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Filter-foraging strategies of captive American paddlefish (*Polyodon spathula*) in relation to food type, density and distribution in the water column

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Abstract

The American paddlefish (*Polyodon spathula*) uses ram filter-feeding to forage for (mainly) zooplankton throughout the water column. It makes an ontogenetic transition from buccal pumping to ram ventilation feeding in the first year. In wild conditions, plankton is often distributed unevenly in time and space; however, this does not always apply to captive conditions. In the present study, two paddlefish were fed on a range of diets and supply methods to investigate the effect on foraging strategy. Insight into influencing foraging strategies could be beneficial for zoos and aquaria for display purposes or for improving welfare conditions. The paddlefish were studied during foraging, and foraging strategy, bout length and usage of the aquarium space were recorded. Three foraging strategies can be distinguished: foraging while swimming in straight lines, foraging while swimming in circulatory paths and particulate foraging. Although these strategies appear to not have a fixed switch-point, a significant difference was found between the foraging strategies for start and end points of certain strategies in relation to food density (P<0.003). Mean time spent on a strategy differed in duration from 1 to 60 seconds. When negative buoyant food sources (e.g. Mysids) were used, the paddlefish foraged in the lower parts of the aquarium. Neutrally buoyant food sources (e.g. *Daphnia pulex*) caused the paddlefish to forage throughout different depths of the aquarium (P<0.001).

Introduction

The American paddlefish (*Polyodon spathula*) is one of the largest freshwater planktivores in the large rivers and lakes of the Mississippi river basin (Jennings and Zigler 2000). Where once populations extended northwards up to the southern parts of Canada, no sightings have occurred there since the early 1900s (Parker 1988). The paddlefish has been an iconic species since its first documented sightings in the 1600s. Their primitive form, in combination with their paddle-shaped snout, the rostrum, have baffled researchers for a long time. It was first assumed that paddlefish would dig for food with their rostrum as the size and shape were considered ideal to plough vegetation and soil in search for small arthropods and fish (Beach 1902; Norris 1923 in Rosen and Hales 1981). However, this idea faced scepticism because of the delicate skin structure of the rostrum and the shallow ampullary pits, better known as ampullae of Lorenzini, which cover about 70% of the rostrum surface (Wilkens and Hofmann 2007; Wojtenek et al. 2001). Spraque (1959) studied stomach contents and concluded that paddlefish feed mostly on zooplankton and that the rostrum is a tool for detecting food particles in the water. Paddlefish were subsequently not considered bottom feeders, though related species of sturgeons in the family Acipenseridae were.

Ram filter-feeding

Filter-feeding in paddlefish varies in duration and speed of swimming. The mouth is stretched fully open for maximum filtration surface and the branchial (gill) arches and opercular flaps are spread, while the paddlefish swims forward to catch planktonic prey (Burggren and Bemis 1992; Rosen and Hales 1981). As a result of this forward swimming motion, the water enters continuously (and not in separate 'bites'), thus known as ram filter-feeding.

During ram filter-feeding, foraging and ventilating are combined, as the water passing through the gills provides planktonic food and oxygen for the gills. Paddlefish make an ontogenetic transition from buccal pumping to ram ventilation in their first year. During buccal pumping water needs to be pumped over the gill filaments, whereas during ram ventilation the forward motion of the fish ensures water flow over the gill filaments. Forward swimming in combination with open gills increases drag due to the resistance of the gills in the water (Burggren and Bemis 1992). This suggests that ram ventilation is energetically costly when foraging. However, during ram ventilation, no energy is used for buccal pumping, leaving it available for, for example, using the swimming muscles of the trunk (Jones and Randall 1979; Roberts and Rowell 1988).

In addition to the gill filaments, gill rakers, which are used to filter tiny prey out of the water, begin to form along the medial side of the branchial arches when paddlefish exceed 65 mm eye-to-fork length (EFL) (Rosen and Hales 1981). In contrast to the ram filter-feeding of juveniles and adults, larval paddlefish 'pluck' individual prey items from the water column. Adult paddlefish specialise in relatively slow-swimming zooplankton such as cladocerans, copepods, and only occasionally prey on small fish (Russell 1986). Almost all paddlefish make the switch to ram filter-feeding within their first year, and all do so eventually. The developmental stage of the respective gill rakers determines when a paddlefish makes this transition. Growth rate of the body, and therefore of the gill rakers, is variable between populations (Jennings and Zigler 2000). Sanderson et al. (2001) suggest that fully developed rakers in adult paddlefish are not directly involved in obtaining food, but that they direct the water flow towards the upper part of the buccal cavity where food particles are retained; however, there is no proof to support this idea.

Diet and growth: Wild vs captivity

Rosen and Hales (1981) studied the stomach contents of paddlefish caught between August 1975 and August 1976. Of the 12 different plankton species found in the stomachs, three were most abundant: *Daphnia pulex* (37.3% of total stomach volume), *D. siciloides* (15.1%) and *D. forbesi* (14.1%). The importance of a diverse diet was demonstrated in the study of Brandt (1978), where growth rate of larval paddlefish on different diets was measured. Commercial diets resulted in a 50% lower survival rate than an hourly dispatched diet mixture. Food type also had a positive correlation with growth rate: growth rate of the paddlefish was on average 2.4mm/day until a body length of 100 mm was reached. After that, growth rate decreased to about 1.0mm/day (Houser and Bross 1959; Kroll et al. 1994; Michaletz et al. 1982; Reed et al. 1992). However, these body growth rates, as well as the growth of the gill rakers, are strongly influenced by environmental factors, such as variation in water flow between lentic (ponds, lakes) and lotic (actively moving water) environments. The ability to effectively detect and capture prey may be influenced by differences in water flow. Therefore, low water velocity is often applied in the tanks of paddlefish nurseries, so that larval paddlefish may forage without having to use extensive amounts of energy (Hintz et al. 2015; Jennings and Zigler 2000; Kozfkay and Scarnecchia 2002).

Much research has been done on the stomach contents of paddlefish; however, the relation between stomach contents and food (zooplankton) availability has not been fully studied (Hoxmeier and Devries 1997; Rosen and Hales 1981). Even in captive conditions, the foraging behaviour of paddlefish is still somewhat mysterious. Until now, ram filter-feeding has been seen as one single strategy without variants; however, it is now known that paddlefish display this foraging behaviour in (at least) two ways. In wild conditions, zooplankton is distributed unevenly, and high densities of zooplankton is likely to occur only in the spawning season of zooplankton (Omori and Hamner 1982). When paddlefish actively forage, or encounter sufficient plankton to initiate foraging, their mouths open completely and foraging is initiated. Then, the paddlefish moves typically in a straight line through the water to catch zooplankton; an aspect of their behaviour which has not been mentioned as such in the literature, to the best of our knowledge. In the present study, we will refer to this phenomenon as foraging along straight paths (FSP). The second ram filter-feeding type involves the paddlefish swimming along circular paths. Our observations show that this behaviour usually occurs with higher densities of food (e.g., when food has just been supplied to the aquarium). In our study, this motion is referred to as foraging along circulatory paths (FCP). Well documented is particulate foraging (PF) of juvenile paddlefish, whereby individuals selectively pluck food particles out of the water.

The goal of the present study is to gather insight into the relationship between food density and foraging behaviour of the American paddlefish. We hypothesise that (i) there is a switch-point for foraging strategies depending on food density, whereby adult paddlefish will switch from ram filter feeding to particulate feeding when food-density is very high; and that (ii) at lower food densities, the time spent foraging will increase, and the foraging strategy will be adjusted to the food density.

If food density does indeed influence foraging behaviour, this should be taken into consideration in the cultivation or holding facilities of captive paddlefish, such as in zoos and aquaria, or in the growing caviar industry into which paddlefish are also being introduced. Although the public display of animals has changed considerably in the last century, the implementation of more natural conditions in captive environments could be beneficial for fish welfare and visitor satisfaction.

Methods

Two semi adult paddlefish (574mm and 345mm) of unknown sex were kept in an octagonal ring-shaped aquarium (300x300x70x80cm [lxwxhxd]) for a total of 10 weeks (Figure 1). Mean temperature was 18±2.9°C. Mean salinity levels were kept at 6.1±1.34‰ pH levels had a mean of 8.5±0.32. Paddlefish were exposed to a light regime of 12:12 L:D. The aquarium pump (I, Figure 1) had a total volume flow of 1,872 litres per hour. The water entered the aquarium via two valves, at a rate of 936 litres per valve per hour. The valves were aimed slightly downwards, directing the water flow towards the aquarium floor (large arrows, Figure 1). Situated directly underneath the aquarium pump was an air pump (II, Figure 1). In combination with the pump inflow, this caused vertical flow of the net water inflow. The overall flow velocity of the water was measured via the tracking of single food particles on video recordings (ImageJ – NIH). The food particles had a velocity of 3.5cm per second at the study area (III, Figure 1). Although the water was pumped into the aquarium in two different directions, the water and the paddlefish went from left to right in the perspective of that in Figure 1.

Frozen plankton from Frozen Fish food Inc. (i.e. Artemia, Mysids and Malawi-mix containing Artemia sp., other shrimps and vegetable proteins and carbohydrates) were thawed and rinsed

in fresh water, and supplied to the aquarium two to six times a day, in different amounts at the same spot in the aquarium (food insertion point, Figure 1). Food was weighed frozen each time and divided into two amounts: High (87±0.1g) and Low (52±0.1g). Paddlefish were given the same diet for five days in a row, of which the first three days were considered an acclimation period for that particular diet. On the fourth day, foraging behaviour was recorded and food density was measured after supplying the tank with the Low amount of food in combination with a certain feeding frequency. On the fifth day, the same procedure was followed after supplying the High amount of food at a certain frequency. After each experimental cycle of five days, there was a resting period of two days with a food supply two times a day. Frequencies of food supply per week per day can be found in Table 1. Following the above procedures, the paddlefish did not go from a low frequency to a high frequency of food supply in a single week, and by increasing the frequency of food supply in steps of two, the effect of habituation was kept to a minimum. Every first, third and fourth day the aquarium floor was suction-cleaned.

The following aspects were recorded during paddlefish foraging: 1) foraging strategy, 2) bout lengths and 3) use of aquarium space. Foraging behaviour was recorded with an Adimec 1000m camera at 25 frames per second, which was mounted directly at the spot where the food was supplied (III, Figure 1). For quantifying the use of the area/space in the aquarium, we focused on the depth the paddlefish was swimming. To give a workable measure of depth, six sections were defined in the aquarium, each of 10cm height, which were clearly visible on the camera images. Depth was determined by picking the tip of the rostrum as a reference point. To measure bout length of the three different foraging strategies, namely foraging along straight paths (FSP), foraging along circulatory paths (FCP) and particulate foraging (PF), the following rules were applied: FSP was recorded when a distance of 1.5 body length was covered in a straight line, without starting FCP. FCP was recorded when paddlefish swam in circles in a relatively small area while foraging, without using the entire aquarium. Selectively plucking food particles out of the water was characterised as PF. The maximum duration of one foraging bout in the particulate foraging strategy was set at two seconds, so particulate foraging would clearly be differentiated from FCP and FSP. Food density was determined by illuminating the food particles for a short time with a green light sheet from a DPSS Laser (SNOC-lasers, 532NM, Pmax=2W) mounted above the tank (Figure 1). Food particles drifted through the 2mm thick laser sheet, and lit up as bright spots that were imaged with the camera. For analysis, images were converted to 8-bit B/W images and inverted; subsequently, particles were counted using a particle count procedure (ImageJ, NIH Image). At each start and end point of a foraging bout, particles in the laser sheet were counted and density was calculated. The density of food particles was converted to particles per litre (p/L). Data were analysed with a Two-Way Anova in IBM SPSS Statistics version 23.

To check for changes in feeding behaviour when supplied with food items similar to a natural diet, a few test trials with thawed *Daphnia pulex* and *Cyclops sp.* were performed after completing the previous experiments. The density of these food items is closer to that of the water, thus making them almost neutrally buoyant so that they occur throughout the water column for a long time. The behaviour of the paddlefish was recorded in the same way as described above. These results are only indicative and will be used for comparison in the Discussion section.

Results

When food is supplied to the aquarium, a dense cloud of zooplankton is observed. Because the density of the zooplankton is higher than that of the water, it slowly sinks to the bottom. In addition, the current made by the circulation pump of the aquarium system causes the zooplankton to be distributed throughout the aquarium. The paddlefish appear to adapt their foraging strategy
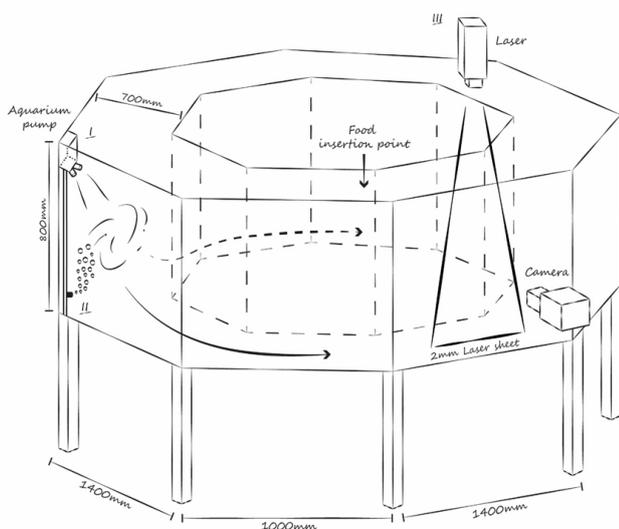

Figure 1. Side view of the research setup. Food was supplied at the food insertion point and food density was determined with an Adimec 1000-m camera and a laser (532NM, 2W)
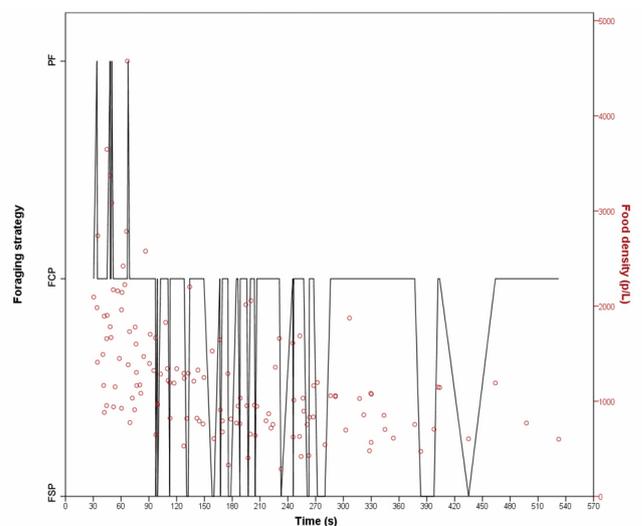

Figure 2. Foraging strategies and food density (p/L) shown over time (n=165). X-axis show time in seconds. On the left y-axis foraging strategies are shown: FSP=foraging along straight paths, FCP=foraging along circulatory paths, PF=particulate foraging

Table 1. Feeding frequencies

Week number	Times per day
1	2
2	4
3	6
4	3
5	5

Table 2. Mean bout length for each foraging strategy for Low and High amount of food supply.

Strategy	Low Bout length (s)	High Bout length (s)
FSP	42.34±28.99	45.13±31.92
FCP	64.34±54.13	66.16±34.17
PF	0.78±0.21	0.94±0.35

to these food density levels (Figure 2). Mean density of plankton during the feeding strategy FSP is 709±330 p/L, during FCP it is 1438±882 p/L and during PF 2513±1134 p/L is observed. Although these strategies have no fixed switch-point, significant differences in food density were found between foraging strategies at the start and end points (P<0.003). Paddlefish showed PF and FCP behaviour with high food densities directly after supplying the food. When food density levels dropped below 2000 p/L, a shift occurred towards FCP and FSP. The minimum food density level for a paddlefish to initiate any foraging behaviour in this experiment was 569 p/L or higher. When a swimming paddlefish encountered a location with a higher food density, it stayed in that location and changed its strategy to FCP. Figure 3 presents the different feeding strategies in relation to food density at the start of a foraging bout. Densities of zooplankton decrease except during the strategy FSP, in which the food density at the start of feeding bouts is lower than that at the end (see Discussion).

Each measurement series consisted of multiple bouts. A bout (measured in seconds) started the moment the paddlefish opened its mouth and stopped as soon as the mouth was closed. Bout length significantly differed between the three foraging strategies (P<0.001). Table 2 gives an overview of the bout lengths per strategy for Low and High amounts of supplied food. In the

strategy of FCP the paddlefish foraged for the longest period of time, followed by FSP, with PF exhibiting the shortest foraging time. However, the amount of food supplied (High or Low) had no influence on the duration of a foraging bout (P=0.11). The short periods between bouts appear to be used to clean the buccal filter and swallow the zooplankton. Irrespective of the strategy used to acquire the food particles, time between two foraging bouts was 4.04±1.65 seconds.

Foraging during this study mostly took place in the lower parts of the aquarium. The paddlefish was in depth-section six for 88.8% of the time, which was the deepest area in the aquarium, in area five for 9% of the time and only in area four for 0.7% and area three for 1.5%. Areas one and two were not used at all for foraging.

Discussion

This study suggests that, at the moment paddlefish encounter zooplankton and/or detect it with their rostrum, the most appropriate foraging strategy is set in motion depending on the detected food density. When food density is high, paddlefish exhibit particulate foraging to gain as much plankton as possible in a short period of time. When food density is low, but high enough to initiate foraging, paddlefish will switch to FSP while swimming
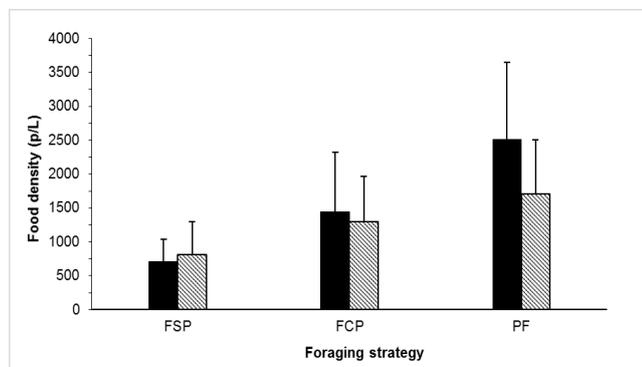
Figure 3. Mean density level of plankton in relation to foraging strategy. Black bars indicate the food density (p/L) at the start point of a foraging strategy, striped bars indicate the end point
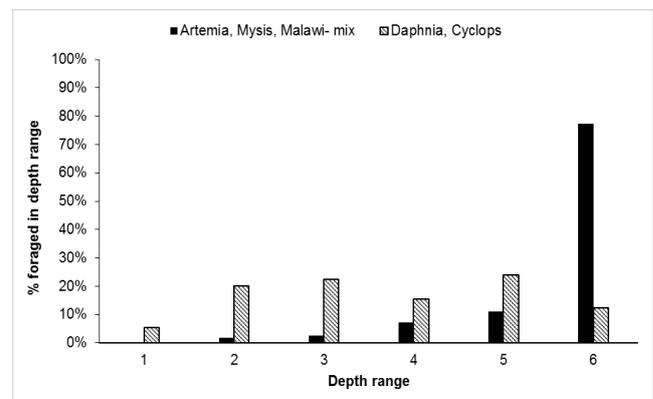
Figure 4. Influence of food source on aquarium area use. The height of each area was 10cm, with area 1 as the highest (shallowest) part of the aquarium and area 6 the lowest (deepest) (n=165 in original experiment; n=129 in additional experiment).

through the water. Ram filter-feeding appears to be preferred when food density is relatively low, but our data suggest that a minimum food density is necessary to initiate this foraging mode.

Since larger paddlefish have further developed gill rakers for filtering zooplankton, body size is expected to influence the switch-point between foraging strategies and may be the cause of the relatively large standard deviation between strategies. This would suggest that larger paddlefish would more often exhibit a filtering strategy (FCP or FSP) than particulate foraging (PF). The two individual paddlefish used in this study had different body lengths. However, no differences were found between the two individuals in choosing feeding strategies in relation to food density and therefore the datasets were combined; small differences might, however, still have caused variations in the final dataset.

The negative buoyancy of the Artemia, Mysids and Malawi-mix caused it to sink towards the aquarium floor. When a paddlefish was swimming just above the gravel covering the aquarium floor, it disturbed previously settled zooplankton by the swimming motion of its caudal fin. This resulted in a cloud of zooplankton of high food density behind the paddlefish which led to two possibilities. First, food density in front of the paddlefish was high enough to initiate circulatory foraging and the paddlefish extended the foraging area size to include the disturbed zooplankton. Second, the food density in front of the paddlefish was not high enough to stimulate FCP. The disturbed zooplankton was subsequently coincidently encountered by the paddlefish during swimming or FSP in the aquarium, again initiating FCP or PF. Figure 2 shows that paddlefish appear to adapt their foraging strategies to density levels of zooplankton. Using the caudal fin to disturb settled zooplankton does not appear to be a deliberate part of the foraging strategy, although we cannot rule this out. Paddlefish seem to react only to the food density levels in front of them, and were not observed to turn around for the higher food density levels behind them created by the action of their caudal fins.

The goal of this study was to investigate if foraging behaviour is influenced by food supply frequency or quantity, and whether this knowledge could subsequently be used to improve the welfare of paddlefish in captivity. Zoos and aquaria with paddlefish on public display could achieve higher customer satisfaction by introducing improved methods of food supply. Feeding times are an important consideration when displaying animals in a zoo. Displaying animals has seen major changes over the last century: in the early 1900s, animals were caged in zoological gardens (Mason 2000) provided with little stimuli encountered in wild conditions. The subsequent transition to displaying animals in a more natural habitat not only caused a decrease in stereotypic behaviour in the animals, but also changed attitudes towards the animals' place in human society (Ballantyne et al. 2007). In case of the paddlefish, food is more than a basic requirement for animals; animal keepers can influence foraging behaviour of paddlefish by changing feeding regimes to display the range of behaviours that would be seen in the wild. Paddlefish are known for their ram filter-feeding. Increasing the duration and frequency of this foraging behaviour would likely increase visitor time in front of the display, thus resulting in higher visitor satisfaction (Mason 2000), while at the same time offering the fish a more natural feeding regime. Stimulating a combination of the FCP and FSP strategies is advised to acquire the desired longer foraging duration to stimulate foraging behaviour as seen in the wild.

Diet can play an important role in the use of the aquarium space. To stimulate the paddlefish to use different parts of the aquarium in terms of depth levels, the choice of food type is apparently of key importance. In an additional experiment the paddlefish were given Daphnia pulex and Cyclops sp. as a food source instead of Artemia, Mysids and Malawi-mix, in the same quantities and frequencies as the original experiment. These food

sources were chosen because of their almost neutral buoyancy in water, meaning that they do not settle on the aquarium floor. When encountering these food types, the paddlefish adjusted their depth in the aquarium. Because the motions of the caudal fins had no effect on food density, paddlefish foraged higher up in the aquarium (Figure 4; area one is the shallowest and six the deepest area of the aquarium). A significant difference was found (P<0.001, paired sample t-test) in area use when fish were fed with the Daphnia and Cyclops. In the original experiment, most foraging occurred in area six. In the additional experiment, foraging shifted evenly towards the other areas. Because the food source was more dispersed throughout the aquarium the two paddlefish could forage simultaneously in the same aquarium section.

Conclusion

Different food sources and food supply regimes can result in different foraging behaviours and foraging bout durations in paddlefish (*Polyodon spathula*). For zoos and nurseries, and paddlefish, this can be beneficial. In this study, paddlefish displayed natural behaviours when food sources were supplied in a more controlled fashion. By additionally introducing neutrally buoyant food items, more animals can forage simultaneously in the same aquarium section at different depths, thus minimising dominance effects that may occur during feeding time in captive conditions. Zookeepers can select certain food sources and supply regimes that stimulate the paddlefish to swim and display foraging behaviour as seen in wild conditions.

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