Visual cues eliciting the feeding reaction of a planktivorous fish swimming in a current

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Summary

The visual plankivorous feeding behaviour of the shiner perch (*Cymatogaster aggregata*) was investigated by means of a flow tank operated at various current speeds. *Artemia salina* was used as prey. In a second set of experiments, *Artemia* was darkened with black ink, to compare the visually mediated behaviour of *C. aggregata* while feeding on dark prey *vs* feeding on natural (i.e. semi-transparent) prey. The positions of the fish and its prey at the time of the feeding reaction of *C. aggregata* were measured in three dimensions. Prey were on average closer and more in line with the fish's axis when feeding reactions to darkened *Artemia* were considered, in comparison with natural *Artemia*. Three potential mechanisms triggering the feeding reaction of *C. aggregata* were explored: the prey may trigger a reaction in *C. aggregata* when it reaches a threshold (1) angular size, (2) angular velocity, or (3) rate of change of the angular size (i.e. loom) of the prey as it is carried passively by the current towards the fish. Our results show that angular velocity may trigger the fish's reaction when using semi-transparent prey, while loom may trigger the reaction to darkened prey. This suggests that feeding behaviour of planktivorous fish is flexible and can use different cues to trigger a motor reaction to prey with different visual characteristics. The feeding reaction appeared to occur at longer distances for semi-transparent rather than darkened *Artemia*. We suggest that semi-transparent *Artemia* were visible at greater distances because of their higher scattering (i.e. diffuse reflectance) that made them appear brighter when viewed against a dark background.

Key words: fish, plankton, predation, vision, *Cymatogaster aggregata*, feeding.

Introduction

High sensitivity to motion across the visual field is characteristic of many visual systems. For example, in many vertebrates, motion detection cells in the brain can have directional sensitivity and maximal responses to stimuli moving at different speeds (Barlow and Hill, 1963; Cronly-Dillon, 1964; Jacobson and Gaze, 1964; Guthrie and Banks, 1974; Kawasaki and Aoki, 1983). In addition, the ability to detect a lower contrast stimulus (i.e. the modulation sensitivity), usually occurs at intermediate presentation frequencies or velocities (Kelly, 1972; Sekuler et al., 1978; Sekuler et al., 1990). The detection of predator or prey by fishes, although it may involve characteristics such as shape, spatial pattern and chromatic aspects, certainly responds dramatically to targets in motion. A central part of any visual stimulus must be the contrast of the target compared with the radiance of the background space light. Because zooplankton are small and usually semi-transparent, in general, they appear as low-contrast objects under viewing conditions that minimize the effects of scatter and reflection of downwelling light into the direction of view. However, near the surface where the downwelling irradiance is high relative to the horizontal irradiance, semi-transparent plankters will scatter downwelling light from their external and internal refractive interfaces and appear as bright targets, as long as the viewing distance is relatively short and the downwelling irradiance is not diffuse (i.e. the plankters are irradiated by the solar beam) (E. R. Loew and W.N.McF., unpublished). With depth, or as the veiling brightness increases with an increase in viewing distance, this phenomenon becomes less obvious. Thus, the contrast of a semi-transparent object when viewed horizontally depends on the veiling brightness, the viewing distance, the depth, the characteristics of the downwelling irradiance (diffuse *vs* beam) and the differences in refractive index between any intra-organismal compartments (Videen and Ngo, 1998).

Planktivorous fishes that feed in currents provide an example where the motion between a fish and its zooplankter prey are

consistent and definable (Hobson, 1972; Hamner et al., 1988). By feeding zooplanktivourous fishes in flumes, Kiflawi and Genin (1997) demonstrated that peak ingestion can occur at intermediate current speeds and McFarland and Levin (2002) showed that individuals will cease feeding at higher speeds. Four phenomena may chronologically occur before a fish reacts to a particle: (a) detection, (b) recognition (c) decision (i.e. threshold of triggering mechanism at the sensory system level) and (d) motor response. Behaviourally, only the feeding reaction can be observed (i.e. the motor response). The timing of the feeding reaction should be, however, largely dependent on the timing of the detection. In particular, the distance at which a feeding reaction is triggered is limited by the maximum detection distance.

In investigating predator–prey interactions, Dill (1974) measured the escape responses of prey and modelled the rate of change in apparent size of a predator (i.e. the loom) as it approached the prey. For fish feeding on plankters in a current, angular velocity, apparent size and loom were described mathematically for particles that approached head-on and at various distances offset from the position of the fish in the current (McFarland and Levin 2002). In that study, the temporal-resolution of a fish's reaction to an incoming plankter was limited by the 2D spatial resolution and by the low temporal resolution of the system used to capture time-sequence images for analysis (McFarland and Levin 2002). In this paper, using a high-speed video system, we examine the reaction of fish under similar conditions and evaluate, in three dimensions, what attribute(s) of a plankter appear to influence the feeding reaction of fish. We test three alternative hypotheses: (1) The feeding reaction of planktivourous fish may be triggered by a fixed apparent size (i.e. angular size) of the approaching particle. (2) Fish may react to plankton once it reaches a given threshold angular velocity as it is carried passively by the current. (3) The mechanism triggering a fish's reaction may be the loom (i.e. the rate of change of the angular size) of the prey while approaching the fish. The experiments were carried out using three different current speeds and two treatments, which provided plankton with different properties of contrast (i.e. semi-transparent and darkened *Artemia*) in order to test the effect of contrast on detection mechanisms.

Materials and methods

Fish collection and maintenance

Shiner perch (*Cymatogaster aggregata* Gibbons) were collected using a beach seine at Jackson Beach, San Juan Island Washington, USA, during August of 2000 (total length 6.7±0.08 cm; mean±S.E.M., N=8), and April 2002 (total length 8.8±0.17 cm; N=8). Fish were held at the Friday Harbor Laboratories in flow-through seawater tanks at 12°C for one week before use. Fish were exposed to a 12h:12h light:dark cycle, provided through fluorescent illumination from above. Integrated irradiance was 5.1×10^{17} photons cm^{-2} s^{-1} over 300–750 nm (OCEAN OPTICS S1000 spectroradiometer; Dunedin, FL, USA).

Apparatus

Experiments were carried out in a flume tank as described in McFarland and Levin (2002) with a working section 50 cm long, 12 cm wide, and a water depth of 17 cm (Fig. 1). The experimental tank was illuminated from above with a daylight fluorescent lamp (two 20 W lights, model F20T12 GE). Integrated irradiance was 8.2×10^{17} photons cm^{-2} s^{-1} over 300–750 nm, measured at the water surface level of the experimental tank (OCEAN OPTICS S1000 spectroradiometer).

Water flow was generated by a two-bladed propeller and current speed controlled by varying the voltage *via* a variac to the AC/DC motor (Dayton AC/DC model 2MO338 motor; Lincolnshire, IL, USA). A catch screen was placed 10 cm downstream from the working section to isolate fish in the flume. To assure repeatability of current speed for different trials, the voltage output of the variac was prescribed through the use of a digital voltmeter. Three layers of collimators (5 cm wide) were positioned upstream to produce a homogeneous flow through the working section. Viewed through the collimators, the upstream aperture of the collimator tubes provided a dark background to the fish. The background radiance from the collimator, as measured with an OCEAN OPTICS S1000 spectroradiometer between 300 and 750 nm, was only 3.1% when compared with the radiance from a white Teflon reflective surface and was similar to the radiance from a black surface (4.3%). Flow speed was calibrated from dye injected in the water upstream from the collimators and filmed at 125 images s^{-1} using a high-speed video camera (Red Lake, model 1000 S series motionscope; San Diego, CA, USA). The current flow as seen by discrete dye travel in the horizontal dimension was laminar over the working section, with minor turbulence only observed just upstream from the catch screen. To avoid wall effects, only trials in which a fish initiated a reaction towards the prey more than 2 cm from the walls, bottom and water surface, were analysed.

Fish movements were recorded at 125 images s^{-1} with the video camera placed perpendicular to the flume. We capture
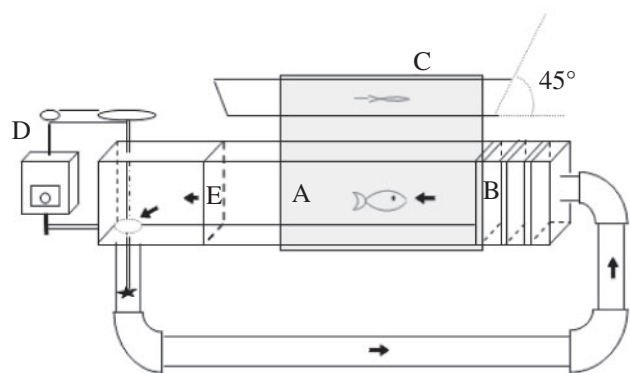

Fig. 1. Flume tank used in the experiments seen from the side (as viewed by the camera). (A) working section, (B) collimators, (C) mirror at 45°, providing top view of the fish, (D) pump, (E) Catch screen. The shaded rectangular section indicates the approximate field of view of the camera.

3D-movements of each fish by positioning a 30 cm×60 cm mirror at 45° above the experimental tank (Fig. 1). Therefore, lateral and top images of the fish were produced at one time, the bottom half of the camera filming the fish laterally to determine height in the water column and position along the length of the flow tank, while the upper half of the camera filmed through the mirror and viewed the fish from above against the floor of the tank, allowing positions across the width of the flow tank to be determined. Frame-by-frame analysis of the horizontal and vertical positions of each fish at the time of first departure from a steady swimming mode and at the moment of engulfment of a planter (*Artemia* nauplii) was accomplished though use of the software Scion Image (NIH image analysis). The 3D-coordinate position (x, y, z) of each fish in the flume was established against two ruled grids, one placed on the backwall of the flume and another on the bottom of the flume. For horizontal positions of the fish (x, y), the midpoint between the eyes of each fish was used as reference, and for the vertical position (z) the centre of the fish's observable (right) eye.

Experimental procedure

Artemia nauplii were used as in Kiflafi and Genin (1997), since they have a shape and size similar to the prey of shiner pearch, calanoid copepods, and because they lack escape behaviour (Coughlin and Strickler, 1990; Trager et al., 1994). Individual fish did not require conditioning to swim in the flume and, even though naïve, fed on *Artemia* when introduced [also reported for natural zooplankton by McFarland and Levin (2002)]. As suggested by Webb (1982) for visual reaction in fish, the size of an *Artemia* (i.e. particle diameter) was considered as the mean between its length and width (mean size 0.053±0.002 cm; *N* of subsample =10).

Two sets of experiments differing in prey type were carried out. Perch collected in August of 2000 were used in the first set of trials, where naturally semi-transparent *Artemia* nauplii were released into the flume-tank (Fig. 2). In a second set of experiments, shiner perch collected in April 2002 were presented with darkened *Artemia* (Fig. 2). A stone for grinding a Sumi ink stick with water was used to make liquid black ink. Darkening was obtained by adding a suspension of black ink (0.037 g in 1 l of water) into the *Artemia*'s tank overnight. The Sumi ink produced a darkening of the *Artemia* gut.

In both experiments, fish were acclimated in the flume tank at zero current speed for 40 min before each experiment. Current speed was then increased slowly over a 2 min period to the chosen trial speed. The order of trial speeds was chosen at random among the six possible combinations of orders using slow (0.52 body length s^{-1} for semi-transparent *Artemia* and 0.66 body length s^{-1} for darkened *Artemia*), intermediate (1.88 body length s^{-1} for semi-transparent *Artemia* and 1.60 body length s^{-1} for darkened *Artemia*), and fast flow speeds (3.12 body length s^{-1} for semi-transparent *Artemia* and 3.01 body length s^{-1} for darkened *Artemia*). These speeds are within the range in which *C. aggregata* swims using pectoral fin locomotion, i.e. they are lower than the gait transition
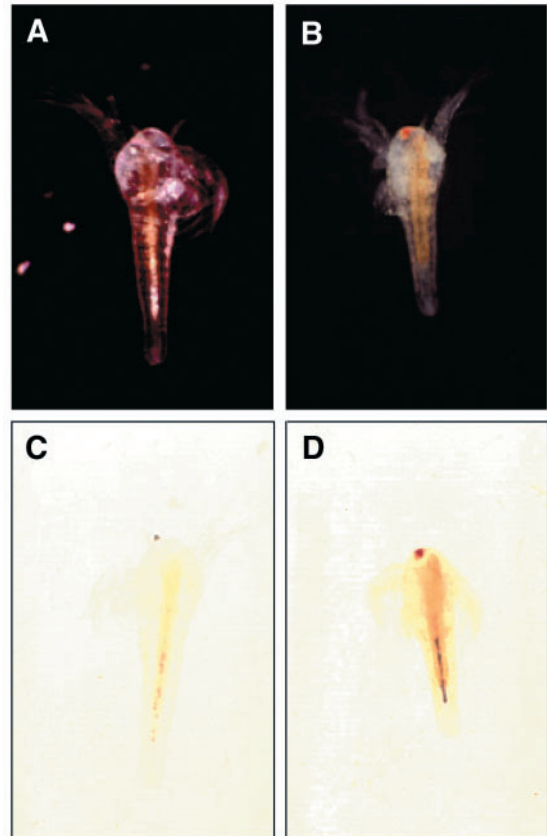

Fig. 2. Images of semi-transparent (natural) (A, under dark-field illumination; C, under bright-field illumination) and darkened (B, under dark-field illumination; D, under bright-field illumination) *Artemia*. Specimens were photographed using a photomicroscope (Wild M400 Photomakroskop) onto Fuji Sensia 100 iso slide film, using two synchronised flashes (Sunpak Auto 383 Super) and a 64× magnification. Scanned (jpg) imaged were obtained using a Scanner UMAX Mirage II Se, at a 200×200 dpi resolution and 342×537 pixels. These images do not necessarily reflect the *Artemia* as perceived by the fish.

speeds (from pectoral fin to caudal fin locomotion), observed in this species and size (Mussi et al., 2002). Ten minutes after a trial speed was reached, live darkened or natural (semi-transparent) *Artemia* nauplii were introduced from behind the collimator baffles and in the approximate centre of the section (i.e. midway between the walls and in midwater). We assumed that, after recirculating in the flow tank (i.e. *Artemia* took a full trip around the flow tank before being preyed upon), the nauplii were distributed randomly over the tank cross section. The numbers of trials for the natural (semi-transparent) *Artemia* experiment were 15, 15 and 19 for slow, intermediate and fast current speeds, respectively, and 10 trials at each current speed were performed using darkened *Artemia*. Each trial involved one single fish. For each individual in both darkened and natural conditions, up to four prey captures were analysed at each current speed.

Fish first reacted to an approaching particle by a noticeable change in position at the time T_R (Fig. 3). Because a latent
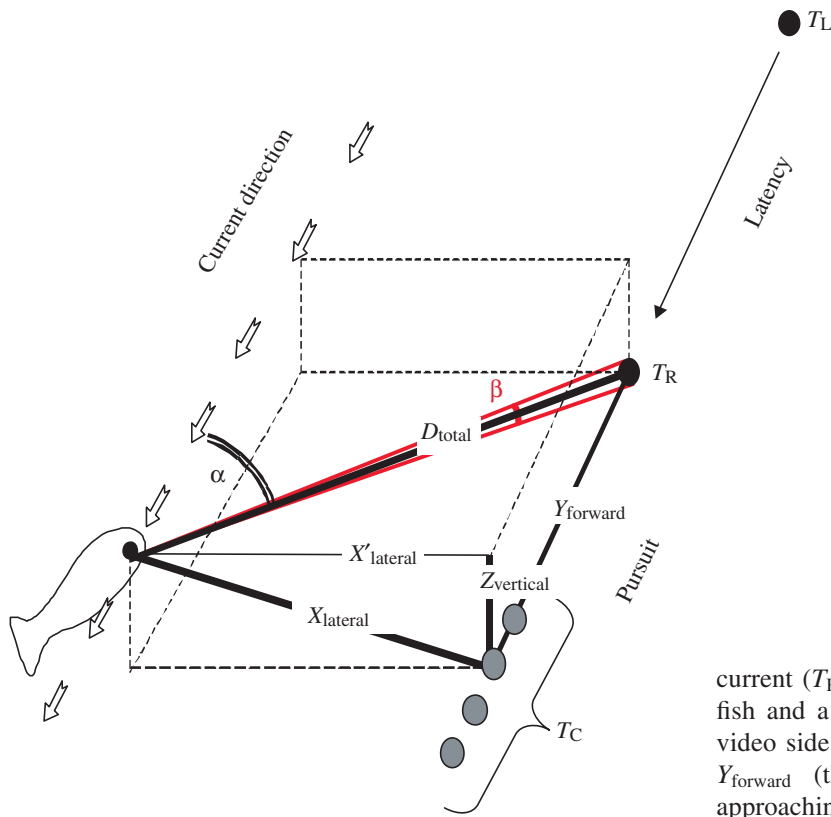
Fig. 3. Geometry of the particle detection and capture in three dimensions. The direction of the current is indicated by empty arrows. A fish's initial detection response is triggered at T_L, and the fish's first visible reaction to an approaching food particle occurs at T_R (i.e. response latency occurs between T_L and T_R). The arrow between T_L and T_R indicates the distance covered by the particle during the response latency. The food particle is captured at T_C, and the distance covered between T_R and T_C corresponds to $Y_{forward}$. Various particles are drawn at T_C because the particle at T_C may be upstream or downstream relative to the fish's eyes at T_R (data not shown). $X'_{lateral}$ is the lateral distance in the horizontal plane. $X_{lateral}$ is the overall lateral distance between the fish's eyes and the axis of motion of the prey along the current. $Z_{vertical}$ and D_{total} are the vertical distance and the total distance, in three dimensions, between fish's eyes and the particle at T_R, respectively. Alpha (α) is the angle between the current direction and D_{total}. Beta (β) is the angular size of the plankton as seen by the fish.

period must occur between when the reaction is triggered by the particle and the actual visible reaction of the fish (Dill, 1974; Domenici, 2002), we have defined the theoretical time at which the particle triggers fishes' 'inner reaction' as T_L (the reaction at the sensory system level). The time of the fish's first 'visible reaction' was defined as T_R (the reaction at the motor level), and the time at which the fish captured the particle was defined as T_C. The hypothesized delay between T_L and T_R would be due to the conductive times of the neurosensory and neuromuscular systems. While we were not able to determine T_L experimentally, its definition is needed in order to facilitate further theoretical considerations.

Neither darkened nor semi-transparent *Artemia* nauplii were visible on the video images. However, the jaw protrusion of the fish that corresponded to the engulfing of an *Artemia* was visible. Previous video recordings from close up at all speeds indicated that the position of the tip of the mouth at maximum mouth protrusion was a good estimator of the position of an *Artemia* at the time of capture along the tank axis. The vertical position of the particle was therefore estimated as the midpoint between the two edges of the mouth tip at maximum protrusion, while the position of the particle across the width of the tank was estimated by using the top image of the tip of the mouth at the time of maximum protrusion, in accordance with previous observations. Therefore, the time T_R and the position of the mouth at T_C when a fish captured a particle (easily detectable by jaw protrusion), were used to estimate the position of the nauplius at T_R. This assumes that nauplii moved passively within the

current (T_R to T_C in Fig. 3). The vertical distance between a fish and a food particle at T_R ($Z_{vertical}$) was estimated from video side views. The video top view provided estimates of $Y_{forward}$ (the distance between the fish and the prey approaching along the current axis), and $X'_{lateral}$ (the lateral distance between the fish and the prey along the axis perpendicular to the current, in the horizontal plane).

The geometry in Fig. 3 was reconstructed for each capture event, and all analyses were done using the plane D_{total} $X_{lateral}Y_{forward}$, where D_{total} is the estimated total distance between the fish's eyes and the food at T_R, and $X_{lateral}$ is the overall lateral distance between the fish's eyes and the axis of motion of the prey along the current. D_{total} is at an angle alpha (α) from the fish's axis. Left and right responses were pooled as if they were all responses to particles approaching on the right side of the fish.

The angular size threshold (β_R, i.e. β at T_R) of the prey was calculated as the angle subtended by the plankton onto the fish's eye at the time of reaction (Fig. 3). The apparent loom threshold (λ_R, i.e. loom at T_R) was calculated as in Dill's (1974) equation, modified for the case of approaching objects not necessarily in line with the fish's body axis, following McFarland and Levin (2002).

McFarland and Levin's equation (equation 26 in McFarland and Levin, 2002), for the general case of a particle coming towards the fish in any direction, corresponds to:

$$\lambda_R = \frac{d\beta}{dt} = \frac{-2R}{(D_{total}^2 + R^2)} \left(U_y \cos \alpha + U_x \sin \alpha \right), \quad (1)$$

where R the radius of the approaching particle, D_{total} is the total distance to the particle at T_R, β is the angular size of the particle as seen by the fish, α is the angle between the line that connects the fish to the particle and the current direction at T_R, U_y is particle speed along the current (with a negative sign if the particle is approaching the fish; McFarland and Levin 2002), U_x

is particle speed perpendicular to the current (note that our y and x axes correspond to the x and y axes, respectively, in McFarland and Levin, 2002). In our case, we assume that U_x is zero as the particles are carried passively by the current, which runs parallel to the axis of the fish. Therefore,

$$\lambda_R = \frac{d\beta}{dt} = \frac{-2RU_y \cos \alpha}{D_{total}^2 + R^2} \ . \tag{2}$$

Using particle diameter $P = 2R$ and considering current speed $U_c = -U_y$ (i.e. considering current towards the fish having a positive speed) for particles approaching, we obtain:

$$\lambda_R = \frac{d\beta}{dt} = \frac{4U_c\, P \cos \alpha}{4D_{total}^2 + P^2} \ , \tag{3}$$

where U_c is current speed, P is the particle diameter calculated as the mean between the particle's length and width (Webb 1982), D_{total} is the total distance to the particle at T_R, β is the angular size of the particle as seen by the fish, and α is the angle between the line that connects the fish to the particle and the current direction, at T_R (Fig. 3).

The apparent angular velocity threshold (i.e. ω_R, the angular velocity of the particle at T_R) was calculated following McFarland and Levin (2002). Their equation (equation 6 in McFarland and Levin, 2002) for the general case of a particle coming in any direction corresponds to:

$$\omega_R = \frac{Y_{forward}U_x - X_{lateral}U_y}{D_{total}^2} \ . \tag{4}$$

Since in our case U_x is equal to zero (see above), the equation becomes:

$$\omega_R = \frac{-X_{lateral}U_y}{D_{total}^2} \ . \tag{5}$$

The minus sign is due to the fact that McFarland and Levin (2002) consider speed as negative when approaching the fish. We switched the sign to positive, as in our case $U_c = -U_y$. In addition, $X_{lateral}$ is equal to $D_{total} \sin \alpha$ (equation 3 in McFarland and Levin, 2002). Therefore, the equation becomes:

$$\omega_R = \frac{U_c \sin \alpha}{D_{total}} \ . \tag{6}$$

The effect of current speed and plankton type (natural *vs* darkened) was tested using two-way ANOVAs (analysis of variance) for each feeding reaction variable (i.e. D_{total}, $X_{lateral}$, $Y_{forward}$, $Z_{vertical}$, α, angular size, angular velocity, loom). To account for multiple simultaneous two-way ANOVAs, the level of significance was adjusted within columns using the sequential Bonferroni technique (Rice, 1989).

Theoretical considerations on how angular size, angular velocity and loom should vary as the particle approaches

If the time at which a particle first triggers a fish's reaction (i.e. the threshold at the sensory system level at T_L), is caused by a given angular size (β_L), angular velocity (ω_L) or loom (λ_L)
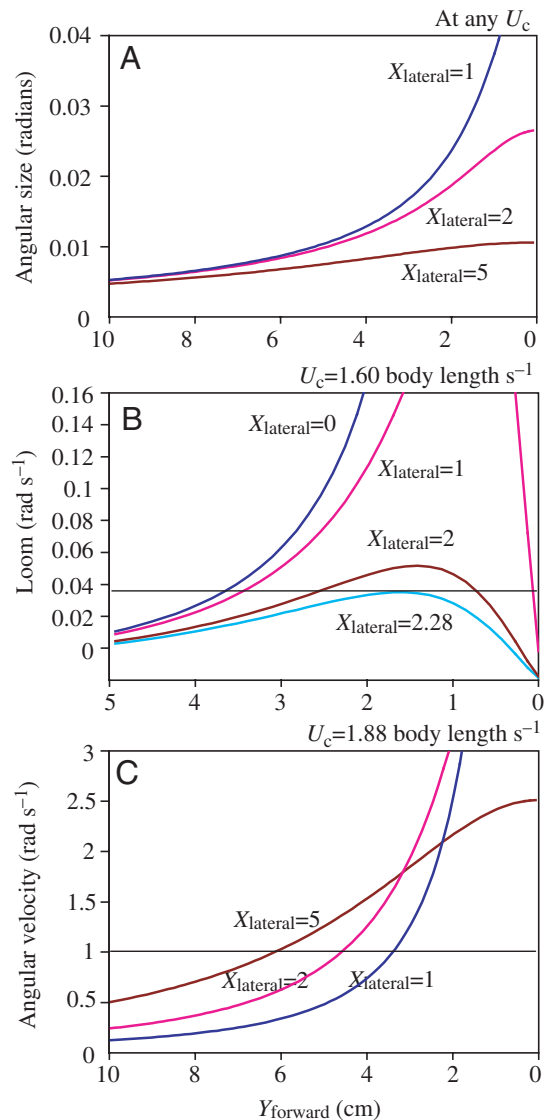

Fig. 4. (A) The relationship between angular size (β_R) and $Y_{forward}$ at various theoretical values of $X_{lateral}$. The graph is valid for all speeds, because angular size is not affected by current speed (U_c). Any given value of β_R is reached at decreasing values of $Y_{forward}$ as $X_{lateral}$ increases. (B) The relationship between loom λ_R and $Y_{forward}$ (the particle distance upstream at the time of T_R), at various theoretical values of $X_{lateral}$, at the intermediate current speed used in darkened conditions. At $X_{lateral}=0$, λ_R is always highest. Horizontal line represents the average experimental values of λ_R found in darkened conditions at intermediate U_c. λ_R is reached at smaller values of $Y_{forward}$ as $X_{lateral}$ values increase. (C) The relationship between angular velocity ω_R and $Y_{forward}$ at various theoretical values of $X_{lateral}$, at the intermediate current speed used for semi-transparent *Artemia*. At $X_{lateral}=0$, ω_R would be equal to zero and it is not represented. Horizontal line represents the average experimental values of ω_R found for semi-transparent *Artemia* at intermediate U_c. Average ω_R is reached at increasing values of $Y_{forward}$ as $X_{lateral}$ values increase.

of an approaching particle, independent of its speed, then the 'apparent' angular size β_R, angular velocity ω_R or loom λ_R (i.e. at T_R), should vary with current speed as the approaching object

Table 1. *Geometry of the visual response*

Artemia type	Current speed	$Y_{forward}$ (cm)	$Z_{vertical}$ (cm)	$X_{lateral}$ (cm)	D_{total} (cm)	α (deg.)
Natural	Slow	4.0±0.5	1.1±0.2	2.1±0.3	4.6±0.5	30.1±3.9
Natural	Intermediate	5.7±0.7	1.2±0.2	2.5±0.3	6.3±0.7	25.5±3.6
Natural	Fast	6.0±0.4	1.0±0.3	2.7±0.3	6.6±0.5	23.2±1.3
Darkened	Slow	3.6±0.4	0.4±0.1	0.6±0.2	3.7±0.4	11.9±4.1
Darkened	Intermediate	3.1±0.3	0.7±0.1	1.3±0.2	3.5±0.2	24.3±6.0
Darkened	Fast	3.2±0.4	0.7±0.2	1.3±0.3	3.6±0.3	25.0±6.5

Data shown are mean ± S.E.M. D_{total} (total distance from plankton at the time of reaction), $X_{lateral}$ (lateral distance), $Y_{forward}$ (forward distance), $Z_{vertical}$ (vertical distance), α (angle between the fish's axis and the plankton).

covers a longer distance between T_L and T_R (assuming a constant latency) when travelling at higher speeds. The potential effect of current speed on the threshold for the fish's response can be visualised by plotting how angular size, loom, and angular velocity vary as a function of $Y_{forward}$ (Fig. 4). Since current speed for each trial is constant, decreasing values of $Y_{forward}$ also correspond to time. The angular size increases continuously as the particle travels along $Y_{forward}$ (Fig. 4A) and its rate of increase is higher the smaller the lateral distance $X_{lateral}$ is. Therefore, assuming the theoretical angular size β_L to be constant at different flow speeds, the experimental angular size β_R should increase with current speed.

Loom increases as the particle travels along the current up to a certain (relatively small) value of $Y_{forward}$, and then decreases again (except if $X_{lateral}$=0 cm). For example, for an $X_{lateral}$ value of 2, loom increases up to $Y_{forward}$ values around 1.5 cm (Fig. 4B). Therefore, if we assume λ_L to be constant at different current speeds, then λ_R should increase with current speed up to $Y_{forward}$ values of about 1.5 cm, as the distance covered by the particle along $Y_{forward}$ would increase with current speed. Loom decreases only when very close to the fish. The angular velocity ω, conversely, increases continuously as the particle travels along $Y_{forward}$, although this increase has different rates depending on $X_{lateral}$ (Fig. 4C). In particular, if we assume ω_L to be constant at different speeds, then ω_R should increase with current speeds (as $Y_{forward}$ gets shorter). Therefore, we expect that the angular variable(s) implicated in the mechanisms triggering the feeding reaction should increase with speed.

For those angular variables that are found to increase with speed, we estimated latency as follows. To find a theoretical constant value of latency for all current speeds, an index of homogeneity (I_H) between each average 'angular variable' (i.e. angular size, angular velocity or loom) calculated at T_L (i.e. assuming a given latency) at different current speeds was calculated using (maximum 'angular variable' – minimum 'angular variable') / minimum 'angular variable'. Each angular variable at T_L was calculated as the theoretical value that the fish would experience if, for each sequence, the particle had triggered a reaction at a position with $X_{lateral}$ at T_L being the same as at T_R (since a straight course was assumed), while $Y_{forward}$ was considered longer at T_L than at T_R by a distance that was calculated as the current speed multiplied by the theoretical latency.

The alternative hypotheses for the three mechanisms triggering feeding reaction were further tested as follows:

(1) The frequency distributions of $X_{lateral}$ were compared between darkened and semi-transparent *Artemia* experiments, since it can be assumed that low values of $X_{lateral}$ may imply that the feeding reaction is triggered by an angular size or a loom mechanism, while high $X_{lateral}$ values suggest a mechanism based on angular velocity. This is because, at any $Y_{forward}$, angular size and loom should be highest for particles coming head on, while the angular velocity should be highest at low values of $X_{lateral}$ only for very small values of $Y_{forward}$ (not observed here; see theoretical values in Fig. 4). Therefore, if an angular size or a loom threshold are used, the first particles to achieve threshold will be those with the smallest $X_{lateral}$. Conversely, if angular velocity is used, the first particles to reach threshold should always be off line from the fish's axis, i.e. at $X_{lateral}$>0.

(2) The potential roles of angular size, angular velocity and loom in the feeding reaction of the semi-transparent and darkened *Artemia*, respectively, was tested by comparing the $Y_{forward}$ and $X_{lateral}$ positions of the particles at T_R and the theoretical values of these positions based on the average experimental angular size, angular velocity and loom at each current speed.

Results

Darkening (dark *vs* semi-transparent *Artemia*) had an effect on most variables measured (Table 1 and 2). In particular, the reaction distance D_{total} was significantly greater for the semi-transparent *Artemia* (Table 1 and 2, Fig. 5). The results from a two-way ANOVA (adjusted using the sequential Bonferroni method; Rice, 1989) revealed that current speed had no significant effect on all reaction distance parameters (i.e. D_{total}, $X_{lateral}$, $Y_{forward}$, $Z_{vertical}$), while darkening did (Table 2). No significant interaction effect of current speed and darkening was found. Neither current speed nor darkening had any effect on reaction angle α (P>0.5 and P>0.05, respectively), and the interaction effect was not significant according to the sequential Bonferroni technique (see Table 2).

Current speed and darkening had no effect on angular size, and no interaction effect between darkening and current speed was found (Table 2 and Fig. 6). Conversely, both angular

Table 2. *Two-way ANOVA for each detection parameter measured*

Variable	d.f.	ms	F	P
$Y_{forward}$				
Intercept	1	1344.261	395.9377	**<0.001**
Speed	2	4.507	1.3276	>0.1
Darkening	1	67.136	19.7743	**<0.001**
Speed×darkening	2	10.230	3.0130	>0.05
Error	73	3.395	–	–
D_{total}				
Intercept	1	1660.845	478.6935	**<0.001**
Speed	2	6.166	1.7771	>0.05
Darkening	1	91.503	26.3732	**<0.001**
Speed×darkening	2	7.622	2.1970	>0.05
Error	73	3.470	–	–
$Z_{vertical}$				
Intercept	1	52.27299	80.65771	**<0.001**
Speed	2	0.25464	0.39291	>0.5
Darkening	1	4.44736	6.86232	**0.0107**
Speed×darkening	2	0.18578	0.28666	>0.5
Error	73	0.64808	–	–
$X_{lateral}$				
Intercept	1	225.2176	196.5117	**<0.001**
Speed	2	2.7245	2.3772	>0.05
Darkening	1	33.8909	29.5713	**<0.001**
Speed×darkening	2	0.0443	0.0386	>0.5
Error	73	1.1461	–	–
α, angle between particle and fish's axis				
Intercept	1	40243.82	196.0764	**<0.001**
Speed	2	104.49	0.5091	>0.5
Darkening	1	632.13	3.0799	>0.05
Speed×darkening	2	714.95	3.4834	0.036
Error	73	205.25	–	–
ω, angular velocity				
Intercept	1	145.0043	79.5432	**<0.001**
Speed	2	21.8438	11.9825	**<0.001**
Darkening	1	12.5417	6.8798	**0.0106**
Speed×darkening	2	7.5108	4.1201	0.020
Error	73	1.8230	–	–
λ, loom				
Intercept	1	0.1352	160.3226	**<0.001**
Speed	2	0.0095	11.3796	**<0.001**
Darkening	1	0.0910	22.5987	**<0.001**
Speed×darkening	2	0.0058	6.9095	**<0.005**
Error	73	0.0008	–	–
β, angular size				
Intercept	1	0.0136	261.5416	**<0.001**
Speed	2	0.0001	2.2211	>0.1
Darkening	1	0.0002	4.7532	0.032
Speed×darkening	2	0.0001	1.9541	>0.1
Error	73	0.00005	–	–

Significant results according to the sequential Bonferroni method (Rice, 1989) are in bold. –, not determined.

velocity and loom were affected by current speed ($P<0.001$ in both cases), as well as darkening ($P=0.0106$ and $P<0.001$, respectively), and the interaction of these two factors was significant for loom ($P<0.005$) (Table 2 and Fig. 6).

Angular variables involved in triggering the feeding reaction to plankton are expected to increase with current speeds, except for loom at very small distances (see above and Fig. 4). While loom may theoretically decrease at small distance from the fish, loom increases with decreasing $Y_{forward}$ when the $Y_{forward}$ and $X_{lateral}$ ranges of all observed speeds are considered (only intermediate speed is shown as an example, in Fig. 4). The results show that with semi-transparent *Artemia*, β_R does not vary significantly with speed (Table 2 and Fig. 6), ω_R increased with current speed, while λ_R was lowest at the intermediate speeds, and higher at the low and the high current speeds. Therefore, an index of homogeneity I_H was calculated only for angular velocity. I_H was highest when a theoretical latency of 385 ms was considered. That is, if we assume a latency of 385 ms, the values for the angular velocity when the fish's 'inner reaction' occurs (ω_L) are relatively constant (i.e. 0.26 rad s^{-1}, 0.28 rad s^{-1} and 0.26 rad s^{-1} for slow, intermediate and fast speeds, respectively).

When darkened *Artemia* were used, the angular size β_R is relatively constant at different current speeds, while both ω_R and λ_R increased with current speed in darkened *Artemia* (Fig. 6). Therefore, I_H was calculated for both loom and angular velocity. However, a maximum I_H was found only for loom, and it resulted in a latency of 230 ms. Using this theoretical latency, λ_L is relatively constant (i.e. 0.013 rad s^{-1}, 0.015 rad s^{-1} and 0.013 rad s^{-1} for slow, intermediate and fast speeds, respectively). Conversely, I_H increased indefinitely when increasing values of latency were applied to ω_L.

The frequency distributions of $X_{lateral}$ of the semi-transparent *vs* darkened treatments were compared using a Chi square test. Four bins (0–1, 1–2, 2–3, >3 cm) were used for the comparison (Fig. 7). The distributions of the two treatments are significantly different (Chi^2 22.69; 3 d.f.; $P<0.0001$). The highest peak in the distribution for the darkened treatment was in the bin $X_{lateral}$=0–1 cm, i.e. for particles almost in line with the fish.

The comparison between the $Y_{forward}$ and $X_{lateral}$ positions of the particles at T_R and the theoretical values of these positions based on the average experimental angular size, angular velocity and loom at each current speed is shown in Fig. 8. For the semi-transparent *Artemia* experiments, the theoretical values of $Y_{forward}$ and $X_{lateral}$ at T_R based on the average angular velocity are closer to the experimental values than those based on the average loom or angular size for the fast current speed (ANOVA; $P<0.01$; Tukey post test, $P<0.01$ and $P<0.05$ for the comparisons between loom and ω_R, and β_R and ω_R, respectively), although differences were not significant for the intermediate and slow speeds (Fig. 8). The theoretical values of $Y_{forward}$ and $X_{lateral}$ based on the average loom for intermediate and fast speeds are closer to the experimental values than those based on angular velocity (intermediate and fast; ANOVA; $P<0.05$; Tukey Post-test, $P<0.05$ in both cases),
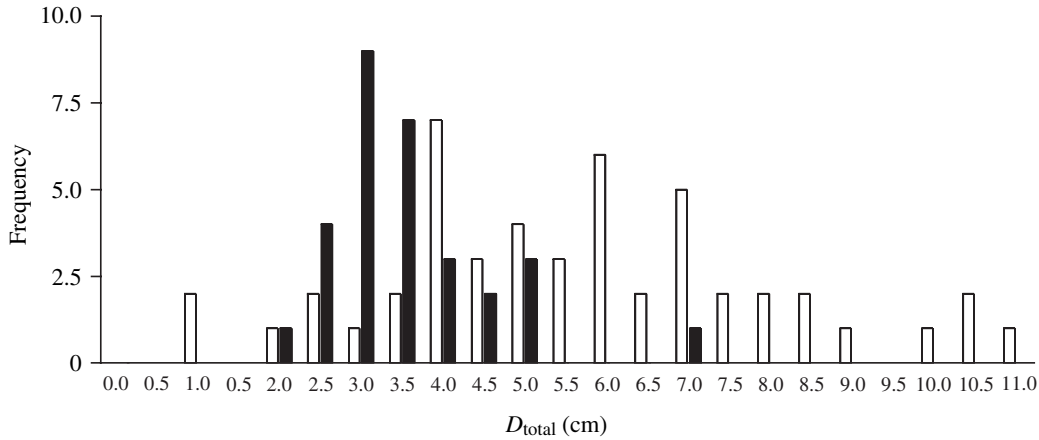
Fig. 5. Frequency distribution of reaction distance D_{total} over all current speeds for both semi-transparent (white bars) and darkened (black bars) *Artemia*.

although there were no significant differences when values based on averages β_R and ω_R were compared. Differences were not significant in any case for the slow speed (Fig. 8).

Discussion

Angular size vs *loom* vs *angular velocity*

Planktivorous fishes typically feed on transient zooplankton delivered by water currents (Stevenson, 1972; Hobson and Chess, 1976, 1978; Thresher, 1983; Hobson, 1991). When a planker is transported by the current towards a fish's visual field, angular size, loom and angular velocity change over time (McFarland and Levine, 2002). These parameters could act

Fig. 6. Angular velocity ω_R (black bars), loom λ_R (white bars) and angular size β_R (grey bars) at different current speeds in the semi-transparent (A) and darkened (B) conditions; error bars show S.E.M.

independently or together as attentive cues to alert a fish to the presence of particles and to trigger a sensory–motor reaction (O'Brien and Slade, 1976; Dunbrack and Dill, 1984; Dill et al., 1997; Raviv, 2000).

The geometry of the particle position and, in particular, its lateral distance, at which the feeding reaction occurs can give us some insights on the main visual mechanism involved. A relatively distant food particle travelling towards the fish at a given lateral distance ($X_{lateral}$) from the nasal–caudal axis has a relatively low angular velocity, which is increasing very slowly. As the particle approaches, a sharp increase in angular velocity takes place, and it reaches a peak (Fig. 4) when $Y_{forward}=0$ and subsequently decreases as the particle travels along its rectilinear path. By contrast, a straight-on particle ($X_{lateral}=0$) has zero angular velocity throughout its approach towards the fish. Conversely, loom and angular size are maximised when lateral distance is minimal. This scenario suggests that preference for particles coming at a lateral distance $X_{lateral}=0$ implies angular size or loom as the mechanisms triggering the feeding reaction. Conversely, if particles coming at small lateral distance are not attacked, then angular velocity may be the mechanism involved in the feeding reaction.

It is reasonable to suppose that fish would capture most particles at low $X_{lateral}$ values for minimizing energy expenditure, if detection mechanisms were not limiting factors. However, in spite of possible energetic advantages of capturing prey in line with fish's nasal–caudal axis, very few particles were taken in when semi-transparent *Artemia* travelled at small $X_{lateral}$ values (i.e. <1 cm; Fig. 7). In fact, most particles produced a reaction when they approached off-axis with peak frequency values of $X_{lateral}$ at 2–3 cm, and with values of $X_{lateral}$ as high as 6 cm (Fig. 7). These results suggested that a threshold angular velocity ω_R might alert a fish to approaching semi-transparent *Artemia*, and promote the feeding reaction to food at greater reaction distances (Fig. 5).

By contrast, with darkened *Artemia*, the peak response frequency occurred when prey approached closest to a fish's nasal–caudal axis. The larger reaction to darkened prey at low $X_{lateral}$ (Fig. 7), suggested that loom or angular size rather than
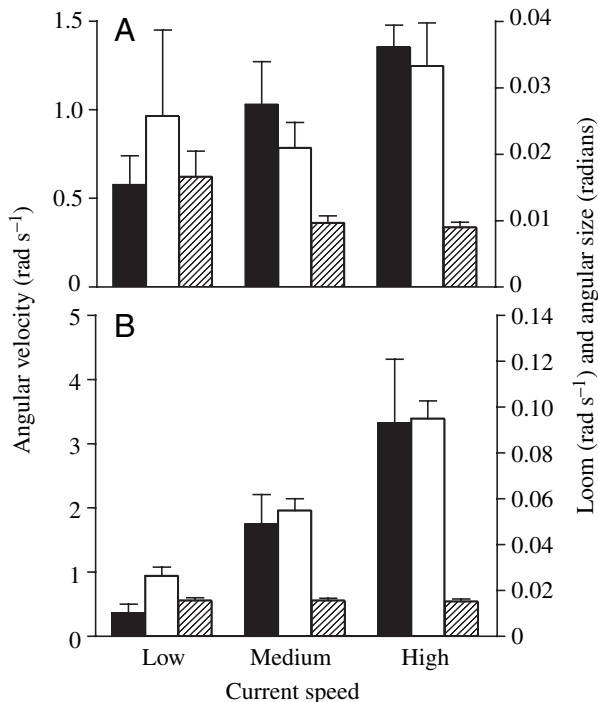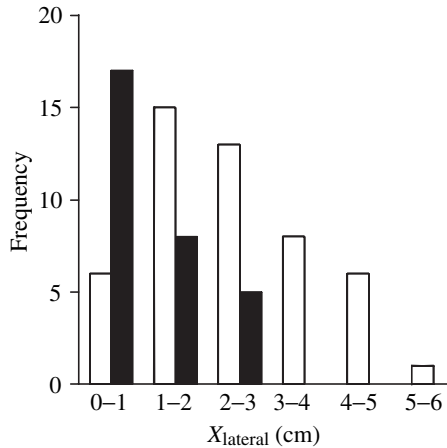
Fig. 7. Frequency distribution of particle lateral distance ($X_{lateral}$) in the darkened (black bars) and semi-transparent conditions (white bars) over all current speeds.

angular velocity might have triggered a fish's reaction to darkened prey (Fig. 8). However, further explanations, are needed to account for the decline in frequency at $X_{lateral}$ values >3 cm in semi-transparent *Artemia* (Fig. 7). This decline may be related to the energetic cost of feeding at larger $X_{lateral}$ and to the fact that peak values of ω_R decline as $X_{lateral}$ increases (Fig. 4C).

The effect of current speed on each angular variable suggests that angular velocity is the mechanism triggering the response to semi-transparent *Artemia*, while loom is the mechanism triggering the reaction to feed on darkened plankton. This is because angular velocity for the semi-transparent *Artemia* and loom for the darkened *Artemia* were the only variables that both (1) increased with current speed as expected if a relatively constant latency and a constant angular threshold are assumed (2) allowed calculation of a reasonable latency. These results are in line with our comparison between the experimental $Y_{forward}$ and $X_{lateral}$ and the expected $Y_{forward}$ and $X_{lateral}$ based on averages angular size, angular velocity or loom. Such a comparison suggests that angular velocity may be the variable that triggers the feeding reaction to semi-transparent *Artemia*, although differences are significant only for high current speed. Conversely, the fitting of the experimental data with the model for the darkened *Artemia* treatment is not significantly different between angular size and loom. This is because the shapes of the curve for angular size and loom are very similar (Fig. 8). However, as discussed above (Materials and methods section), if angular size was the mechanism triggering the feeding reaction, one would expect the position of the particle at the apparent reaction time (T_R) to be different for different current speeds. Let us consider a realistic example in which the sensory threshold occurs at a given angular size corresponding to a distance of 10 cm at T_L. Let us consider a given latency of 200 ms. In this case, at T_R, high-speed particles should be closer to the fish, at approximately 5 cm distance from the fish *vs* 9 cm distance for slow speed particles. This assumes the same time interval (200 ms) between when the sensory threshold is reached (i.e. T_L) and the motor response (i.e. T_R)
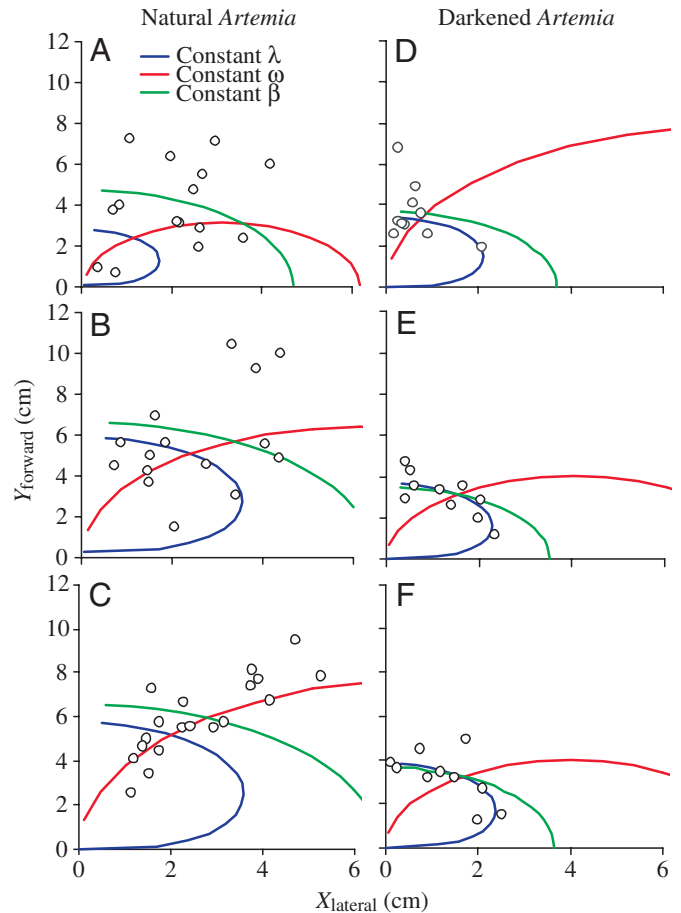

Fig. 8. Experimental values of $Y_{forward}$ and $X_{lateral}$ at low, intermediate and high current speed in semi-transparent (A, B, C, respectively) and darkened (D, E, F, respectively). Blue, red and green lines represent values corresponding to a constant loom, angular velocity and angular size, respectively (i.e. the average loom, angular velocity and angular size for each given speed, respectively).

in the fish at all current speeds. Conversely, if a loom mechanism is considered, higher current speed would cause both (1) higher rate of change of the looming angle and (2) a longer distance travelled between T_L and T_R. Higher loom in high speed would cause reaching the sensory threshold from a larger distance. As a realistic example, let us consider that sensory threshold (i.e. at T_L) of loom may be reached at 10 cm for high speed particles *vs* 6 cm for slow speed particles. However, this difference may be in large part cancelled out, at least in our experimental conditions, by the longer distance travelled by the high speed particles. Following our example, during a given latency period of 200 ms, higher speed would allow particles to travel approximately 5 cm *vs* 1 cm travelled at slow speed. This would cause slow and fast particles to be at a similar distance (i.e. 5 cm according to our example) from the fish at the time of the fish's response. Therefore, loom, but not angular size, can explain particles travelling at different speeds to be in similar positions (Fig. 8D–F) relative to the fish at the time of reaction (T_R). We conclude that loom is the most

likely variable involved in triggering the feeding reaction of fish preying on darkened *Artemia*.

Latency and speed

The reaction models based on average angular velocity ω_R or loom λ_R fit better at high, rather than at low, current speed for darkened and semi-transparent *Artemia*, respectively (Fig. 8). An explanation could be that variability in the time for reaction may decrease with current speed (i.e. when a fish needs to minimize latency to successfully capture the particle). Previous work on escape response in zebra danio (*Brachidanio rerio*) showed that predator speed had no effect on the apparent loom threshold, while it had an effect on the reaction distance and, therefore, latencies were considered negligible (Dill, 1974). However, latencies of escape responses are likely to be shorter than those of feeding reactions, as escape responses are triggered by the Mauthner cells, a pair of giant neurons in the hindbrain of most fish species (Eaton and Hackett, 1984). Batty (1989) reported escape response latency to visual stimuli to be about 40 ms. The reaction to an approaching prey (e.g. plankton), may have a longer latency of the order of 100–300 ms, because more time is needed to process a prey's movement and trajectory, and then to direct an attack. This range corresponds approximately at the values found for maximizing I_H (i.e. assuming that fish respond to a given value of angular velocity or loom at all current speeds).

At higher current speeds (e.g. 40 cm s^{-1}) than those used here, *C. aggregata* swam in a flume but did not attempt to capture plankton (McFarland and Levin, 2002). This may have been due to sensory–motor constraints, which influenced the fish's reaction time preventing successful capture when plankton approached at high speeds. Furthermore, feeding may become energetically costly at very high current speeds, even if fish may be capable of capturing the prey.

Plankton visibility

Transparency in the aquatic environment represents a significant adaptive cryptic mechanism (Johnsen 2001a,b, 2002). However, visual adaptations, such as UV and polarization vision, have evolved among planktivores to increase apparent visual contrast (Lythgoe and Hemmings, 1967; Lythgoe, 1979; Loew et al., 1993; McFarland and Loew, 1994; Cronin et al., 1994; Shashar et al., 1998). Foraging success in planktivores is also strongly dependent on the light, turbidity, background space light, and visibility of pigmented parts, such as the eyes or the gut of the prey (Vinyard, 1980; McFall-Ngai, 1990; Thetmeyer and Kils, 1995; Johnsen and Widder, 1998; Tsuda et al., 1998; Utne-Palm, 1999; Utne-Palm and Stiansen, 2002). Under the same background light conditions, fish predation was shown to be higher when transparent prey with larger eyes were used *vs* prey with small eyes (Zaret 1972), and reaction distances for transparent prey were significantly lower than those for pigmented prey (Thetmeyer and Kils, 1995; Tsuda et al., 1998; Utne-Palm 1999). However, it was shown by video imaging in the near field that transparent zooplankton irradiated from above when viewed horizontally against a darker background appeared as bright targets due to light scattering off their bodies (Loew and McFarland, 2000). Some planktivorous fish search for prey outside Snell's window (i.e. a cone angle of about 97.2° through which the terrestrial hemisphere can be seen), because prey are seen against a dark background (Lythgoe, 1979).

In our study, feeding reaction to zooplankton appeared to occur at longer distances for semi-transparent *Artemia* than for a darkened one. This result would be in line with Loew and McFarland's (2000) observations, and is in agreement with the general observation that changes in prey contrast may cause differences in reaction distances, although most observations are on pigmented prey against a light background (e.g. Utne-Palm, 1999). In our study, the dark background of the collimator tubes would enhance the visibility of semi-transparent plankton; therefore, semi-transparent *Artemia* should be visible at a greater distance due to their higher light scattering (diffuse reflectance) against the dark background. Because light was weakly reflected from a dark *Artemia*'s body there would be less contrast between the target and the background in darkened *Artemia* (Fig. 2 and E. R. Loew and W.N.McF., unpublished).

The higher visibility of the natural (semi-transparent) plankton at longer distances, however, does not explain why shiner perch did not react to semi-transparent particles coming straight on. At small $X_{lateral}$, fish could theoretically react to a threshold angular velocity, although such a threshold would be reached at very small values of $Y_{forward}$ (Fig. 4) (i.e. when it may be too late for the fish to react in time to catch the prey). Alternatively, fish could have used loom as a mechanism triggering their feeding reaction. A threshold loom would be reached at relatively high values of $Y_{forward}$ for the case of small $X_{lateral}$ (Fig. 4). If we assume that the apparent size of semi-transparent and darkened particles was the same, then a $Y_{forward}$ of about 6 cm should trigger a reaction when $X_{lateral}$=0, as in the semi-transparent *Artemia* at intermediate speed. Because relatively few fish reacted to natural plankton at small $X_{lateral}$ values, it is possible that the apparent size of the darkened plankton was greater than that of the natural plankton, although there we have no evidence that darkening can cause a change in apparent size. If semi-transparent *Artemia* had a relatively small apparent size, for any value of $X_{lateral}$ and $Y_{forward}$, loom for a darkened *Artemia* would be greater than for a semi-transparent *Artemia*. In this case, it would be possible that when using semi-transparent *Artemia*, a threshold loom may have occurred when the prey was too close to the fish to react in time for prey capture. Alternatively, it may be possible that shiner perch do not have enough behavioural flexibility in order to shift from a reaction based on angular velocity mechanism to one based on loom within a single feeding session, and it may be 'locked' in using the most favourable mechanism of detection for any given contrast conditions. However, we are not aware of any supporting evidence from other sources, and therefore this suggestion remains highly speculative.

Under the conditions of our experiments, we may be dealing

with both positive and negative contrast situations. For the natural prey irradiated from above viewed against the darker background there may be positive contrast due to internal scatter. However, for the darkened prey the contrast may be negative. Since on- and off-channels use separate pathways that may differ in properties, it is possible that some of the observed differences in feeding reaction mechanisms may be due to the way the visual system handles positive and negative contrast (Wheeler, 1982).

Limitations of our study

We have examined a fish's response to food in a flume tank where turbulence in the water flow was minimized, and where the detection of plankton was constrained by the dimensions of the flume. Therefore, this study was simplified compared with foraging in natural water currents. In nature, turbulence (Aksnes and Giske, 1993; Kiorboe and Saiz, 1995; McFarland and Levin, 2002), as well as schooling can affect foraging behaviour in planktivores (Ryer and Olla, 1991; O'Driscoll, 1998; Lachlan et al., 1998; Foster et al., 2001). Nevertheless, individual responses in a flume to approaching zooplankton allowed us to standardize feeding reaction parameters and to define a fish's reaction to plankton.

In our study, fish reaction to approaching zooplankton was assumed to be independent of the particle shape or its intrinsic motion. In order to standardize prey size and behaviour, we used only *Artemia* nauplii. *Artemia* is a non-evasive prey since no significant escape motion has been recorded (Coughlin and Strickler, 1990) and, generally, planktivores preferentially select non-evasive prey items, even when the evasive prey are larger (Drenner et al., 1978; Vinyard 1980, 1982). Although *Artemia* is not a natural prey of shiner perch, perch showed similar behavioural patterns when feeding on natural plankton (McFarland and Levin, 2002). In addition, by staining Artemia with black ink, we provide an artificial set-up that may have affected the behaviour of *Artemia* or its physiology (e.g. any chemical cues it may provide). However, as suggested by its lack of significant evasive behaviour (Coughlin and Strickler, 1990), *Artemia* was most likely just passively carried by the current and therefore its behaviour should not have affected our results.

The dark background we used does not correspond to the most common environment where plankton is found. However, certain environmental conditions, i.e. twilight, as well as in certain conditions of turbidity, cloudiness and depth, may also provide a relatively dark background. Nevertheless, conditions of visibility created in laboratory set-ups such as ours are quite different from natural conditions, and it would be interesting to investigate the feeding reactions of planktivorous fishes to a variety of plankton types in natural conditions.

Conclusions

Our results showed that at high current speeds, angular velocity was the likely cue for triggering the feeding reaction when semi-transparent *Artemia* were used. Loom appeared to be the main mechanism when prey were darkened. It is possible that both mechanisms act in concert during some of the feeding phases (detection, pursuit, capture), although one mechanism might eventually prevail in detecting certain prey characteristics (e.g. motion type, prey contrast).

As our major conclusion, we suggest that prey contrast dramatically affects detection and the subsequent feeding reaction. When prey contrast was high due to scattering (semi-transparent prey), feeding reactions occurred at greater distances and at increasing X_{lateral} values where angular velocity tends to be higher. When prey contrast was low (darkened treatment), reaction distances diminished and feeding reactions occurred for prey approaching at smaller lateral distance (X_{lateral}). This study showed that visual behaviour of planktivores is highly flexible because fish appear to be able to utilize different visual properties of the approaching object for their reaction to prey. Although angular velocity was the main cue for triggering feeding reactions to semi-transparent plankton at high current speeds, it is still possible that during the tracking of a plankter after a prey's detection, loom may have a role in determining the time of engulfment. This and other issues will be explored in a further paper dealing with the pursuit and capture of plankton.

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