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PREY DETECTION IN SELECTIVE PLANKTON FEEDING BY THE PADDLEFISH: IS THE ELECTRIC SENSE SUFFICIENT?

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Summary

The long rostrum of the paddlefish *Polyodon spathula* supports an extensive array of ampullary electroreceptors and has been proposed to function as an antenna for detecting planktonic prey. Evidence in support of this hypothesis is presented in experiments that preclude the use of other sensory mechanisms for plankton detection. Paddlefish swimming in a recirculating observation chamber are shown to feed normally in the dark when prey-related chemical and hydrodynamic sensory cues are masked or attenuated. Specifically, we demonstrate that the spatial distribution of plankton captured by paddlefish is little changed when the plankton are individually encapsulated in agarose, when a high background concentration of plankton extract is added to the chamber, when the nares are plugged and under turbulent water flow conditions. Paddlefish also discriminate between encapsulated plankton and 'empty' agarose particles of the same size. Although capture distributions differed somewhat under certain conditions, the general pattern and effectiveness of prey capture were not disrupted by these procedures. These results support the conclusion that paddlefish, as zooplanktivores, rely on their passive electric sense for prey detection.

Key words: paddlefish, *Polyodon spathula*, electrosensory, planktivore, prey detection, *Daphnia magna*, *Artemia salina*

Introduction

The large freshwater paddlefish *Polyodon spathula* is a planktivore, feeding primarily on tiny crustaceans that it strains in enormous numbers from the water using comb-like gill rakers (Rosen and Hales, 1981). However, as juveniles (<20 cm long), paddlefish feed selectively, capturing plankton one at a time (Rosen and Hales, 1981; Michaletz et al., 1982). We have studied selective particulate feeding in small juvenile paddlefish prior to the development of their filtering apparatus (Wilkens et al., 1997; Russell et al., 1999) and have shown that selective feeding involves passive electrosensory detection of plankton by ampullary electroreceptors (Jørgensen et al., 1972) in the elongated rostrum or paddle. Thus, the paddle functions as an electrical antenna for locating planktonic prey, and it is extended, appropriately, in front of the mouth in these ram-ventilating fish (Burggren and Bemis, 1992). Although the passive electric sense has a well-established role in prey capture in elasmobranchs, including several species of shark (Kalmijn, 1971; Kalmijn, 1978; Tricas, 1982; Tricas and McCosker, 1984), the paddlefish is the only fish thought to rely on the passive electric sense for plankton feeding.

The present study was designed to demonstrate that the electric sense is the primary sensory modality for particulate feeding and that it alone is sufficient for successful prey capture by young paddlefish. Prey capture is undiminished in the dark (Wilkens et al., 1997; Rosen and Hales, 1981), demonstrating that vision is not required for effective feeding. In these experiments, we show further that paddlefish capture plankton with great facility under conditions that preclude the use of either their chemo- or mechanosensory systems.

Materials and methods

Paddlefish *Polyodon spathula* Walbaum were obtained from fish hatcheries in Missouri, USA, approximately 2 months after hatching. Fish were housed in a large biofiltered holding tank (approximately 2000 l) containing dechlorinated tap water raised to a salinity of 2‰ by the addition of stock salt to control fish ick. The fish were fed daily with a diet of commercial fish pellets, frozen bloodworms and live brineshrimp. Prior to an experiment, the fish were conditioned for 2 days in a freshwater tank adjusted to a conductivity of $760\pm10\,\mu S\,cm^{-2}$. Fish were not fed on the day prior to an experiment. The Institutional Animal Care and Use Committee approved all procedures.

We studied prey capture of plankton by small paddlefish (12–17 cm) as they swam in place in a 32 l recirculating, laminar-flow tank (Vogel and LaBarbara, 1978; Wilkens et al., 1997). The water velocity was adjusted to match that of free-swimming fish (approximately $10\,cm\,s^{-1}$) in the holding tanks. The paddlefish were restricted to an observation chamber

(13.5 cm×13.5 cm×40 cm, width × height × length) with glass sides and bottom to permit lateral and ventral views of the fish. All experiments were conducted under near-infrared illumination (λ_{max}=880 nm) using 60 W light-emitting diode illuminators (American Dynamics, model 1020/6020) projecting into the observation chamber from the upstream and downstream ends. Gel filters (Kodak no. 87C) placed between the light sources and chamber further restricted wavelengths below 780 nm. The fish were monitored by two infrared-sensitive closed-circuit video cameras (Baxall, model CD6212/IR) using a 45° mirror for the ventral view. The images were combined using a digital beam splitter (American Dynamics, model 1479) and recorded on video tape with a video recorder (Panasonic, model AG-1970P).

For each experiment, the flow tank was filled with water from the conditioning tank, and a fish was placed in the observation chamber to acclimate for 30–60 min prior to feeding. Live adult plankton, either natural prey, the water flea (*Daphnia magna*) or the brineshrimp (*Artemia salina*), were introduced remotely into the flow tank through a tube passing through a small hole in the wall of the room and inserted into the downstream end of the chamber. Plankton circulated freely, emerging from the grille in front of the observation chamber in near-uniform cross-sectional distribution (D. F. Russell, B. A. Wettring and L. A. Wilkens, in preparation). Throughout the experiment, plankton concentrations remained constant at a relatively low density of 1–2 l^{-1}. This was achieved using the following procedure. Prior to and during an experiment, 10 plankton were placed into cups containing 50–60 ml of tank water. Thus, with the addition of each cup of water, samples of 10 plankton were added to the experimental chamber. A feeding trial was initiated with 30–40 plankton. Additional samples were added at intervals approximating the rate of plankton capture by the fish, as estimated by monitoring feeding behavior during the course of the experiment.

In addition to live, free-swimming plankton, the paddlefish were presented with live plankton encapsulated in agarose to eliminate swimming motions and to restrict the diffusion of chemical signals from the plankton into the water. Individual plankton were grasped carefully with forceps and dipped briefly into a solution of low-melting-point agarose (2% w/v in tank water; Sigma type 1-A) at 45 °C. After gelling, the plankton were dipped a second time to ensure a thorough coating. Selected teardrop-shaped, agarose-coated plankton were visually inspected using a dissecting microscope to determine viability. Although no appendage or other exterior movements were observed, peristaltic gut contractions and heartbeats (in *Daphnia magna*) were visible internally. In other experiments (L. Wilkens and E. Wagner, unpublished results), electrical signals were recorded from encapsulated *Daphnia magna* and *Artemia salina* to confirm viability. Paddlefish captured and engulfed encapsulated plankton, although one fish spat out approximately 50% of the agarose-coated *Daphnia magna* following capture.

In several experiments, paddlefish were also presented with agarose particles of a size approximating the encapsulated plankton. Blocks of 2% agarose were forced through a No. 10 sieve (2.0 mm mesh size), and particles of near-uniform size were selected individually. Both encapsulated plankton and agarose particles were added in samples of 10, as for the free-swimming plankton. The total number of plankton or agarose particles introduced during an experiment was recorded, and an accurate count of feeding events was determined by subtracting the number of plankton/particles remaining at the conclusion of the experiment. A fine-mesh dip net was used to collect and count uneaten items. These feeding estimates agreed well with capture numbers resulting from the analysis of video recordings. Experiments usually continued to satiation of the fish. In the experiments included in this study, the number of plankton captured per fish ranged from 16 to 193.

Feeding was also examined under conditions designed to interfere with chemical and hydrodynamic sensory systems. In the former, brineshrimp (*Artemia salina*) extract was added to the recirculating water to create a high-background chemical environment. Brineshrimp extract was prepared by blending 40–100 g of rinsed, blotted brineshrimp (>10 000 individual plankton) in 275 ml of tank water for 1 min (Waring, medium speed). The mixture was centrifuged for 25 min at 82 000 ***g*** and yielded supernatants with conductivities of 850–1000 μS cm^{-2}. Increases in conductivity in the flow tank resulting from the addition of brineshrimp extract were minor. We also tested chemosensory-impaired feeding by plugging the nares of five paddlefish with drops of 2% (w/v) agarose gel.

Plankton feeding was tested further under conditions of turbulent, non-laminar water flow. Turbulence was created immediately upstream of the observation chamber by vigorous aeration and insertion of a small, insulated propeller driven at high speed by a drill motor (Dremel). Plankton exhibited a distinct tumbling motion as they drifted through the observation chamber.

Analysis of video-taped feeding, as described previously (Wilkens et al., 1997; Russell et al., 1999), involved stopping and reversing the tape following each successful feeding capture. The video recorder jog shuttle was used to align the 'captured' plankton in register with the tip of the rostrum. This video frame was transferred to computer as a digitized image (SigmaScan, Jandel Scientific, San Rafel, CA, USA) in which the positions of the plankton or other captured particles and of the rostrum tip were marked by cursor in both lateral and ventral views. These pixel coordinates were transferred to a spreadsheet program (SigmaPlot, Jandel Scientific, San Rafel, CA, USA) to plot plankton locations and to calculate their distance, relative to the central axis of the rostrum, using a 10 cm videotaped scale for calibration. Thus, each captured plankton was logged at a fixed reference point, a vertical plane at the tip of the rostrum, and each of these represented the 'detection distance' of the plankton as measured from the center of the rostrum. Detection distance is used synonymously with capture distance elsewhere in the text.

For maximum accuracy in comparing feeding events under different conditions, data points accepted for analysis were limited to feeding events meeting certain requirements. For

example, captures were rejected for fish turned sideways in the observation chamber by more than 15 ° relative to the current flow in the video reference frame (plankton at tip of rostrum). At these angles, the effective distance between the prey and the rostrum would have been biased. Such captures constituted a relatively small proportion of all the feeding events. Other feeding responses excluded from analysis included aborted swings towards the prey, unsuccessful strikes and looping backward in the chamber to capture prey that had drifted past the mouth. These data will be analyzed separately in relation to feeding kinematics.

The distributions of captured plankton are presented for certain conditions as scatterplots. These represent the detection distances in the vertical plane at the tip of the rostrum. To quantify these distributions, the radial distance from the center of the rostrum was determined for each plankton. Capture frequency *versus* detection distance approximated a log normal function (SigmaPlot, nonlinear regression analysis), from which maximum detection distances (x_o) could be determined. Data sets were normalized for comparison of prey capture under different conditions. Since detections distances were not distributed normally, statistical comparisons of the data sets were made using a one-way nonparametric analysis of variance (ANOVA: SAS Institute Inc., 1998).

Results

Each of the experiments reported here was performed under infrared illumination to eliminate the visual detection of planktonic prey. Additional experimental procedures were used as controls for electrosensory-based feeding, i.e. to examine prey capture in the absence of chemo- and/or mechanosensory information. The water flea *Daphnia magna*, which we cultured in the laboratory, is the natural prey of the paddlefish and was the primary plankton species used in these experiments.

Daphnia *prey capture*

The distribution profile for a large sample (N=2299) of captured *Daphnia* is illustrated in Fig. 1A. This scatterplot shows plankton locations relative to the horizontal and vertical midlines of the rostrum in the vertical plane at the tip of the rostrum. For this and subsequent figures, data have been pooled for three or more fish. The overall distribution is compressed vertically, with plankton locations extending laterally from the midline to a greater extent than above or below the rostrum, as reflected in the absolute means for the x (13.3 mm) and y (9.0 mm) coordinates. The distribution of captured *Daphnia* is nearly symmetrical above and below the rostrum (45 % *versus* 51 %; mean y coordinate −0.4 mm), whereas there is a degree of lateral asymmetry, i.e. more plankton were captured on the right side of the rostrum than on the left (57 % *versus* 39 %; mean x coordinate +4.0 mm). The lateral asymmetry for *Daphnia* captures appears to be an experimental bias, with two of every three fish tested exhibiting a small right-side offset. None had a left-side bias. A similar bias was observed for fish feeding on brineshrimp in the same flow chamber (Wilkens et al., 1997). A basis for the capture asymmetry would exist if the fish had a swimming preference for the left side of the chamber, thus restricting feeding opportunities on that side. The chamber is asymmetric only to the extent that the left side is clear for viewing while the right side has a black background. Since all experiments were performed in the dark, differences in the sides of the chamber are unlikely. Alternatively, more plankton may enter the observation chamber on the right side. This too seems unlikely since plankton appeared to enter the chamber uniformly (D. F. Russell, B. A. Wettring and L. A. Wilkens, in preparation).

Curiously, fewer plankton were captured near the vertical or horizontal midlines of the rostrum. These ‘gaps’ have been seen previously in brineshrimp data. We believe these gaps are real. Although it is possible that plankton approaching the tip of the rostrum at the horizontal midline might be deflected up or down by a bow pressure wave, the existence of the vertical gap, in the absence of an equivalent vertical pressure wave, suggests that the gaps are not an artifact of our analysis criteria. The physiological basis for these gaps will be addressed in a separate paper.

The distribution of *Daphnia* captured as a function of radial detection distance from the center of the rostrum is illustrated in the histogram in Fig. 1B (based on the x and y coordinates of the scatterplot data in Fig. 1A). Capture frequency is greatest for plankton located 8–20 mm from the center of the rostrum (56 %), decreasing steadily with further increases in distance. A relatively small number (4.3 %) were captured at distances of more than 40 mm, with a maximum capture distance of 83 mm. The capture frequency falls off steeply close to the rostrum, consistent with the gaps seen in the scatterplot. Thus, capture distances for *Daphnia* are not distributed normally.

Species comparison in plankton capture

Selective plankton feeding by the paddlefish was studied initially (Wilkens et al., 1997) using the brineshrimp *Artemia salina*, available commercially in bulk. In the present study, we also used the somewhat smaller water flea *Daphnia magna*, the natural prey of the paddlefish. The distribution profile of captures is similar for these two free-swimming planktonic organisms. As with *Daphnia*, the overall distribution for *Artemia* is vertically compressed, with a vertical mean of 10.4 mm and a horizontal mean of 13.9 mm. These values are proportionately equivalent (within 3 %) to those for *Daphnia* (9.0 mm and 13.3 mm, respectively). Although distribution profiles cannot be compared in scatterplot overlays, a comparison of radial detection distance (see inset, Fig. 1B) shows overlapping data points and log normal best-fit curves. For both species, relatively few plankton (fewer than 3 %) that pass within 5 mm of the rostral surface, or at distances greater than 40 mm from it (*Daphnia* 4.3 %; *Artemia* 3.8 %), are eaten. However, there is a slight increase in detection distance for *Artemia*, as reflected by a shift to the right for these data. Both

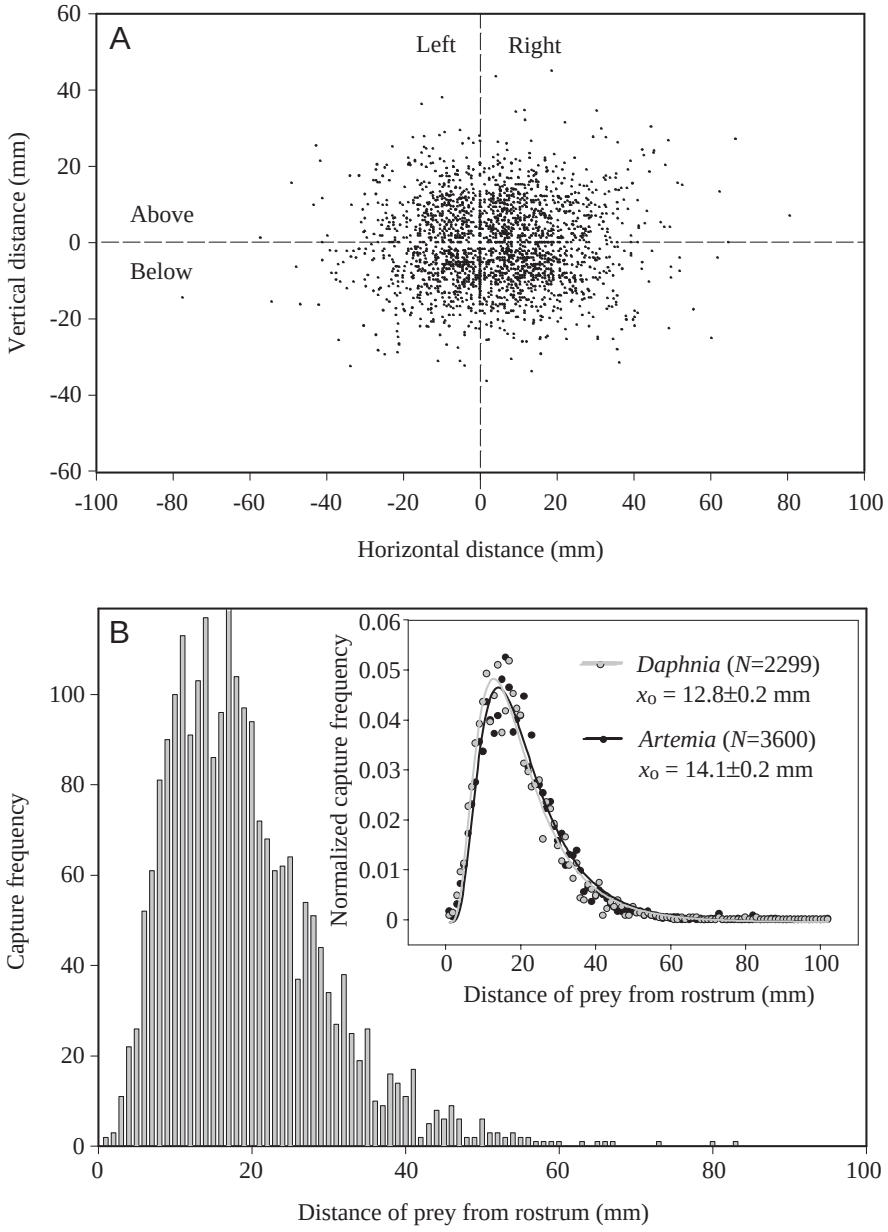

Fig. 1. Distribution of 2299 water fleas (*Daphnia magna*) captured by the paddlefish. (A) Scatterplot of plankton locations (detection distances) as seen in a vertical plane centered at the tip of the rostrum of the paddlefish. Dashed lines indicate the horizontal and vertical midlines of the rostrum. The mean rostrum width at its widest point is 19.7 mm (range 16–22 mm). (B) Histogram of *Daphnia* capture frequencies based on detection distances from the center of the rostrum, calculated from the data points in A. Inset: capture frequencies comparing *Daphnia magna* and *Artemia salina* distributions. The data from the histogram have been normalized for comparison (gray and black circles), with corresponding curves for best-fit non-linear regression analysis. Values for peak detection distances (x_0) are from the regression curves and are presented as means ± S.E.M.

the median and peak detection distances are also somewhat greater for *Artemia* (median distance by 1.5 mm; peak distance by 1.3 mm). Overall, detection distributions for the two species differ significantly (P<0.0001) in a nonparametric one-way analysis of variance (ANOVA).

Capture of encapsulated plankton

Paddlefish swimming in the recirculating observation chamber readily detect and capture plankton encapsulated within agarose, the locations of which are shown in scatterplot format (inset, Fig. 2). This figure also illustrates capture frequencies for encapsulated *Daphnia* compared with free-swimming *Daphnia* (data from Fig. 1B). Although there is a slight shift to the right for encapsulated capture data, these distributions do not differ significantly (P<0.7745), as reflected also by small differences in the median (by 0.2 mm) and peak (by 0.7 mm) detection distances for encapsulated *versus* free-swimming *Daphnia*.

Brineshrimp were used in several experiments to test the capture of agarose-coated plankton. As with *Daphnia*, paddlefish readily captured encapsulated brineshrimp, although the distributions for this smaller sample (N=409, P<0.0001) differed from those of free-swimming *Artemia* (Fig. 3). The median (increased by 3.0 mm) and peak (increased by 3.0 mm) detection distances for encapsulated brineshrimp were again somewhat greater. Thus, encapsulation results in small increases in overall detection distances for both species.

In three feeding experiments using encapsulated *Daphnia*, paddlefish were presented with equal numbers of ‘empty’ agarose particles. The particles, together with the encapsulated plankton, remained suspended and circulated freely through the flow chamber. A relatively small number of agarose

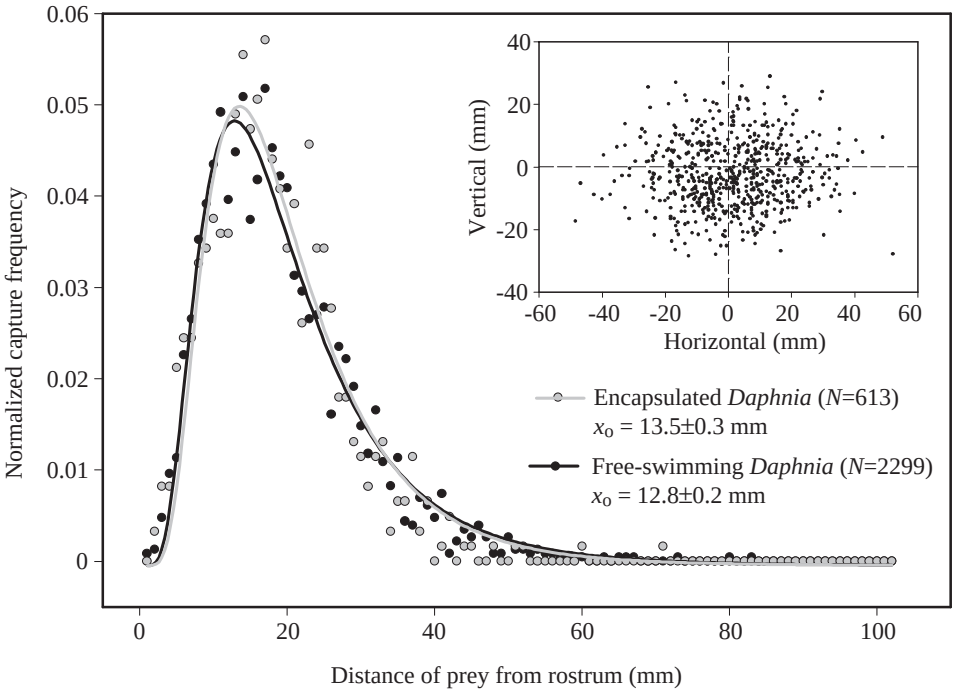

Fig. 2. Detection distances for *Daphnia magna* encapsulated in 2 % agarose. The data are illustrated in scatterplot format (inset) and as normalized capture frequency relative to the distance from the center of the rostrum, for comparison with free-swimming *Daphnia* sp. (*N*=2299, data from inset in Fig. 1B). Values for peak detection distances (x_o) are from the regression curves and are presented as means ± S.E.M.

particles were captured (21) in contrast to the capture of encapsulated *Daphnia* (368), results illustrated in Fig. 4. All agarose particle captures were close to the rostrum, the majority within 10 mm. These data correspond to a rate of capture of 1.7 min^{-1} for encapsulated *Daphnia* and 0.1 min^{-1} for the agarose particles over the combined 212 min of videotaped feeding. It should be noted that the distribution of encapsulated *Daphnia* for this data set (*N*=368) was not significantly different (P<0.1793) from those in the three remaining experiments with encapsulated *Daphnia* (*N*=245). The combined results of these two data sets are presented in Fig. 2 (total *N*=613).

Feeding choice experiments using encapsulated brineshrimp yielded equivalent capture distributions (not shown). In four experiments, paddlefish feeding was first examined using encapsulated *Artemia*, then, after removal of all prey items, with agarose particles alone and finally with equal numbers of encapsulated brineshrimp and agarose particles. Only two

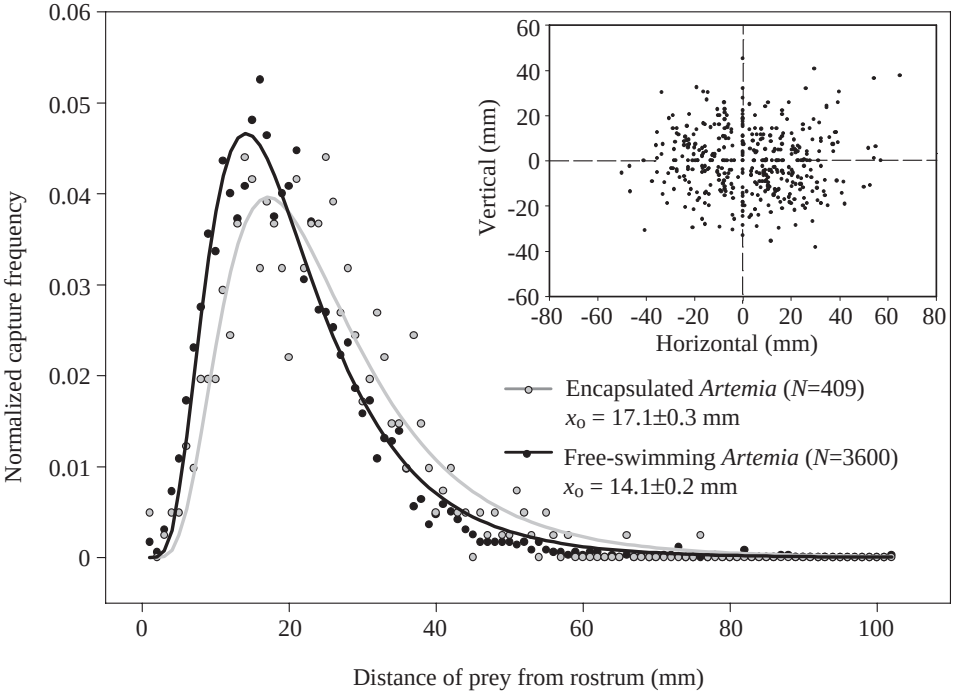

Fig. 3. Detection distances for *Artemia salina* encapsulated in 2 % agarose. The data are illustrated in scatterplot format (inset) and as normalized capture frequency relative to the distance from the center of the rostrum, for comparison with free-swimming *Artemia* (data from inset in Fig. 1B). Values for peak detection distances (x_o) are from the regression curves and are presented as means ± S.E.M.

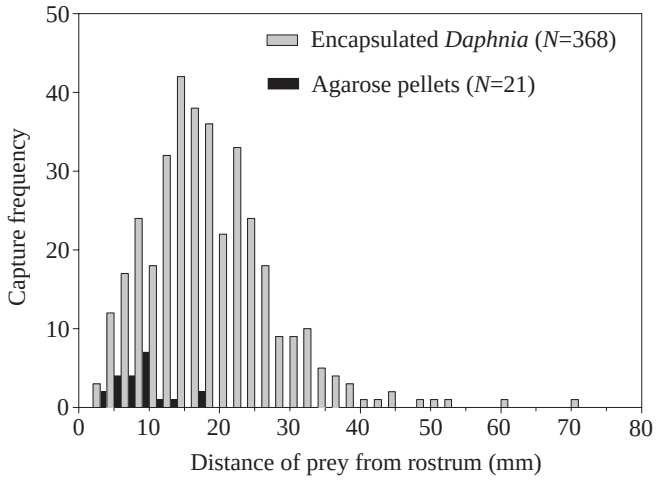

Fig. 4. Comparison of detection distances for agarose-encapsulated *Daphnia magna* and equivalent-sized agarose particles. The encapsulated *Daphnia* data (*N*=368) are a subset of the results presented in Fig. 2.

agarose particles were captured in 138 min of particle-only feeding (a feeding rate of 0.01 min^{-1}), and only three particles were taken in 172 min in the feeding-choice experiments (a feeding rate of 0.02 min^{-1}). In contrast, paddlefish captured encapsulated brineshrimp at nearly identical rates of 0.84 min^{-1} when presented alone (98 captures) and 0.82 min^{-1} under feeding-choice conditions (145 captures).

Chemosensory effects on feeding

Two additional procedures were used to test the role of chemosensory detection in prey capture. First, *Artemia* capture was tested in the presence of a concentrated chemical background, using an extract prepared from the prey species itself. Paddlefish fed aggressively under these conditions at a mean rate of 2.61 captures min^{-1}. This exceeds the mean rate of feeding (1.81 captures min^{-1}) for the large sample of free-swimming brineshrimp (*N*=3600) in control feeding experiments. Prey-capture distributions (Fig. 5A) differed significantly ($P<0.0212$), with median distance increasing by 1.0 mm and peak capture distance by 1.8 mm in the presence of brineshrimp extract. In a second chemosensory test (Fig. 5B), we blocked the nares of the paddlefish with agarose plugs. These fish also fed aggressively, with a mean brineshrimp capture rate of 2.80 captures min^{-1}. Again, the detection distribution with the nares blocked differed from that for control feeding ($P<0.0001$). Both median and peak detection distances decreased (median distance by 1.9 mm and peak distance by 2.2 mm).

Prey capture in turbulent flow

Prey capture under nonlaminar turbulent flow conditions was tested in a single experiment. Paddlefish fed actively, capturing 63 brineshrimp in a 12 min sample period. A statistical comparison was not made because of the small sample size. Nevertheless, capture distributions were similar in form, with few captures at short distances (<5 mm), the majority of captures (60 %) between 14 and 30 mm, and a maximum capture distance of 58 mm.

Discussion

The present experiments support the hypothesis that small paddlefish using the selective feeding mode use their elongated rostrum as an electrical antenna to detect and capture planktonic prey. To strengthen this argument, we have examined planktonic feeding under conditions that eliminate or greatly reduce the effectiveness of the other sensory modalities. These ‘control experiments’ include encapsulating individual plankton to immobilize their appendages and to create a chemical barrier, adding a concentrated plankton extract to disrupt or mask spatial chemical cues, plugging the nares to block olfaction and generating turbulence to interfere with hydrodynamic signals produced by the swimming plankton. All experiments were performed in the dark to eliminate visual cues.

Our experiments mirror the procedures used by Kalmijn (Kalmijn, 1971) with sharks and rays in which the role of the electric sense in feeding was first established. Sharks were trained to attack flatfish prey buried in the sand, and therefore invisible, after which they also attacked fish concealed by agar plates that masked their chemical and hydrodynamic signals and artificial electric fields simulating prey (see also Kalmijn, 1982). Similarly, the bioelectric potentials of fish prey trigger bites by the swell shark (Tricas, 1982). As with sharks, an artificial electric field triggers feeding responses by the paddlefish. Previously (Wilkens et al., 1997) and in the companion paper (Wojtenek et al., 2001), paddlefish are shown to strike at dipole electric fields as if capturing plankton.

Sufficiency of the electric sense for particulate feeding

The present study demonstrates that paddlefish exhibit normal feeding behavior under experimental conditions that preclude the use of other sensory modalities. A survey of plankton distributions in each of the feeding experiments reveals a consistent pattern of prey capture. Experiments using different plankton species, plankton encapsulated in agarose and procedures inducing other sensory deficits are all characterized as follows: low numbers of prey captures close to the rostrum, a steep rise to maximum captures in the range 12–17 mm and an exponential decline in captures with increasing distance. Thus, the general feeding pattern of the paddlefish remains unchanged despite a variety of perturbations of the sensory environment, except for the electric sense. We conclude that the paddlefish electric sense is sufficient for the detection of prey in selective planktivorous feeding. Our results suggest further that the paddlefish electric sense is the primary, if not the sole, sensory modality for detecting planktonic prey.

Electrosensory prey detection remains somewhat of a novelty among the feeding strategies used by fish. This is especially so for particulate feeding, which generally implies the capture of zooplankton by a much larger predator. Further,

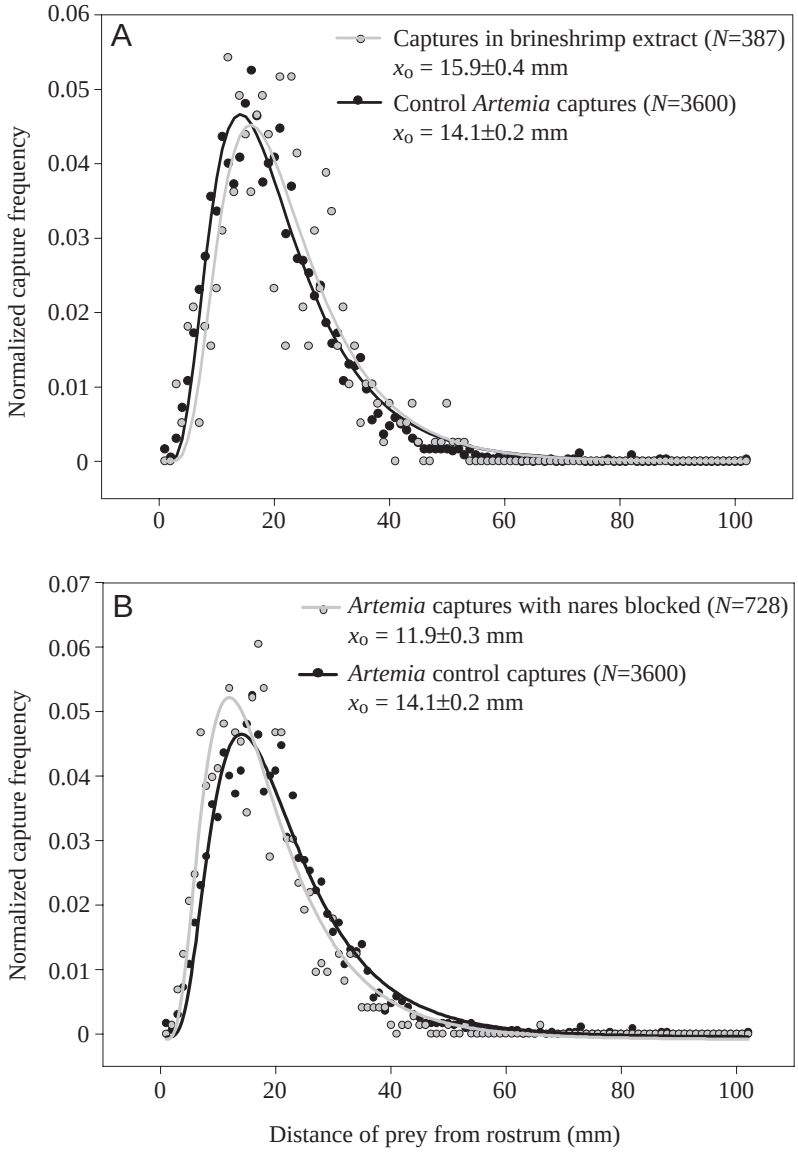

Fig. 5. Prey capture with chemosensory interference. (A) Brineshrimp (*Artemia salina*) detection distances in the presence of high background concentrations of brineshrimp extract. (B) Brineshrimp detection distances with the nares blocked. Data points and regression analyses are as in previous figures. Values for peak detection distances (x_o) are from the regression curves and are presented as means ± S.E.M.

particulate feeding is generally associated with visual mechanisms of prey detection (Gerking, 1994; Gliwicz, 1986; Maddrell, 1998; O'Brien, 1979). Both the paddlefish (passive electrosensory) and the weakly electric fish (active electrosensory) are exceptions to the rule of visually based planktivory. These two unrelated groups of freshwater fish scan their planktonic prey electrically. Juvenile paddlefish scan plankton as they drift alongside the rostrum (Wilkens et al., 1997), whereas weakly electric fish, e.g. *Apteronotus albifrons*, swim (knife) forwards and backwards in the process of localizing their planktonic prey (Lannoo and Lannoo, 1993; MacIver et al., 1997; Nelson and MacIver, 1999). Paddlefish are unique in another respect: they switch to a filtering mechanism as they grow larger, although utilizing the same zooplanktonic resources. Filtering, i.e. suspension feeding, is non-selective by definition, implying that prey capture is indiscriminate. Prey selection is determined passively by the filtering mechanism, here the spacing of the gill raker teeth (Rosen and Hales, 1981), and further reduces the need for sharp vision. However, assuming that it retains its extraordinary sensitivity in large paddlefish, the electric sense may continue to play a role in feeding, e.g. in assessing plankton density.

Chemo- and mechanosensory intervention has minimal effects on prey capture

Although distributions of captured prey in each type of experiment follow the same general pattern, there are nevertheless subtle differences in capture distributions. For example, brineshrimp capture distances are slightly greater than those for the water flea *Daphnia*. This holds true for both free-swimming (see curve shifts, inset Fig. 1B) and encapsulated (peak detection distance is 3.6 mm greater for encapsulated *Artemia*, cf. encapsulated x_o values in Figs 2 and 3) plankton. The maximum detection distance for brineshrimp is also greater (*Artemia*, 102 mm; *Daphnia*, 83 mm). The

greater detection distances for *Artemia* may be related to the more extensive electric fields of brineshrimp (L. Wilkens and E. Wagner, unpublished results). Encapsulation also tends to increase detection distances, e.g. curves for the encapsulated plankton are shifted to the right (Figs 2, 3), although only significantly so for *Artemia*. Encapsulation does not increase the strength of the plankton electric field (L. Wilkens and E. Wagner, unpublished results).

Two points should be considered in evaluating the small but consistent feeding differences observed for different plankton species and encapsulation. First, relatively large data pools are presented for each experiment to ensure a representative sample of behavioral measurements. However, these data were obtained over a period of several months. Standardized procedures were used to the extent practical, but it is possible that variables such as the effect of handling stress on individual fish, relative satiation, the time of day of the experiment or general condition of the fish may have affected the results. Water quality is especially critical since stressed fish feed poorly or not at all. Thus, while these experiments show some differences in capture distribution, their effects are subtle and do not alter the conclusion that paddlefish feed primarily by the electrosensory detection of plankton.

This conclusion is also consistent with the results from feeding experiments in the presence of brineshrimp extract, with the nares blocked and under turbulent water flow. The small differences in the overall distribution of plankton captures are as yet unexplained, but feeding dexterity is relatively unaffected by any of these procedures. However, the feeding rate does appear to be influenced positively by the presence of brineshrimp extract, as reflected by a 44 % increase (from 1.81 to 2.61 captures min^{-1}). This effect might be anticipated since it triggers animated swimming, a behavior characteristic of actively feeding fish. Feeding paddlefish exhibit accelerated swimming (see also Sanderson et al., 1994) and more frequent turns, whether presented with live plankton or artificial fish food. Indeed, water drained from frozen blood worms, essentially an extract, by itself triggers animated swimming characteristic of feeding fish. Plugging the nares also stimulated feeding behavior, as indicated by a 55 % increase in capture rate (to 2.80 min^{-1}). Thus, both brineshrimp extract and blocked nares appear to stimulate feeding activity, but not the mechanics of feeding as judged by capture locations. These rate increases must be viewed cautiously, however, since the data are compared with those from unimpeded feeding experiments. A more definitive comparison would have been to establish a feeding rate for each fish prior to the addition of extract, although this would have been impractical for naris blocking.

Although olfaction appears to stimulate feeding, it is unlikely to be involved in prey capture. The nares are at the base of the rostrum, adjacent to the eyes and mouth, and other analyses (D. F. Russell, B. A. Wettring and L. A. Wilkens, in preparation) demonstrate that the reaction distance of paddlefish peaks when the plankton have passed only one-third of the length of the rostrum, well in front of the nares. Gustation can also be discounted because there is no contact with plankton prior to capture. Indeed, the fact that paddlefish engulf and swallow both free-swimming and encapsulated plankton, even plain agarose pellets, suggests that taste plays a limited role in feeding, although one paddlefish was observed to 'chew' and then spit out half the encapsulated *Daphnia*. In contrast, the largemouth bass *Micropterus salmoides* relies heavily on gustatory food quality before swallowing (Linser et al., 1998), as demonstrated in the rejection of sight-captured but 'tasteless' food balls.

The most dramatic evidence for electrosensory feeding is seen in the food-choice experiments in which paddlefish were presented with encapsulated plankton in equal numbers with agarose particles. Whereas 368 encapsulated *Daphnia* were captured, only 21 agarose particles were eaten (Fig. 4), 5 % of total captures. In experiments with encapsulated *Artemia*, only three particles (2 %) were taken. Clearly, paddlefish can distinguish between inanimate and 'live' agarose particles, which have identical physical characteristics except for the electrical component of the plankton. The fact that paddlefish take empty agarose particles, prepared with water equal in conductivity to their environment, is further evidence of a highly sensitive electrosensory system.

Hydrodynamic detection of plankton is also an unlikely sensory explanation, and our experiments showed no effect of turbulence on prey capture. In general, turbulent fluctuations are weak at the scale of small crustacean zooplankton as a result of water viscosity (Lazier and Mann, 1989). However, copepods and cladocerans produce measurable wakes, trails that approximate the width of the plankton (a few millimeters) and produce water velocities up to 20 mm s^{-1} (Yen and Strickler, 1996), but these also attenuate rapidly. Flow speeds generated by the swimming motions of tethered *Daphnia* decrease by as much as d^{-14} (where d is distance) (Kirk, 1985). Nevertheless, planktonic flow fields represent turbulent trails in a laminar environment, signals available for potential mates and predators. For example, midge (*Chaoborus trivittatus*) larvae attack *Daphnia* at a mean distance of 3.1 mm, where equivalent water flow is 3.4×10^{-4} mm s^{-1} (Kirk, 1985). For copepods, escape hops leave conspicuous toroidal vortices, whereas swimming motions are barely discernible. These wakes signal the presence of predator or prey and trigger appropriate responses by another copepod (Yen and Strickler, 1996). Male copepods also use female wakes in tracking mates (Yen et al., 1998). Nevertheless, the size of a planktonic wake is small compared with the capture distances for paddlefish, a few millimeters *versus* up to 8–9 cm, and there is as yet no evidence that fish use the hydrodynamic wakes of even larger organisms, e.g. fish, for prey detection (Hanke et al., 2000).

In the present study, we have shown that sensory systems other than the electric sense are most unlikely to contribute to the highly specialized particulate (zooplankton) feeding strategy of paddlefish. These results support the conclusion that the paddlefish rostrum has evolved as a highly sensitive electrosensory system capable of prey discrimination during selective feeding in the wild.

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