Integration of Undulatory Swimming Kinematics and Ram Suspension Feeding in A Model American Paddlefish

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Integration of Undulatory Swimming Kinematics and Ram Suspension Feeding in a Model American Paddlefish

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Thesis presented to the Graduate Faculty of The College of William & Mary in Candidacy for the Degree of Master of Science

Biology

The College of William & Mary
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Master of Science

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ABSTRACT

Ram suspension-feeding fishes are a taxonomically diverse group that is both economically and ecologically important. However, many questions remain pertaining to how they feed, including the types of prey they are capable of capturing, the metabolic costs associated with feeding, and the process of manipulating and transporting food around the oral cavity. Recent research has shown that the American paddlefish (*Polyodon spathula*) employs vortical cross-step filtration, in which vortices that form posterior to the branchial arches organize crossflow filtration processes into a spatial structure across the gill rakers. Potential temporal organization of filtration mechanisms in ram suspension-feeding fish has not been studied previously. Because ram suspension feeders swim forward with their mouths open to capture prey, we investigated the effect of the locomotor kinematics associated with undulatory swimming on intra-oral flow patterns and food particle transport. We constructed a mechanized model to simulate the swimming of suspension-feeding paddlefish, and recorded fluctuations of flow speed and pressure within the model. We also showed that swimming kinematics aided the transport of food particles from the gill rakers to the posterior margins of the gill slots. These findings suggest strong integration between locomotor and feeding systems in ram suspension-feeding fishes.
# TABLE OF CONTENTS

Acknowledgements .............................................. ii
Dedication ........................................................ iii
List of Tables ..................................................... iv
List of Figures ..................................................... v

Chapter 1. Introduction ........................................ 1

Chapter 2. Methods ..............................................
   a. Physical model ........................................... 6
   b. Analysis of live paddlefish swimming kinematics .... 9
   c. Operation of the models ................................ 15
   d. Particle capture and transport ......................... 16
   e. Pressure and flow speed ................................ 17
   f. Flow patterns ............................................ 20

Chapter 3. Results ..............................................
   a. Particle capture and transport ......................... 21
   b. Pressure and flow speed ................................ 23
   c. Flow patterns ............................................ 27

Chapter 4. Discussion .......................................... 30
   a. Ecological implications .................................. 34
   b. Future directions ....................................... 37

References ....................................................... 39
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Many thanks to Dr. Ken Semmens of Kentucky State University’s aquaculture program and to Big Fish Farms for generously providing dead paddlefish specimens. Thanks also to Drew Rotunno and Will Laney for their physical computing expertise and their help designing our model’s Arduino program, and to Tom Meier for his help constructing the model mechanism.
This thesis is dedicated to my parents. Thanks for telling me to go play outside.
LIST OF TABLES

1. Morphometric measurements of preserved paddlefish specimens and analogous measurements of the 3-D printed model  8

2. Kinematic measurements of live, suspension-feeding paddlefish  14
# LIST OF FIGURES

1. A digital rendering of the 3-D printed model used in all experiments 9
2. Proportion of analyzed mesh area covered by *Artemia* cysts during 3-minute trials 21
3. Particle coverage of mesh after three minutes in mechanized and control trials 22
4. Particle capture as a proportion of seeded mass in 3- and 4-minute mechanized and control trials 23
5. Representative pressure and flow speed recordings in mechanized and control trials 24
6. Pressure and flow speed recordings filtered using a 1.8 – 2.6 Hz bandpass Fourier filter 25
7. Power spectrum comparisons of pressure and flow speed recordings 26
8. Vortices in stationary control trials 27
9. Dye stream visualization of flow in a mechanized trial at the anterior cannula 28
10. Dye stream visualization of flow in a mechanized trial at the branchial arch cannula 29
Introduction

Suspension-feeding fish, which feed on prey items that are too small to be efficiently pursued and captured individually, are both ecologically (Zamon 2003, Tanaka et al. 2006) and economically important (Food and Ag. Org. of the UN 2016). These fish may engulf their prey by oral pumping, which generates a suction that is used to force water through the oral cavity, allowing water currents and filter structures to separate prey from the water. Alternatively, suspension-feeding fish may force water through their oral cavities by simply opening their mouths and swimming forward, or “ramming.” Ram feeding and suction feeding are not discrete classifications, but describe two ends of a spectrum (Norton and Brainerd 1993). However, the morphologies and feeding behavior of ram suspension-feeding fish are particularly extreme, more so than other ram feeders, and their oral anatomies are distinctly adapted for the capture of very small prey. In addition to an unusually large gape (Ferry et al. 2015), these adaptations may include filter pads, as in whale sharks and the mobulid rays (Paig-Tran and Summers 2014), or thin bony or cartilaginous structures attached to the branchial arches called gill rakers, as in the paddlefish (Rosen and Hales 1981), basking shark (Paig-Tran and Summers 2014), and teleost suspension feeders (Friedland et al. 2006, Sanderson et al. 1996, Castillo-Rivera et al. 1996). Ram suspension-feeding fish may also have elaborations of the filter structures including denticles, lobes (Paig-Tran and Summers 2014), or branchiospinules (Friedland et al. 2006, Castillo-Rivera et al. 1996).
Until fairly recently, the gill rakers present in most suspension-feeding fish were assumed to function as a dead-end sieve, in which water flowed through the rakers and food particles larger than the inter-raker space were retained, as in bream (Hoogenboezem et al. 1993, Hoogenboezem 2000). Additional mechanisms for the capture of particles include inertial impaction and direct interception by filter structures (Rubenstein and Koehl 1977, LaBarbera 1984, Shimeta and Jumars 1991), often with the aid of mucus (Sanderson et al. 1991). The sieve filtration model that had long been assumed to describe filtration in all taxa of suspension-feeding fishes has been replaced for many species by a crossflow filtration model. In crossflow filtration, particle-laden water flows across the surface of a filter, rather than perpendicular to the filter. Particles in crossflow remain in suspension and are transported posteriorly as water is forced out of the oral cavity through the rakers (Sanderson et al. 2001, Brainerd 2001). Importantly, crossflow filtration mechanisms allow the capture of particles smaller than the spaces between filter structures, and reduce fouling of the filter (Brainerd 2001, Callan and Sanderson 2003, Cheer et al. 2012).

In industrial crossflow filtration, some filter fouling does occur, increasing the filter’s internal pressure and reducing its efficiency (Jaffrin 2012, van Dinther et al. 2011). However, crossflow alone does not appear to be entirely responsible for the lack of filter fouling in suspension-feeding fish (Sanderson et al. 2001, Brainerd 2001). Elaborations of the fish crossflow model have been developed recently to address the vortices formed posterior to the branchial arches and how they change the spatial structure of filter mechanisms in ram
suspension feeders with rib-and-groove branchial arch and gill raker arrangements, specifically the American paddlefish and the basking shark (Sanderson et al. 2016). While Brooks et al. (in preparation) have shown that the angle at which ram suspension feeders encounter flow influences the functioning of this cross-step filtration mechanism in paddlefish, no research to date has shown how continuous motion related to swimming kinematics influences introral flow patterns or reduces fouling during filtration.

The most common modes of swimming in fishes require the passage of an undulatory wave along the length of an individual’s body, providing thrust and allowing the fish to propel itself forward through the water (Webb 1975). The characteristics of these waves, as well as the size and morphology of the fish to which they belong, determine a fish’s swimming speed and how quickly it can accelerate (Tytell et al. 2010, Webb et al. 1984). Even in the undulatory swimmers with very low amplitude undulatory waves, as in tuna, there is some yaw (lateral rotation of the head about a vertical axis as a consequence of undulatory wave production), and there is no point on the body of the fish where the amplitude of the propulsive wave is zero (Dewar and Graham 1994, Webb 1992). As a consequence of the wave having a nonzero amplitude across the fish’s entire body, heave (linear motion perpendicular to the swimming direction, effectively half the amplitude of an undulatory wave at a given point) is an important measurement to describe the wave at a point on the fish’s body. Amplitude, and therefore heave, must increase towards the caudal end to provide a propulsive force (Webb 1975, Shelton et al. 2014, Weihs 2002). It has
also been observed that there is a phase difference between yaw angle and heave, and this phase difference may have important functional implications (Lighthill 1993, Rowe et al. 1993, Akanyeti et al. 2016). Among these, locomotor kinematics, including yaw, heave, and the phase difference between them have been shown experimentally (Akanyeti et al. 2016) and theoretically (Lighthill 1993) to improve lateral line sensing by the reduction of self-generated pressure noise. Akanyeti et al. (2016) have also demonstrated that locomotor regulation of pressures surrounding the head is likely used by fish to reduce the energetic cost of opercular pumping for respiration. However, the possible effect of locomotor kinematics on intra-oral flow speed and pressure dynamics during ram suspension feeding have not yet been explored.

Kane and Higham (2015) suggest that by taking an integrative approach to the study of different biological processes, we can better understand how these processes interact to influence performance and fitness outcomes. To the extent that processes interact, variation in one process may influence performance of the other, ultimately resulting in variable fitness outcomes and at population scales potentially influencing evolution (Kane and Higham 2015, Higham et al. 2016). Although Kane and Higham (2015) use locomotor and feeding systems of fish to demonstrate the benefits of an integrated approach to biomechanics, they suggest that ram suspension feeding fish exhibit only weak integration between these systems. We demonstrate here, using an American paddlefish model, that the kinematics of undulatory locomotion and the function of branchial arches and gill rakers as filtration structures are in fact strongly
integrated, both in space and in time. We conducted experiments showing that in a 3-D printed model, the yaw and heave that we quantified in live, filter feeding paddlefish cause fluctuations in intra-oral pressures and flow speeds. We also visualized these flow patterns generated by locomotor kinematics using dye streams, and used *Artemia* cysts to show the influence of cyclical flow patterns on food particle capture and transport in a 3-D model of a ram suspension-feeding paddlefish.
Methods

Physical model

To simulate the oral cavity of a paddlefish, we designed a 3-dimensional model using SketchUp Make software (version 16.1.1451), and printed of nylon plastic (fine polyamide PA 2200) by Shapeways Inc. (Figure 1) The model’s features were derived from measurements of *P. spathula* specimens preserved in as close as possible to ram suspension-feeding position. The measurements of branchial arch angles were derived from measurements of three preserved specimens (32.5 - 45.5 cm total length, TL; 18 - 29 cm eye-fork length, EFL; Brooks et al., in preparation). These three plus an additional fourth specimen (39 cm TL, 22 cm EFL), all obtained on ice from aquaculture facilities within 24 hours of death (William and Mary Institutional Animal Care and Use Committee approval 07/30/14; Virginia Department of Inland Fisheries Approval 07/24/14), were used to confirm that the proportions of the model were realistic and to estimate the TL and EFL of a paddlefish with an oral cavity the size of the model (36.9 cm TL, 21.1 cm EFL, Table 1).

The model included four branchial arches. The three anterior arches extended from the ventral midline to the dorsal midline, and the fourth branchial arches extended only over the ventral portion of the model. This reflects the arrangement of the branchial arches and gill slots in paddlefish, in which the dorsal terminus of the gill slot posterior to the fourth branchial arch is only slightly above the ceratobranchial-epibranchial joint (Burggren and Bemis 1992). The gill slots of the model were covered with a nylon mesh to simulate gill rakers. The
mesh had a pore diameter of 140µm, a thread diameter of 50µm, and was 55% open area (Component Supply Co.). In order to cover the model’s rounded shape, some stretching of the mesh was required, but this did not have any apparent effect on particle retention or flow patterns. No mesh fabric can perfectly simulate the rakers of a paddlefish, which run parallel to each other rather than crossing each other like the woven fabric of the mesh. However, we believe the mesh we have chosen is the best option available to simulate the inter-raker distance and the thickness of the rakers themselves, which are approximately 42 µm and 100 µm, respectively, for the size of paddlefish we simulated (approximately 21 cm EFL [Table 1], Rosen and Hales 1981). The fluid exit ratio (the total open pore area for water to exit from the model, divided by the open area of the gape; Brooks et al., in preparation) was 1.23. In addition to the mesh, a clear, flexible vinyl sheet (20 gauge) attached to the model immediately posterior to the oral gape was used to simulate an operculum by covering all the model's gill slots.

The aspect ratio of the model’s first gill slot was calculated using two straight lines drawn along the central coronal plane of the model between the posterior and anterior edges of the first gill slot in SketchUp. One line connected the medial edges of the gill slot on the interior of the model, and the other connected the lateral edges on the exterior of the model. Using the length of the interior line and the minimum distance between the two lines when measured along an axis perpendicular to the posterior end of the interior line, we calculated the aspect ratio of the first gill slot to be 3.95.
This model was attached by a 0.95 cm diameter wooden dowel to a servo motor, which controlled yaw, and to a DC motor on a repurposed printer printhead, belt, and stabilizer bar, which controlled lateral heave. We controlled these motors using Arduino Uno and Arduino MotorShield hardware, and a program we designed using Arduino software (version 1.6.8). This apparatus allowed us to control yaw about a vertical (Z) axis, and heave, or lateral motion perpendicular to flow. We were also able to control the phase difference between yaw and heave, which Akanyeti et al. (2016) have noted is an important, but often ignored, kinematic variable in undulatory swimmers.

<table>
<thead>
<tr>
<th>Fish</th>
<th>1</th>
<th>2</th>
<th>3</th>
<th>4</th>
<th>Mean</th>
<th>SD</th>
<th>Model</th>
</tr>
</thead>
<tbody>
<tr>
<td>Total Length</td>
<td>32.5</td>
<td>35.5</td>
<td>45.5</td>
<td>39.0</td>
<td>38.13</td>
<td>5.59</td>
<td>36.92*</td>
</tr>
<tr>
<td>Eye-Fork Length</td>
<td>18.0</td>
<td>19.0</td>
<td>29.0</td>
<td>22.0</td>
<td>22.0</td>
<td>5.0</td>
<td>21.1**</td>
</tr>
<tr>
<td>Esophagus - Anterior Maxilla</td>
<td>4.8</td>
<td>6.0</td>
<td>8.5</td>
<td>6.3</td>
<td>6.4</td>
<td>1.54</td>
<td>6.84</td>
</tr>
<tr>
<td>3rd Branchial Arch - Anterior Maxilla</td>
<td>4.3</td>
<td>5.2</td>
<td>7.1</td>
<td>5.5</td>
<td>5.53</td>
<td>1.17</td>
<td>5.44</td>
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<tr>
<td>Gape Width</td>
<td>3.8</td>
<td>4.5</td>
<td>5.4</td>
<td>4.2</td>
<td>4.48</td>
<td>0.68</td>
<td>4.24</td>
</tr>
<tr>
<td>Gape Height</td>
<td>3.4</td>
<td>3.2</td>
<td>2.0</td>
<td>2.1</td>
<td>2.68</td>
<td>0.73</td>
<td>4.18</td>
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</table>

<table>
<thead>
<tr>
<th>Total Length Ratio (X/TL)</th>
<th></th>
<th></th>
<th></th>
<th></th>
<th>Mean</th>
<th>SD</th>
</tr>
</thead>
<tbody>
<tr>
<td>EFL</td>
<td>0.55</td>
<td>0.54</td>
<td>0.64</td>
<td>0.56</td>
<td>0.573</td>
<td>0.045</td>
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<tr>
<td>Esophagus - Anterior Maxilla</td>
<td>0.15</td>
<td>0.17</td>
<td>0.19</td>
<td>0.16</td>
<td>0.166</td>
<td>0.016</td>
</tr>
<tr>
<td>3rd Branchial Arch - Anterior Maxilla</td>
<td>0.13</td>
<td>0.15</td>
<td>0.16</td>
<td>0.14</td>
<td>0.144</td>
<td>0.001</td>
</tr>
<tr>
<td>Gape Width</td>
<td>0.12</td>
<td>0.13</td>
<td>0.12</td>
<td>0.11</td>
<td>0.118</td>
<td>0.008</td>
</tr>
<tr>
<td>Gape Height</td>
<td>0.10</td>
<td>0.09</td>
<td>0.04</td>
<td>0.05</td>
<td>0.073</td>
<td>0.029</td>
</tr>
</tbody>
</table>

* The estimated Total Length for the model is a mean of the TLs calculated using the four specimens’ mean 3rd Branchial Arch - Anterior Maxilla / TL and Gape Width / TL ratios.

** The estimated Eye-Fork Length was calculated using the TL, obtained as described above, and the specimens’ mean Eye-Fork / TL Ratio.
Analysis of live paddlefish swimming kinematics

Kinematic variables were measured using video (30 frames s⁻¹) recorded directly overhead of live paddlefish (36 – 45 cm TL, 22 – 29 cm EFL) ram suspension feeding in a round tank (1.2 m diameter x 0.2 m deep, Sanderson et al. 1994). Nine clips (mean length 2.7 s ± 1.4 s SD) of the video were used to measure kinematic variables. We selected clips in which the fish in the tank swam in a reasonably straight line without colliding with any structures or other fish in the tank. The measured paddlefish were ram suspension feeding during at least a portion of all nine clips. The yaw and heave measurements used were taken from three separate fish, each of which appeared in three of the selected video clips. Although fish did not exhibit steady swimming in these clips, these
methods enabled us to measure kinematics of fish that were actively ram suspension feeding at voluntary swimming speed.

Yaw
This experimental design allowed the paddlefish to ram suspension feed at a voluntary swimming speed. However, the use of a circular tank required that the yaw angle be corrected for the potential effects of a circular trajectory while swimming in the tank. For each frame of video in a given clip, we measured the angle of the midline of the fish’s rostrum relative to a horizontal line on the video, using the protractor tool in ImageJ 1.49 (National Institutes of Health). A linear trend line was obtained in Microsoft Excel 15.30 representing the change in these measured rostrum angles over the duration of the clip.

The difference between the measured angle and the trend line at the corresponding time point was recorded as the yaw. The two points used as yaw maxima in each stride had the largest and smallest differences between the measured rostrum angle and the trend line. The absolute value of the difference between consecutive yaw maxima was divided by two, providing a mean maximum yaw angle for each stride (two tailbeats). These mean maximum yaw angles were then averaged for each clip. This procedure corrected for the circular trajectory of the fish while swimming voluntarily in the tank.
Stride Length and Swimming Speed

Absolute measurements of the lengths of individual fish in the videos used to calculate swimming kinematics were unavailable. Therefore, measurements of speed of the swimming fish and stride length (the forward distance traveled during one complete undulatory wave) were found in pixels and then converted into body lengths (TL) by dividing by the fish’s TL (in pixels). To minimize the effect of yaw on these calculations, only the frames of video from which peaks in the yaw series were measured were used, so stride length and swimming speed were measured per stride. This resulted in calculations for two sets of strides; one including frames with yaw maxima to the left, and one including frames with yaw maxima to the right.

To calculate stride length in ImageJ, we measured the linear distance in pixels traveled by the tip of the rostrum between the frames of video showing the yaw maxima. We then divided each stride length by the time elapsed between frames to calculate speed (pixels s⁻¹). We calculated the average speed and stride length over each series (yaw maxima to the left, and to the right) by using the harmonic mean of speeds and stride lengths calculated for each stride, and then by finding the mean of both stride series from each clip. Harmonic means of speeds were weighted by the duration of each stride. Unweighted standard errors of harmonic means were calculated for each clip.
Heave

In each frame of video from the nine clips used to measure yaw, we placed a single point on the dorsal midline of the fish at the anterior edge of the oral cavity (location approximated using lateral expansion of the fish’s gape). The locations of these markings were tracked between frames using the Cartesian coordinates of their pixels in ImageJ, and the Euclidean distance was calculated between each pair of consecutive points. The distance traveled on the X axis and the distance traveled on the Y axis between each pair of consecutive frames were both divided by the Euclidean distance traveled between frames, each yielding a number between -1 and 1. This process was repeated for all pairs of consecutive frames in each clip, and yielded one series of numbers between -1 and 1 for each axis. In Excel, we fit polynomial trend lines to both series that resulted from these calculations (one for the X axis and one for the Y axis). Taking the difference between each trend line and the corresponding value between -1 and 1, and multiplying it by the total Euclidean distance traveled between frames yielded a deviation distance from the trajectory for each pair of consecutive frames.

At this point, the course of a fish’s swimming occasionally required that the calculated values be inverted. For instance, when a fish swimming in a counter-clockwise direction turned from swimming in a positive direction along both axes, to swimming in a positive direction along the Y axis and a negative direction along the X axis, the values for the Y axis were inverted, to correct for the fact that heaves to the left and right of the trajectory switched from moving in positive
and negative directions to moving in negative and positive directions along the Y axis, respectively. From the deviations calculated along the X and Y axes, we used the Pythagorean Theorem to determine deviation from the fish’s trajectory in two dimensions. We added these deviations from all consecutive frame pairs in a video clip to calculate cumulative heave distances for each frame pair. In each stride, heave maxima to both sides of the fish were identified, and the heave to either side was found by dividing the difference between consecutive heave maxima by two. All heave distances were converted into body lengths from pixels by dividing by the TL of the fish (in pixels) from the clip.

Application of Live Paddlefish Kinematics to the Model

All measurements were found using 9 video clips, three video clips for each of three fish. All means were weighted by the number of measurements per clip. All standard deviations are mean standard deviations for a clip, weighted by the number of measurements per clip. Mean yaw maximum was $6.07^\circ \pm 2.13^\circ$ SD (82 total measurements) and mean measured heave maximum was $0.013$ TL $\pm 0.004$ TL SD (74 total measurements). The mean phase difference between yaw and heave cycles was 0.146 yaw cycles $\pm 0.215$ cycles SD ($52.6^\circ \pm 77.2^\circ$, 73 total measurements). Mean stride length, stride period, and speed were $0.356$ TL, $0.480$ s $\pm 0.090$ s SD, and $0.754$ TL s$^{-1}$, respectively (72 measurements each). The mean stride frequency (the inverse of the mean stride period) was 2.08 Hz. The mean speed of $0.754$ TL s$^{-1}$ is equivalent to $27.8$ cm s$^{-1}$ for our model of a 36.92 cm TL paddlefish. Measurements for each clip are shown in
Table 2. Although comparable measurements were not always available for all these variables in the literature, most available measurements were similar to or larger than those that we recorded (Webb 1986, Akanyeti et al. 2016, Müller et al. 2002, Webb 1988, Webb 1975). The exception was the phase difference between yaw and heave, which we measured to be larger at this swimming speed than Akanyeti et al. (2016) possibly due, at least in part, to the influence of the paddlefish’s long rostrum on its swimming.

Due to the small scale of the measured heave maxima in live fish, it was not possible to heave the model at these distances. In a test of the model, the mean heave distance to either side measured over four strides at a point approximately 7 mm posterior to the anterior dorsal edge of the model was 1.10

<table>
<thead>
<tr>
<th></th>
<th>Yaw (Deg)</th>
<th>SD</th>
<th>No.</th>
<th>Stride Length (TL)</th>
<th>SE</th>
<th>Stride Period (s)</th>
<th>SD</th>
<th>Speed (TL/s)</th>
<th>SE</th>
<th>No.</th>
<th>Phase Difference</th>
<th>SD</th>
<th>No.</th>
<th>Heave (TL)</th>
<th>SD</th>
<th>No.</th>
</tr>
</thead>
<tbody>
<tr>
<td>Fish 1</td>
<td>5.62</td>
<td>2.38</td>
<td>5</td>
<td>0.490</td>
<td>0.040</td>
<td>0.883</td>
<td>0.196</td>
<td>0.557</td>
<td>0.044</td>
<td>4</td>
<td>0.091</td>
<td>0.264</td>
<td>4</td>
<td>0.017</td>
<td>0.008</td>
<td></td>
</tr>
<tr>
<td>Fish 2</td>
<td>4.70</td>
<td>0.83</td>
<td>8</td>
<td>0.259</td>
<td>0.018</td>
<td>0.414</td>
<td>0.042</td>
<td>0.626</td>
<td>0.037</td>
<td>7</td>
<td>0.170</td>
<td>0.099</td>
<td>8</td>
<td>0.008</td>
<td>0.003</td>
<td></td>
</tr>
<tr>
<td>Fish 3</td>
<td>5.04</td>
<td>2.90</td>
<td>8</td>
<td>0.253</td>
<td>0.026</td>
<td>0.469</td>
<td>0.143</td>
<td>0.564</td>
<td>0.035</td>
<td>7</td>
<td>-0.211</td>
<td>0.560</td>
<td>7</td>
<td>0.009</td>
<td>0.002</td>
<td></td>
</tr>
<tr>
<td>Total</td>
<td>5.05</td>
<td>1.98</td>
<td>21</td>
<td>0.308</td>
<td>0.539</td>
<td>0.116</td>
<td>0.586</td>
<td>18</td>
<td>0.013</td>
<td>0.335</td>
<td>19</td>
<td>0.010</td>
<td>0.003</td>
<td>20</td>
<td></td>
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</tr>
</tbody>
</table>

Table 2. Kinematic measurements of live, suspension-feeding paddlefish. Stride length, stride period, and speed were obtained using the same points, so these calculations used the same number of measurements in each video clip. Measurements for each of three clips are shown in the first three rows for each fish. Phase difference is presented as the lag of a heave maximum in relation to the maximum of the concurrent yaw cycle. The value shown is a proportion of a yaw cycle, so that a value of 0.250 indicates that heave maxima occurred 25% of a yaw wave after yaw maxima. A negative value for this calculation indicates that the heave maxima preceded the yaw maxima. The final row for each fish includes totals for that fish. All grand totals and totals for individual fish are weighted by the number of measurements per clip or per fish, and all SD totals were calculated from pooled variances weighted by number of measurements per clip or per fish. Harmonic means were calculated for stride length. Harmonic means weighted by stride period were calculated for speed. Arithmetic means are shown for all other measurements. Standard errors were calculated only for harmonic means, and are unweighted.
cm (± 0.01 cm SD, n = 8, 2 heave measurements per stride over 4 strides), compared with a mean heave of 0.013 TL ± 0.004 TL measured from videos of live fish, or 0.465 cm ± 0.153 cm for a 36.92 cm TL. However, analogous measurements made at the nose of subcarangiform fish have found amplitudes ranging from 0.04-0.07 TL, or 0.02-0.035 TL heaves (0.74-1.29 cm in a 36.92 cm fish), which show much greater agreement with our model (Webb 1975, Bainbridge 1958, Bainbridge 1963, Pyatetskiy 1970a, b in Webb 1975, Webb 1971). Our model may even be conservative compared with the 0.14 TL minimum amplitude measured at the center of mass of a rainbow trout (Webb 1988).

**Operation of the Models**

All stationary control trials were conducted with the model positioned parallel to flow in a recirculating flow tank (18 x 18 x 90 cm working area, 100 L total volume). Based on our kinematic measurements of suspension-feeding paddlefish, all mechanized trials were conducted using a yaw of 5° to either side of the direction of flow, a phase difference of 72° (20% of one undulatory wavelength, which is equivalent to one stride) between yaw and heave, and a stride frequency (corresponding with tail beat frequency in kinematic studies of live fish) of 2.2 Hz. All trials were conducted at a target flow velocity of 28 cm s⁻¹. Average recorded flow velocity in the recirculating flow tank during experimental trials was 28.32 cm s⁻¹ (SD = 0.38 cm s⁻¹, min. = 27.60 cm s⁻¹, max. = 28.87 cm s⁻¹).
Particle Capture and Transport

Two types of experiments were conducted to examine the effect of yaw on particle capture and transport. Both sets of experiments included stationary control and mechanized model trials. In all trials, the flow tank was seeded with 1.20 g of brine shrimp cysts (*Artemia*, 210-300 µm diameter, density 1.09 g cm\(^{-3}\), 20 ppm volume concentration). Trials began 10 seconds after seeding and lasted for 3.00 minutes, and were recorded on video at 240 frames s\(^{-1}\).

A rectangular area was demarcated on the exterior of the model, including the entire anterior to posterior width of the first four gill slots, and excluding the fifth gill slot. In the first set of experiments, mesh coverage by particles was analyzed in ImageJ using color thresholding and the “Analyze Particles” tool on still frames taken from the video at five-second intervals. Because the mechanized model was in motion but needed to be in comparable positions in all analyzed frames for coverage analysis, it was not possible to use frames of the mechanized model at exact 5 s intervals. Frames analyzed for the mechanized model were sampled from no more than 0.45 s after each 5 s interval, except in the case of the final time point, when frames were used from the last stride of each mechanized trial. Proportion of mesh area covered within the demarcated region was calculated in each of these still frames. Areas of mesh in contact with exterior surfaces of branchial arches were excluded from these calculations. Care was taken in the analysis of mechanized trials to use frames of video that captured the model at an angle as close to parallel with respect to flow as possible. We used SPSS (IBM SPSS Statistics, Version 24) to conduct a two-
way repeated measures ANOVA to compare particle coverage of the mesh throughout the trial, and for the purposes of comparison, frames from mechanized trials were compared with frames from control trials sampled at precise 5 s intervals.

For the second set of experiments, the model gape was blocked after the completion of three-minute control and mechanized trials and four-minute control and mechanized trials, which were again conducted with 1.20 g of brine shrimp cysts. We rinsed *Artemia* cysts from the model into a Nalgene 310-4000 filter holder fitted with a previously weighed Nalgene 205-4045 membrane filter (0.45 µm pore size), then dried the filter membrane and retained cysts for at least 48 hours in a drying oven (Cat. No. 400, Chicago Surgical & Electrical Co.) at 37º C. Dried cysts from each trial were weighed after being allowed to cool for five minutes. To compare captured particle masses, we conducted a nonparametric two-way ANOVA after performing an aligned rank transformation (ART) on our data using the ARTool package in RStudio (RStudio version 1.0.136, Wobbrock et al. 2011). The response variable used was the mass of captured particles as a proportion of particle mass initially seeded into the flow tank.

**Pressure and Flow Speed**

To measure pressure and flow speed, three 2.38 mm diameter holes were drilled in the model, two of them in the portion anterior to the first gill slot, and the third through the first branchial arch. Each of these holes was fitted with a polyethylene cannula (1.57 mm inner diameter, 2.08 mm outer diameter,
Intramedic PE-205) through which thermistor flow probes or pressure transducers were inserted. The cannulae anterior to the first gill slots were oriented approximately perpendicular to the interior surface of the model, and were positioned opposite each other on either side of the anterior-posterior midline, and ventral to the model's lateral midline. The cannula through the first branchial arch was oriented so that the opening protruded through the posterior surface of the arch. Each cannula was flush with the interior surface of the model.

To measure flow speed, we used a probe constructed using a glass bead thermistor (1.09 mm diameter, 112-101BAJ-01, Fenwal Electronics) and connected to a circuit modified from LaBarbera and Vogel (1976). We measured pressure using a Millar Mikro-tip SPC-330 catheter pressure transducer (1.0 mm) and a PCA-2 preamplifier and calibration unit. Both the flow speed and pressure were sampled at 200 Hz by a Sonometrics TRX-4A/D convertor. In previous studies (Patterson 1991, Smith and Sanderson 2008) this circuit with a glass bead thermistor of this size was described as having a frequency response of approximately 5 Hz, meaning events less than 200 ms in duration may not be detected consistently.

Flow speed and pressure were recorded from 30-second stationary controls in each cannula. Three replicates of 90 s readings were taken of the mechanical models from each cannula. To assess whether a higher frequency signal appearing in the readings was an artifact of the model mechanism, we
also conducted a trial in which two 90 s recordings were taken from both anterior cannulae simultaneously.

Flow speed and pressure readings were analyzed by subsampling 75 seconds of data from each stationary control and mechanized trial. The first two and final two strides in each of the 90 s recordings were excluded from the 75 s subsamples. We filtered the subsamples using a bandpass Fourier filter in the ifilter: Interactive Fourier filter function (version 4.1) add-on for MATLAB (version R2016a, 0.0.0.341360). The filter band had a range of 1.8-2.6 Hz. We also used the ifilter function’s power spectrum analysis tool to compare signal strength of various signal frequencies in mechanized and control trials.

To associate regions of pressure and velocity waveforms with particular portions of the model’s stride, we conducted trials in which either flow speed or pressure was recorded at the model’s left anterior cannula using the same setups as described above. Pressure and flow speed data were synchronized with video recorded using an Ektapro Hi-Spec motion analyzer 1012/2 (250 frames s⁻¹, Kodak, San Diego, CA), which was prompted to begin recording by a TTL-compatible trigger signal connected to the A/D convertor. This allowed events in the video to be associated with concurrent pressure and flow speed data. Peaks and troughs of pressure and flow speed were recorded, and were detected in 7-point moving averages of recorded pressure traces. When equivalent maximum or minimum pressure values occurred at multiple time points within a single stride, the earliest point with that value was used. We recorded the times of the model’s observed yaw maxima to either side, and calculated the mean delay

19
between maximum yaw angles and recorded flow speed and pressure minima and maxima. The flow speed and pressure recordings made during these trials were used to calculate the differences between maximum and minimum recorded values in a stride.

**Flow Patterns**

We used dye streams in the models in both mechanized and stationary control trials in order to visualize and qualitatively describe flow patterns through the model. Videos were recorded (240 frames s\(^{-1}\)) as rhodamine water-tracing dye (Cole Parmer) was slowly introduced by syringe through the same polyethylene cannulae used for flow speed and pressure experiments.
Results

Particle Capture and Transport

In experiments to quantify mesh coverage by particles during 3-minute trials, stationary control trials exhibited significantly greater coverage of the portion of mesh analyzed than mechanized trials ($p = 0.0005$), and there were also significant interactions for time and between treatment and time ($p < 0.0005$ for both, two-way repeated measures ANOVA, $n = 4$ trials per group, 36 measurements per trial, Fig. 2). After the completion of 3-minute trials, models in control trials averaged $86.6\% \pm 7.3\%$ (95% CI) mesh coverage, while models in

![Graph](image)

Figure 2. Proportion of analyzed area of mesh covered by Artemia cysts during 3-minute trials. Coverage for trials in each treatment is shown at five-second intervals throughout trials. Bars represent 95% confidence intervals of the mean measured mesh coverage of trials within each group at a given time point. Thick blue and red lines represent the means of mechanized and control groups, respectively.
mechanized trials averaged 23.5% ± 21.4% (95% CI) mesh coverage. In mechanized trials, particles were most often captured on the mesh along the posterior margins of each gill slot. By contrast, captured particles were more evenly distributed across the mesh in control trials (Fig. 3).

No differences were detected between the masses of particles captured in control and mechanized trials ($p = 0.113$), between three-minute and four-minute trials ($p = 0.787$), or for the interaction between mechanization and duration ($p = 0.589$, non-parametric ART two-way ANOVA, $N = 12$, $n = 3$). Three-minute control trials captured a mean of 11.2% ± 1.2% SD of seeded mass and four-minute control trials captured a mean of 10.7% ± 0.2% SD of seeded mass. Three-minute mechanized trials captured a mean of 11.4% ± 0.3% SD, and four-minute mechanized trials captured a mean of 11.9% ± 0.9% SD of seeded particle mass (Fig. 4). However, some *Artemia* cysts were observed to have settled to the bottom of the flow tank in all trials. Consequently, reduction of

Figure 3. Particle coverage of the mesh is shown in lateral view after three minutes in a mechanized trial (A) and a stationary control trial (B). In control trials, particles collected fairly evenly across much of the mesh. In mechanized trials however, particles tended to collect in large aggregations in the posterior portions of the gill slots, especially in the ventral portion of the model. Scale bars represent 1 cm.
particle density in the tank, as well as the small sample size, may have contributed to these results.

**Pressure and Flow Speed**

In all pressure and flow speed experiments, mechanized trials exhibited cyclical fluctuations at a frequency of 2.2 Hz, corresponding with the frequency of the model's strides (Fig. 5). In stationary control trials, no regular fluctuations in pressure or flow speed were observed or detected in Fourier transform analyses. Signals processed using a bandpass Fourier filter with a 0.8 Hz range centered around 2.2 Hz (Fig. 6), and a power spectrum analysis using 75 s segments of flow speed and pressure recordings (Fig. 7) both revealed that mechanized trials
experienced pronounced increases in the amplitude and power of the signal at 2.2 Hz, as expected.

Secondary peaks were also detected in pressure and flow speed mechanized trials. It remains unclear whether these secondary peaks are a consequence of vortical flow patterns, an artifact of the model mechanism, or both. However, in mechanized tests of the model in which pressure was recorded simultaneously by probes inserted through both left and right anterior

![Graphs showing pressure and flow speed recordings in mechanized trials and stationary control trials.](image)

*Figure 5. Representative pressure recordings in mechanized (A) and stationary control trials (B), and flow speed recordings in mechanized (C) and stationary control trials (D), all from the left anterior cannula. Pressure values shown are 7-point moving averages of data recorded, and are presented as deviation from the mean value of each sample series.*
cannulae, secondary peaks were recorded in comparable locations of both waveforms. These results indicate that if the secondary peaks did result from artifacts, the artifacts occurred at comparable times in both portions of the model’s stride (left and right).

By using the pressure and flow data that had been synchronized with videos of the mechanized model’s yaw maxima, we were able to determine that, when pressure is recorded at the left anterior cannula, there is a mean lag of 0.080 s (SD = 0.014 s) between the maximum yaw to the model’s right and the minimum recorded pressure in each stride, and a lag of 0.083 s (SD = 0.018 s) between the maximum yaw to the model’s left and the maximum recorded pressure in each stride (data pooled from 3 series, each of n = 44 strides for both calculations). At the same cannula, we measured a mean lag of 0.092 s (SD = 0.050 s) between the maximum yaw to the model’s right and the minimum

![Graphs showing pressure and flow speed recordings](image_url)

*Figure 6. Pressure (frames A and B) and flow speed (frames C and D) recordings that have been filtered using a 1.8 - 2.6 Hz bandpass Fourier filter, which excluded all signals of frequencies outside that range. Filtered signals from mechanized recordings are shown in frames A and C, and signals from control recordings are shown in frames B and D.*

25
recorded flow speed, and a mean lag of 0.130 s (SD = 0.033 s) between maximum yaw to the model’s left and the maximum recorded flow speed (data pooled from three series, for first calculation n = 43, 45, and 44 strides, for second calculation n = 43, 44, and 44 strides).

The mean difference between minimum and maximum pressures recorded at the anterior cannula was 0.461 mmHg (SD = 0.045 mmHg, data pooled from three series, N = 392 total calculations, two per stride, n = 113, 149, 130). The mean difference between minimum and maximum flow speeds was 5.26 cm s\(^{-1}\) (SD = 1.13 cm s\(^{-1}\), data pooled from three series, N = 394 total calculations, two per stride, n = 103, 191, 100). In one case, a stride was excluded from these calculations, because no peak in flow speed was detected.

Figure 7. Power spectrum comparisons of waveforms recorded during pressure and flow speed trials. All power analyses shown were computed using 75 s segments of recordings. Recordings from mechanized trials excluded at least the first two and final two strides of the model’s operation in a trial. Data from pressure trials are displayed in frames A and B, and data from flow speed trials are displayed in panels C and D. The frames on the left show data recorded through the cannula in the branchial arch. The frames on the right show data recorded through the anterior cannula.
in that stride, and thus the difference between the minimum and maximum values could not be calculated.

**Flow Patterns**

In control trials, sustained vortices formed downstream of all cannulae through which dye was introduced. When dye was introduced through the cannulae positioned anterior to the first gill slot, a prominent vortex formed along the anterior margin of the first gill slot (Fig. 8A). This vortex traveled continuously along the margin of the gill slot, primarily in a dorsal direction until dye dispersed. Most dye in this vortex exited the model through the mesh near the posterior-most portion of the anterior margin of the first gill slot, just above the model’s central coronal plane. This location approximately corresponds to the ceratobranchial-epibranchial joint in the paddlefish oral cavity. Dye introduced through the cannula inserted through the first branchial arch formed smaller vortices downstream. (Fig. 8B)

*Figure 8. Vortices in stationary control models. The left anterior cannula is shown in panel A, and the branchial arch cannula is shown in panel B. Vortices (V) are indicated downstream of flow. Scale bars represent 1 cm.*
vortices along the anterior margin of the second gill slot, which were made visible by the rhodamine dye only intermittently (Fig. 8B). Dye introduced at this location exited the model directly through the mesh at the anterior margin of the second gill slot, with minimal travel along the posterior surface of the first branchial arch in either the dorsal or ventral direction.

In mechanized trials, vortices that formed in the anterior portion of the gill slot repeatedly formed and shed, with entrained dye often traveling posteriorly through the model after shedding of the vortex, before exiting through the mesh (Fig. 9). These vortices tended to shed as the model yawed to the side opposite the dye stream, although in some instances, a vortex would shed only partially and rotation would persist throughout a stride. The vortices that formed along the anterior margin of the first gill slot were often accompanied by a second type of vortex that formed anterior and dorsal to the opening of the cannula in the anterior portion of the model (Fig. 9B). These vortices rotated in the same direction as the first type described, but formed less frequently, and were more

![Figure 9. Dye stream visualization of flow in a mechanized trial of the model. In frame A, a vortex (V₁) has formed on the interior of the mesh, directly behind the backwards-facing step at the anterior edge of the first gill slot. In frame B, the first vortex (V₁) has begun to become disorganized, and a second vortex (V₂) has formed anterior to the step. In frame C, both vortices are shed, and dye streams disperse downstream, tending to travel towards the posterior of the model before passing through the mesh. Frame A occurs 0.225 s before frame B, which precedes frame C by 0.104 s. Frame A precedes the maximum yaw angle by 0.096 s. Scale bars represent 1 cm.](image-url)
disorganized and shorter-lived. Vortices also briefly formed when dye was introduced through the cannula in the first branchial arch (Fig. 10). The speed at which the dye traveled in the time between exiting the model’s mesh in the second gill slot and leaving from the simulated operculum appeared to vary between portions of the model’s stride, indicating a change in the pressure gradient between the interior and exterior of the model. This dye stream appeared to move the fastest at and shortly following peak yaw towards the same side as dye introduction.

Figure 10. Dye stream visualization of flow in a mechanized trial of the model. A vortex (V) is shown in panel B, and shed through the mesh in panel C. Panel A occurred 0.067 s before the maximum yaw to the model’s left, and preceded panel B by 0.163 s. Panel B preceded panel C by 0.108 s, which occurred 0.021 s before the model’s maximum yaw to the right. Scale bars represent 1 cm.
Discussion

We found that locomotor kinematics cause regular, cyclical fluctuations in flow speed and pressure in a model ram suspension-feeding paddlefish, as well as the formation and shedding of vortices posterior to the backward-facing steps formed by simulated branchial arches. These cyclical flow dynamics resulted in the transport of food particles from the surface of the mesh simulating the gill rakers to aggregations of particles near the posterior margins of the gill slots. This reduced fouling of the filter, and moved particles to an area where they may be easier to manipulate and transport towards the esophagus. Reduction of filter fouling and increases in particle transport have been shown to result from bidirectional oscillatory flow and unidirectional pulsations in flow and transmembrane pressure in a variety of industrial and medical crossflow filtration systems (Jaffrin 2012). Analogous flow manipulations have been quantified in pump suspension-feeding fish (Sanderson et al. 1991, Callan and Sanderson 2003, Smith and Sanderson 2008). Repetitive oscillatory and pulsatile flow patterns quantified in pump suspension-feeding fish have been suggested as defouling processes (Callan and Sanderson 2003, Smith and Sanderson 2008). Whale sharks have also been observed to employ coughs at irregular intervals to clear their filter structures (Motta et al. 2010).

Previous investigations of the biomechanics of ram suspension-feeding fishes have used preserved specimens (Sanderson et al. 2016), physical models (Paig-Tran et al. 2011, Sanderson et al. 2016), and computational models (Cheer et al. 2012, Cheer et al. 2001) to study the flow of water and food particles
through the oral cavity and their interactions with gill rakers and branchial arches. However, while these studies have considered flow speed as a variable that is relevant to food particle size selectivity and the interactions between flow patterns and gill rakers, none have considered other kinematic variables associated with the undulatory locomotion used by most fish (Webb Ch. 2, 1975) as they relate to ram feeding. Sanderson et al. (1994), in the only known flow speed recordings taken from the interior of the oral cavity of live, ram suspension-feeding fish, showed that the flow speed measured during paddlefish suspension feeding (22 – 29 cm EFL) fluctuated at regular time intervals, though the cause of these fluctuations was not investigated at the time. Also, Burggren and Bemis (1992) recorded buccal pressure in a paddlefish (13.0 cm fork length) during ram ventilation and ventilation by buccal pumping, noting that pressure oscillations during ram ventilation reflected tailbeats.

Our findings indicate that in addition to the spatial organization of particle retention described in the vortical cross-step filtration mechanism of Sanderson et al. (2016), there also exists a strong temporal component to the organization of filtration mechanisms and particle retention patterns in ram suspension-feeding fish. The fluid dynamics of our model appear analogous to the unstable vortices resulting from pulsatile flow over a fixed backward-facing step (Dol et al. 2014), albeit with changes in the directionality of flow relative to anatomical structures as a consequence of yawing. A temporospatial cross-step filtration model that includes a kinematic mechanism for aggregating food particles at the posterior portion of the gill slot is applicable in both the paddlefish and the
basking shark, two species which have convergently evolved rib-and-groove arrangements of their branchial arches. In these species, the gill rakers abduct from the distal portion of the branchial arch to form the porous floor of a groove that is roughly rectangular in cross-section (Imms 1904, Matthews and Parker 1950, Sanderson et al. 2016, Sims 2008). This temporal organization of the cross-step model also clarifies the function of the mucus-secreting cells present on the branchial arch epithelium along the bases of the gill rakers in both the paddlefish and the basking shark. These mucus-secreting cells were previously presumed to be related to feeding, but, as the rakers themselves do not have mucus, were apparently of limited utility (Paig-Tran et al. 2014, Rosen and Hales 1981, Matthews and Parker 1950, Sims 2008). Since our study demonstrates that fluid dynamics result in the transport of particles to the posterior margin of the gill slot, the mucus secretions of the branchial arch may function to form aggregations of food particles and mucus into a bolus or string that can be easily manipulated.

Although our experiments were conducted using a physical model of a rib-and-groove branchial arch structure, our results may also be applicable to teleost fishes using more typical crossflow filtration mechanisms (Sanderson et al. 2001). The ram suspension-feeding mechanisms in teleosts are not well studied compared with pump suspension feeding in teleost fishes that rely on suction, but the arrangement of the gill rakers on the branchial arches tends to be very different from the rib-and-groove arrangement of paddlefish and basking sharks. Instead of having gill rakers that protrude from the distal portions of the branchial
arces, the gill rakers of ram suspension-feeding teleosts are attached to the medial edges of the arches (Sanderson et al. 1996, Sanderson et al. 2016). However, in the pump suspension-feeding blackfish (*Orthodon microlepidotus*, Cyprinidae, Sanderson et al. 1991) and blue tilapia (*Oreochromis aureus*, Cichlidae, Smith and Sanderson 2008), regular fluctuations in flow speed have been recorded that were similar to those we measured in our physical model as well as those that Sanderson et al. (1994) measured in live paddlefish. Furthermore, influence of crossflow is strong enough in pump suspension-feeding cichlids that fish may feed effectively even when gill rakers are surgically removed (Smith and Sanderson 2007, Smith and Sanderson 2013, Drenner et al. 1987). Transport of food particles may be facilitated in an analogous manner in teleost ram suspension feeders by kinematically modulated hydrodynamic processes that influence pressure gradients and flow patterns, which in turn minimize contact with gill rakers or resuspend captured particles from the filter apparatus.

In addition to aiding in the manipulation of food towards the esophagus, the clearing of food particles from the surface of the filter apparatus during ram suspension feeding is likely to allow more efficient respiration by permitting a larger volume of water to flow through the gill slots than would otherwise be possible. This would at least partially resolve the functional conflict between respiration and suspension feeding that Feder et al. (1984) demonstrated in *Xenopus* larvae, and Sanderson et al. (1994) predicted to exist in fish, in which maximizing prey capture reduces the effectiveness of respiratory structures.
Burggren and Bemis (1992) suggested that ram suspension feeding permits more efficient use of energy in ram ventilators, and that the evolution of suspension feeding in the *Polyodon* genus (Grande and Bemis 1991) was made more likely by the “preadaptation” of ram ventilation because simultaneous ram feeding and ventilation reduces the metabolic costs of both foraging and opercular pumping. This view would be further supported by showing that clearing of gill rakers by flow dynamics associated with swimming kinematics increases respiratory efficiency compared to rakers clogged with food particles.

**Ecological Implications**

Because swimming during ram suspension feeding is much more metabolically expensive than routine swimming as a result of the increased drag that results from swimming with a large open gape (James and Probyn 1989, Durbin et al. 1981), ram suspension feeders require certain threshold densities of zooplankton to feed at a net energy gain (Sims 1999, Sims 2000). These prey threshold densities are measurable in several different ways, yielding relatively consistent results in mass of prey per volume of water (Sims 1999). However, Sims (2000a) also noted that basking sharks swim more slowly during suspension feeding than the speeds at which they had been predicted to maximize net energy gain based on evidence from teleost ram suspension feeders. This was partially attributed to the increased effect of skin friction drag in basking sharks, but could also be partly explained by increased functionality of the filter apparatus, at least for small particles, at lower speeds. Using a computational
fluid dynamics model, Cheer et al. (2012) demonstrated that the gill rakers of ram suspension feeders are less leaky at low Reynolds numbers. Because flow speeds, as well as pressure and the incident angle of flow are constantly changing in association with swimming kinematics, it is possible that these variable affect the size selectivity of particles smaller than the inter-raker space.

Rubenstein and Koehl (1977) have previously hypothesized that filter-feeding organisms might move more quickly than when cruising as a way to increase particle capture using filtration mechanisms, and Pepin et al. (1988) provide strong empirical evidence that this is the case in ram suspension-feeding Atlantic mackerel (Scomber scombrus). However, this was proposed in the context of filter fibers capturing particles by inertial impaction, with retention often facilitated by mucus, or sieving (Shimeta and Jumars 1991). In the context of crossflow filtration, in which fish retain food particles primarily by inertial lift and shear-induced diffusion as water passes across, rather than through, a filter apparatus (van Dinther et al. 2011), there could be combinations of flow speeds, and particle sizes and densities, that might allow the capture of more, rather than fewer, small particles at slower speeds. Furthermore, although the inter-raker distances are unavailable for S. scombrus, if the relationship between body length and inter-raker distance is similar to that observed in the congeneric Pacific mackerel (S. japonicus, Molina 1996), then all size classes of plankton used by Pepin et al. (1988) would have been larger than the inter-raker space, and thus easily retained by the fish irrespective of swimming speed.
Paig-Tran et al. (2011) found that retention of particles smaller than their model’s mesh pore diameter improved at higher flow speeds (60 cm s\(^{-1}\) compared to 45 cm s\(^{-1}\)). However, they compared capture at the filter mesh in their models, and in a fish employing crossflow filtration, particles smaller than the inter-raker space would not tend to be captured at the surface of the rakers. In addition, Paig-Tran et al. only measured particles captured at their model’s simulated esophagus from 45 cm s\(^{-1}\) trials. Particle separation has also been shown in a biomimetic crossflow filter design to decline at increasing, but biologically relevant flow speeds (Hung et al. 2012). Therefore, because it is now clear that swimming kinematics including yaw and heave result in changes in intra-oral flow speeds and patterns, it is conceivable that fish adjust swimming kinematics in order to modulate mechanical size selectivity of the filter apparatus and increase the amount of prey captured, especially when available zooplankton are smaller than the inter-raker distance. This hypothesis could be tested in laboratory experiments by quantifying the swimming speeds and kinematics of ram suspension-feeding fish in aquaria seeded with zooplankton prey of sizes larger than the fishes’ inter-raker space, and comparing these with the speeds and kinematics of fish ram suspension-feeding in aquaria seeded with zooplankton prey of sizes smaller than the fishes’ inter-raker space.

Determining with as much detail as possible how ram suspension feeders are able to filter prey from the water column is of substantial importance, as many of these species are of great economic importance (Food and Ag. Org. of the UN 2016) and serve as ecologically important links between phytoplankton or
zooplankton and larger piscivorous predators. As a consequence, the ability to develop more accurate predictive models of population growth and decline would be of value to both commercial fisheries and conservation efforts. For example, Annis et al. (2011) specifically report that more information regarding size selectivity in Atlantic menhaden would be likely to produce population and growth models more capable of responding to trends in plankton communities. Without a better understanding of the mechanics of filter feeding, however, this remains difficult, especially due to the complex nature of prey selection. Researchers have shown, for instance, that texture in addition to size is important in determining the ability of a fish to capture certain prey items, that suspension-feeding fish prey on the eggs and larvae of other fish (Garrido et al. 2007), and that in some closely related species, including the menhaden Brevoortia gunteri and B. patronus, seasonal partitioning of food resources takes place on the basis of prey size, despite similar gill raker structures (Castillo-Rivera 1996).

**Future Directions**

Our experiments have shown that there is strong integration between feeding and swimming kinematics in ram suspension-feeding fish. However, to build a more complete understanding of ram feeding and how ram suspension-feeding fish respond to and influence aquatic and marine communities in light of this work, it is necessary for researchers to conduct experimental studies using model ram suspension-feeding teleosts to show the impact of swimming kinematics on feeding in species without the rib-and-groove filter structure of
paddlefish and basking sharks. Ideally, these studies should incorporate investigations of various kinematic parameters including swimming speed, yaw angles, phase difference between yaw and heave, and stride frequency. Computational fluid dynamics (CFD) studies incorporating kinematic motions are necessary to determine the interactions between water and the branchial arches and gill rakers of ram suspension feeders. Similar physical model-based, CFD, or live animal studies of kinematic influence on feeding in the whale shark, megamouth shark, and mobulid rays, all of which have filtration structures that are highly divergent from those in the paddlefish and basking shark (Paig-Tran and Summers 2014), should also be pursued. Finally, CFD studies that investigate how locomotor kinematics influence size selectivity of filter structures, especially for very small particles, would establish a strong link between the functional morphology and biomechanics of ram suspension-feeding fishes with the ecological implications of this mode of feeding.
References


