing scaled strain relative to flow speed at one-half gape distance from the mouth and scaled distance in gape diameters. The deviations of individual profiles from the mean profile averaged over all individuals were moderate (average residual = 17.9% of the strain rate expected at one-half gape  $\pm 22.3\%$ ). Bow wave-induced flows and strain rates did not conform to the above scaling.

Spatiotemporal pattern of flow in the prey's frame of reference—To assess the potential effect of the flow source on prey's response, we measured suction- and bow wave–induced water deformation rates (measured at the prey and bow wave points) and compared response time and response distance for each of the sources. Bow wave–induced disturbance underestimated the prey's response distance by an average of  $19\% \pm 5\%$  (mixed-effect model, p < 0.001; Fig. 4A). The magnitude of the bias was threshold dependent, decreasing with increasing response threshold of the prey. In contrast, there was no significant difference in response time between bow wave–induced and suction flow–induced strain (mixed-effect model, p > 0.4; Fig. 4B; average difference  $11\% \pm SD = 6\%$ ).

The similarity in response times measured at the prey and the bow wave points can be due to the bow wave signal overriding suction-induced flows, or by the fish timing its strike so that suction flows will hit the prey as late as



Fig. 2. (A) Temporal and spatial patterns of flow speed and (B) strain rate in front of the mouth of a suction-feeding bluegill. Before suction starts ("cold" blue colors, see inset in A) water is being pushed away from the fish (positive flow speeds in A) at low speeds ( $< 0.05 \text{ m s}^{-1}$ ) resulting in moderate strain rates a short distance from the fish (B). When the mouth opens to generate suction flows ("warm" colors), water is drawn into the mouth (negative flow speeds in A) and the spatial reach of the flow is extended following the increasing gape diameter. Note the strong gradients over millimeters and milliseconds during suction. Dotted vertical line represents the maximal distance of the entrainment volume, ~18.7 mm (measured using particle tracking as the distance between the center of the mouth at 20% of TTPG to the last particle entering the mouth; Higham et al. 2006). The distance between the prey and the mouth when the mouth started to open was 6.9 mm. The inset in (A) denotes gape size as a function of time.

possible, just before bow wave–induced flows are sensed. To assess the likely source of disturbance at the prey, we asked for each sequence whether disturbance rose above a threshold level before suction commenced (i.e., when mouth size was <20% of maximum gape). Disturbance rose above  $0.2 \text{ s}^{-1}$  before suction started in  $\sim39\%$  of the strikes (Fig. 4C), indicating that sensitive prey could sense bow wave–induced flows in those strikes. However, the proportion of strikes in which disturbance rose above the threshold before suction commenced decreased rapidly with increasing threshold, and was below 15% for most of the response threshold range (Fig. 4C).



Fig. 3. Consensus profiles of (A) scaled flow speed and (B) strain rate in front of the mouth of suction-feeding bluegill. During suction, much of the spatial and temporal variation in flow speed and strain rate (Fig. 2) can be removed by scaling flow speed and strain rates by flow speed at one-half gape distance away from the mouth and scaling distance by gape diameter. The empirical formula for the scaled flow speed (FSs; speed relative to that at one-half gape distance) at scaled distance x (in mouth diameters) was  $FSs_{(x)} = 0.13x^4 - 1.12x^3 + 3.49x^2 - 5.01x + 2.73$ (mixed-effect model;  $R^2 = 0.88$ ,  $F_{1,59} = 207.5$ , p > 0.001). Scaled strain rate (Strain<sub>s</sub>; scaled by speed at one-half gape distance) at scaled distance x was  $\text{Strain}_{s(x)} = -126.3x^4 + 879.8x^3 - 2373.2x^2$ + 3003.3x - 1605.4 (mixed-effect model;  $R^2 = 0.77$ ,  $F_{1.59} = 71.2$ , p > 0.001). Colored lines indicate profiles for five individual fish based on 12 strikes per individual. Black profile is the consensus profile for all five fish.

Measurements of response time of the tethered prey in our experiments were likely biased, because the prey could not advance with the suction flows into the mouth. To account for prey movement, we modeled the prey as a particle of water and asked, what is the response time, given published magnitudes of suction flows (Higham et al. 2006)? Compared to the bow wave-induced disturbance, response time decreased with increasing suction flows and was significantly shorter than the bow wave disturbance at



Fig. 4. Inferred response times and distances of prey following a threshold hydrodynamic disturbance in the suction flows and bow wave. (A) Distance from the mouth when threshold disturbance (x axis) is met, (B) time from the threshold disturbance to ingestion, (C) proportion of strikes in which the response threshold was reached before gape exceeded >20% of peak gape, indicating prey response to bow wave and not suction flows. The average  $(\pm SE)$  distance between the predator and the prev at that time point was  $8.13 \pm 0.54$  mm. Overlaid are threshold deformation rates of planktonic organisms, obtained from siphon experiments: cf, Calanus finmarchicus; at, Acartia tonsa (adults); ea, Eurytemora affinis; pr, Polyarthra remata (Rotifer); er, Euchaete rimana; osp, Oithona sp.; px, Pleuromamma xiphias; lm, Labidocera madurae; atn, Acartia tonsa (nauplii); tl, Temora longicornis (Kiørboe et al. 1999); atl, at6, Acartia tonsa nauplii stages 1 and 6; tl1, tl6, Temora longicornis nauplii stage 1 and 6; ea1, ea 6, Eurytemora affinis nauplii stages 1 and 6 (Green et al. 2003). Threshold deformation rates for the latter four species are outside the axis, ranging from 4.6 to  $6.5 \text{ s}^{-1}$ . In the biologically relevant response threshold range ( $\geq 0.4 \text{ s}^{-1}$ ), those prey species are expected to respond to the bluegill's suctioninduced flows, rather than to bow wave-induced disturbance.

flow speeds >0.6 m s<sup>-1</sup> (mixed-effect model, p < 0.001; Fig. 5).

Comparison with potential flows—prey's frame of reference—Both constant and time-dependent potential flows greatly overestimated the prey's response time and distance (Figs. 6, 7). Compared to a suction-induced disturbance, constant potential flow overestimated prey's response time and distance by a factor of 11 and 4, respectively (mixed-



Fig. 5. The distribution of response times following a threshold hydrodynamic disturbance, with increasing magnitudes of suction flows (dotted lines). Full lines indicate the observed response times for bow wave-induced (light blue) and suction-induced disturbance (dark blue). The prey was modeled as a particle of water, to account for its movement towards the mouth. Shown are data over the range of reported copepod response thresholds (Kiørboe et al. 1999; Green et al. 2003)

effect model, p < 0.001; Fig. 7A,B), whereas timedependent potential flow overestimated prey's response time and distance by a factor of 12.5 and 2 (mixed-effect model, p < 0.001; Fig. 7A,B), respectively. In all those cases, the relative bias (measured as the difference in response time [or distance] normalized to response time [or distance] in suction flows) was threshold dependent (mixedeffect model, p < 0.001 for all cases; Fig. 7A,B). Compared to suction-induced flows, response time bias decreased with detection threshold for constant and time-dependent potential flows, and for response distance bias in constant potential flows. However, response time bias increased with increasing threshold for constant potential flows (mixedeffect model, p < 0.001).

#### Discussion

In this study we characterized the hydrodynamic disturbance produced by swimming and feeding fish, and compared it to the disturbance generated by constant and time-dependent potential flows. Our results indicate that bluegill suction flows generate much lower disturbance at the prey than potential flows, even when the flow at the orifice is identical. We attribute the reduced signal to the remarkable skull kinesis in fishes that permits both timedependent mouth diameter and mouth displacement through upper jaw protrusion. Utilizing this kinesis, bluegill can start the strike far enough away from the prey so that their presence is not disclosed by the bow wave disturbance (Fig. 4). Then, as the mouth opens, the spatial reach of the suction flow is quickly extended (Fig. 2), so that the prey is hit by an already developed suction flow. The forward displacement of the mouth (by jaw protrusion and swimming) contributes to the shortening of response time by rapidly moving the center of the mouth, where flow

is higher, towards the prey. Mouth opening that occurs as the suction flow is being developed, together with jaw protrusion, allows bluegill to generate suction flows that appear abruptly at the location of the prey item, giving the prey animal little time to respond to the strike.

*Implications for fish feeding*—Considering the bow wave disturbance as the minimal disturbance a fish can produce while moving thought the water, the close overlap between the response time and distance for bow wave and suction flows indicates that bluegill coordinate their strike to produce a minimal disturbance at the prey. Thus, the observed prey capture strategy of bluegill can be interpreted as an "ambush" strike, as opposed to a "pursuit" strike. Ambush strikes are expected to include slow ram speed or braking before striking (Higham 2007) to reduce the bow wave, and fast mouth opening with jaw protrusion to reduce the time the prey has to respond. Interestingly, these features of ambush strikes also increase the forces exerted on prey (Day et al. 2005; Holzman et al. 2008b,c). A lowdisturbance mechanism for capturing evasive prey was previously described by Coughlin and Strickler (1990), who suggested a decoupling of the timing of jaw protrusion and the production of suction flows so that the prey is engulfed due to protrusion of the jaws before suction commences. However, such decoupling has not been observed in flow visualization studies of other fishes (Higham et al. 2006; Nauwelaerts et al. 2007) or in kinematic-based modeling (Muller et al. 1982; Van Leeuwen and Muller 1984).

How the morphology and behavior of fish are adapted to capture prey by means of suction is a central and longstanding question in functional morphology (Van Leeuwen and Muller 1984; Ferry-Graham and Lauder 2001; Westneat 2006). Traditionally, the prevailing view has been fish-centric, focusing on the fish's ability to produce low pressure in the buccal cavity (Lauder 1980; Svanback et al. 2002; Van Wassenbergh et al. 2006) and the corresponding ability to produce high flows at the mouth aperture (Day et al. 2005; Higham et al. 2006; Van Wassenbergh and Aerts 2009). After adoption of a physically relevant view of the forces acting on prey in those suction flows, an understanding of the importance of fluid acceleration, mouth size, strike accuracy, and jaw protrusion speed has begun to emerge (Wainwright and Day 2007; Wainwright et al. 2007; Holzman et al. 2008b). We investigated the disturbance produced by suction-feeding fish as a step into incorporating the prev animal's response into a model of hydrodynamic interactions between fish and their prey. Our study, together with Coughlin and Strickler (1990), suggests that the ability to approach the prey without generating detectable disturbance before suction forces hit the prey is an important, yet largely overlooked, axis of adaptation to predation on zooplanktonic prey.

Fish strikes are characterized by high variability in ram speed, gape size, strike effort, and the relative timing of cranial events (Wainwright et al. 2001; Higham et al. 2006; Holzman et al. 2008*b*), which can all potentially affect the hydrodynamic signal available to the prey. These can change within species as a function of prey type, as well as between species (Wainwright et al. 2001). For example, our use of



Fig. 6. (A, B) Representative plots of flow speed and (C, D) principal strain rates from artificial and biologically relevant flow sources as a function of time (left panels) and distance (right panels). Data for suction- and bow wave-induced flows (circles) are based on PIV measurements from a representative strike. Flow speeds and strain rates for constant potential flows (full lines) were calculated using the consensus profiles (Fig. 3) for a passively drifting prey in front of a siphon with a diameter equal to mouth diameter, and steady flow speed equal to the maximal flow at the mouth. Flow speeds and strain rates for time-dependent potential flows (dash-dot lines) were similarly calculated but with time-dependent flow based on the observed speed profile and with observed strike initiation distance. Flow speeds and strain rates for linearly accelerating flows (dotted lines) were calculated based on the observed acceleration in the strike. Note that linearly accelerating flow has a uniform spatial distribution and therefore no strain component. In the strike presented, the mouth started opening at 40 ms, when the distance between the prey and the mouth was 4.2 mm. Peak gape was achieved 38 ms later.

nonmotile prey likely produced slower strikes than would have been induced with living evasive prey (Wainwright et al. 2001). Therefore, the observed difference between bow wave– induced and suction-induced disturbance is likely a conservative estimation of the realized difference because fish are expected to produce faster flows with live prey (Wainwright et al. 2001).

Two predictions can be made for the effects of ram speed and fish size on the signal available for the prey. First, in low Reynolds numbers (where fish larvae frequently feed), flow speed and strain rates are expected to decay slower compared to their decay at high Reynolds numbers (as a function of the distance squared, not cubed; Kiørboe and Visser 1999; Kiørboe et al. 1999). The prey of approaching fish larvae would thus be more heavily affected by bow wave-induced disturbance. To mitigate this effect, larvae can adopt lowram behavior or larger gape size (relative to body size) to extend the reach of their suction flows. Secondly, ram speed can be an important axis of diversification in strike behavior of predatory fish (Wainwright et al. 2001). Faster ram speed is accompanied by stronger bow wave-induced flows, and can therefore inform strain-sensitive prey of the approaching fish. However, many animals relay primarily on vision to detect predators. It might be that strikes with fast ram are employed by species adapted to feed on visually oriented prey (such as krill, shrimp, and other fish), which can detect the predator before the bow wave hits the prey. Slow-ram strikes would then be reserved to surprise planktonic prey that detect their prey through hydrodynamic cues.

Understanding prey behavior and sensory ecology—It is widely accepted that fish predation has a strong effect on many aspects of the ecology, behavior, population structure, and life history of prey animals. In lakes, the presence or absence of fishes can determine the overall trophic state of the ecosystem (Kerfoot and Sih 1987). Predation by fish is also considered the main reason for the evolution of zooplankton diel vertical migration in lakes (Gliwicz 1986), oceans (Bollens and Frost 1989), and coastal waters (Alldredge and King 1985). Not surprisingly, the morphology and physiology of sensory systems in these prey animals are thought to be well equipped to detect the relevant hydrodynamic signals of the approaching predator. The antennae of copepods are covered with an array of setae, which are highly sensitive to fluid motions (Yen et al. 1992; Kiørboe et al. 1999). Specifically, the setae are



Fig. 7. (A) The distribution of response distances and (B) times following a threshold hydrodynamic disturbance in the case of suction flows (black circles), constant potential flows (gray lines), and time-dependent potential flow (black dotted lines). Response distance (A) is the distance from the mouth when threshold disturbance (x axis) is met; response time (B) is the time from the threshold disturbance to ingestion. Error bars represent standard errors.

sensitive to velocity gradients along their length, i.e., shear strain, and much less sensitive to speed or linear acceleration (Yen et al. 1992). In larval fish, changes to the flow environment are perceived through deflection of the sensory hairs of the lateral line system. The boundary layer that is formed over the body has an important role in filtering the signal, causing laminar flows to produce strain because of the velocity gradient along hair cells (Van Trump and McHenry 2008; McHenry et al. in press). These designs seem well suited to the signal available from suctionfeeding fishes, rather than to the signal produced by tactile predators.

To identify the hydrodynamic signals perceived by copepods, previous researchers used artificially generated fluid disturbances such as siphon flows (Fields and Yen 1997; Viitasalo et al. 1998; Kiørboe et al. 1999), moving and oscillating bodies (Buskey et al. 2002; Heuch et al. 2007), and flow chambers (Haury et al. 1980; Kiørboe et al. 1999; McHenry et al. in press). Although these approaches have been instrumental in defining the sensory capabilities of copepods, the signal produced by these artificial sources of hydrodynamic disturbances does not accurately mimic the relevant disturbances produced by suction-feeding fishes. Importantly, these artificial sources overestimate response time and distance for the prey by 3-12 times, leading to unrealistic prediction of the ability of the prey to successfully respond to the feeding strike of its predators. Our data indicate general agreement between response distance to the bow wave and suction flows (Fig. 4), so that estimating response distance of copepods to approaching

fish might be a reasonable approximation (Viitasalo et al. 1998). However, the interpretation for a copepod's escape is critically different because suction flows allow the prey much less time to escape, even at the same distance (Fig. 5). We estimated response times for 17 zooplankton species by comparing their published response thresholds (Kiørboe et al. 1999; Green et al. 2003) to the response time inferred for bluegill feeding on small prey (Fig. 5). The median response times were extremely short, ranging  $\sim 9$  ms for the mean observed flow speed and 4 ms for suction flows of 2 m s<sup>-1</sup>.

The ability of the prey to escape depends not only on its timely response to the approaching predator but also on its ability to swim fast and far from the mouth, opposing suction flows. We estimated the strike's outcome by parameterizing a model of water flow around the prey (Holzman et al. 2007; Wainwright and Day 2007) with flow speed and strike kinematics from an arbitrarily selected bluegill strike. Prey (3 mm in diameter) was modeled to escape directly away from the fish with an escape force ranging from 1.5 to  $2.5 \times 10^{-4}$  N, with response latency of 3 ms and overall jump duration of 25 ms (Lenz and Hartline 1999; Buskey et al. 2002). Prey's response was triggered at threshold strain rates ranging from 0.2 to 6 s<sup>-1</sup>. Strain rate at the prey was calculated based on the distance from the mouth, using consensus profiles of speed and strain rate. Our analysis indicates that the encounter's outcome depended on the magnitude of suction flows, prey's sensitivity to the hydrodynamic signal, and the escape force (Fig. 8). In the fastest strike, only sensitive prey that could elicit vigorous escape response could escape. However, with flow speed of  $0.5 \text{ m s}^{-1}$ , only slow and insensitive prev were taken (Fig. 8). Thus, the interaction between prey sensitivity and escape force can be critical in determining a strike's outcome. A strategy of low sensitivity can be beneficial for the prey, for example, in areas of high shear because it limits "false escapes," which can be energetically costly and may attract predators (Fields and Yen 1997; Buskey et al. 2002). On the other hand, our simulations (Fig. 8) indicate that such a strategy requires the ability to exert high escape forces to compensate for the low sensitivity. Although much is known on the sensitivity of copepods' strain rates (Kiørboe et al. 1999; Green et al. 2003), these sensitivities have rarely been integrated with data on escape response. Note that strike outcome can potentially be affected by a variety of other factors, including the involvement of other sensory modalities in locating the predator (vision, olfaction, touch; Buskey et al. 2002), escape trajectory (Lenz and Hartline 1999; Buskey et al. 2002), the predator's efficiency in eliciting low hydrodynamic disturbance, and the predator's ability to elicit the maximal force on its prey (Holzman et al. 2008b).

In this study, we use a single deformation rate as the threshold, ignoring micro-gradients across the body or antennae. Furthermore, strain rates are the ratios of flow speeds in different flow axes, and as such they contain no information on flow magnitude. Both spatial gradients in fluid velocity and flow magnitude carry additional information, which can be captured by hairs or sensory cells integrating spatial gradients in fluid velocity at different scales. Thus, our calculations are likely a simplification of



Fig. 8. Response threshold, prey's escape force, and predator's strike effort interact to determine the strike's outcome. Using a model of water flow around the prey (Wainwright and Day 2007) and characteristic prey response (Lenz and Hartline 1999; Buskey et al. 2002), we estimated response threshold and escape force needed to evade bluegill's strikes with peak flow speeds ranging  $0.5^{-2}$  m s<sup>-1</sup>. Prey (treated as a sphere 3 mm in diameter) was modeled to escape directly away from the fish with an escape force ranging from 1.5 to  $2.5 \times 10^{-4}$  N (similar to that reported in Lenz and Hartline 1999). Prey started its escape after strain rates reached a response threshold, with response latency of 3 ms and overall jump duration of 25 ms (Buskey et al. 2002). The forces exerted on the prey in the suction flow field are the sum of drag, pressure gradient force, acceleration reaction, and prey escape force, calculated at 0.3-ms intervals (Wainwright and Day 2007). Drag coefficient and the coefficient of added mass for the prey were taken from Vogel (1994). The sum of those forces determined prey acceleration and speed at each time point. In the absence of suction flows, prey escape force is expected to induce peak prey speed of 1.3 m s<sup>-1</sup> and peak prev acceleration of 55 m s<sup>-2</sup>, on par with values reported by Buskey et al. (2002) Gray areas indicate prey escape; white areas indicate capture.

aquatic signal perception. However, little is known about the pattern of neural stimulation across the sensory array that is necessary to evoke an escape reaction (Fields and Weissburg 2005). Also, our scaling analysis (Fig. 3) indicates that in the case of bluegill, strain rates were correlated to the flow speed so that higher strain rates are associated with higher flow speed. Thus, for our data, flow magnitude carries little additional information compared to strain rates.

The evolution of skull complexity and kinesis in fishes—In experiments and modeling of predator—prey interactions of fish and zooplankton, the bow wave produced by the swimming fish is typically thought to be the primary source of hydrodynamic signal available to the prey (Viitasalo et al. 1998; Kiørboe and Visser 1999; Heuch et al. 2007). However, the vast majority of fish species use suction to capture and transport prey, and this is especially true for capturing small prey (Lauder 1980). Yet the flow patterns produced by suction-feeding fishes have not been accounted for to the best of our knowledge. The estimated response time expected for a bluegill's bow wave—induced flows is shorter than that expected for suction-induced flows (Figs. 6, 7). However, this result should be cautiously generalized in the absence of data from other species, because of potential diversity in strike kinematics and strategies (Norton 1991; Norton and Brainerd 1993; Higham et al. 2006).

The comparison between the disturbances generated by potential flows and suction-induced flows highlights an important yet overlooked difference between the feeding ecology of active suspension feeders (represented by potential flows) and suction-feeding fishes. These two groups represent vastly different ecologies and foraging strategies, driven by their different lifestyles (sessile vs. motile) and sensory capabilities (strong visual vs. weak sensory response to prey). Here we add another relevant ecological factor that is likely important in driving the diet differences between these groups. The ability of fishes to rapidly open their mouth and protrude their jaws towards the prey makes their suction flows apparently much less conspicuous than those of active suspension feeders.

One of the main trends in the evolution of ray-finned fishes is the increase in skull kinesis, particularly the evolution of maxillary rotation and jaw protrusion mechanisms that have arisen more than once and characterize some of the most successful radiations of teleosts (Lauder 1982; Wainwright 2006; Westneat 2006). In this study we showed that the implications of skull kinesis for prey capture performance are more complex than previously thought, and require a hydrodynamic perspective to be better understood. Although the ability of fishes to produce strong negative pressure gradients within their mouth cavity, and high suction flow velocities, is a major axis of fish diversification (Collar and Wainwright 2006; Westneat 2006), skull kinesis and gape morphology appear also to be important in determining the force exerted on aquatic prey by suction-feeding fishes (Holzman et al. 2007; Wainwright and Day 2007; Wainwright et al. 2007). The present study indicates that jaw protrusion also plays an important role in mitigating the hydrodynamic disturbance created by suction feeders and that prey animals can use to detect striking predators.

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