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MUCUS ENTRAPMENT OF PARTICLES BY A SUSPENSION-FEEDING TILAPIA (PISCES: CICHLIDAE)

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Summary

A miniature fiberoptic endoscope was used to observe the processes of particle encounter and retention inside the buccopharyngeal cavity of suspension-feeding tilapia. Small particles (38 μm to 1.0 mm in diameter) were trapped in strands and aggregates of mucus, which usually slid posteriorly on the ceratobranchials of arches I–IV towards the esophagus while the fish pumped water through the buccopharyngeal cavity. During stage 1 of periodic reversals of water flow inside the buccopharynx, mucus-bound particles usually lifted off the arch surfaces and travelled a short distance in an anterior or anterodorsal direction. During stage 2 of a reversal, the mucus usually resumed travel in a posterior or posteroventral direction and exited the field of view. Mucus was present less often during feeding on large particles (3–10 mm in diameter) than on small particles, and large particles were rarely observed to be attached to mucus. We discuss the advantages to suspension-feeding fishes of using aerosol filtration by mucus entrapment rather than sieving, and predict that many cichlid and cyprinid suspension feeders that consume bacteria and phytoplankton use mucus for aerosol filtration.

Key words: tilapia, *Oreochromis niloticus*, suspension-feeding, mucus entrapment, aerosol filtration, gill rakers.

Introduction

Suspension-feeding fishes filter massive volumes of water to extract minute prey (approximately 5 to >3000 μm) that are too small to be sensed and engulfed as individual particles (reviews in Sanderson and Wassersug, 1993; Gerking, 1994). These fishes, belonging to at least eleven orders, have extensive effects on the structure and function of freshwater ecosystems (review in Northcote, 1988) and comprise approximately one-third of the total world fish catch (FAO, 1993). Despite this ecological and economic importance, the mechanisms of particle retention used by suspension-feeding fishes remain unknown for all but two cyprinid species (Hoogenboezem *et al.* 1991; Sanderson *et al.* 1991).

The sites and ways in which food particles are retained are of interest for four primary reasons. First, the method of retention determines the particle selectivity of the filtering apparatus (Rubenstein and Koehl, 1977). The ability to select particles according to particle characteristics such as size, density, surface charge, toxicity and nutrient content can be affected strongly by the method of retention. For example, species that retain particles on the slits between the branchial arches (e.g. van den Berg *et al.* 1994*a*) may be able to prevent the retention of toxic algal cells by simply increasing interarch distances, whereas species that retain particles on sticky, mucus-covered oral surfaces (e.g. Sanderson *et al.* 1991) may be unable to avoid completely the retention of undesirable particles, even during respiration (Beveridge *et al.* 1993; Keshavanath *et al.* 1994; Sanderson and Cech, 1995). Second, the selection pressures on prey to escape retention are likely to be dependent on the mechanism of particle retention. Third, in the absence of information on particle retention mechanisms, interspecific comparisons of the morphological features relevant to suspension feeding cannot be made. Fourth, the size–frequency distribution of the retained particles is the proximal parameter that is the most important in shaping the effects of suspension-feeding fishes on aquatic communities. The ability of a suspension-feeding species to retain the smallest phytoplankton, for example, could profoundly affect lacustrine plankton community ecology and marine plankton patchiness.

To expand on the limited research that has been conducted on particle retention mechanisms in suspension-feeding fishes (Hoogenboezem *et al.* 1991; Sanderson *et al.* 1991), we studied the sites and ways that food particles are retained by suspension-feeding tilapia (Cichlidae: Tilapiini). Suspension-feeding tilapia have substantial impacts on phytoplankton and zooplankton community structure (e.g. Drenner *et al.* 1984*b*, 1987*a*; Vinyard *et al.* 1988). They can also have dramatic

adverse effects on native fish populations when introduced into freshwater and marine environments (e.g. Randall, 1987; De Vos *et al.* 1990; Ogutu-Ohwayo, 1990; McKaye *et al.* 1995). However, they are valuable components of commercial fisheries and the aquaculture industry (Pullin, 1991; FAO, 1993; Kolding, 1993).

To determine the sites and mechanisms of particle retention in a suspension-feeding tilapia species (*Oreochromis niloticus*), we made direct observations inside the buccopharyngeal cavity of actively feeding fish using a fiberoptic endoscope inserted through the preopercular bone. In freshwater lakes, *O. niloticus* consumes primarily phytoplankton (Moriarty and Moriarty, 1973) and benthic diatoms (Onyari, 1983), with small quantities of crustaceans and insect larvae (Onyari, 1983; Getachew, 1993). In the laboratory, *O. niloticus* has been shown to ingest suspended bacteria (Beveridge *et al.* 1989), planktonic cyanobacteria (Northcott *et al.* 1991; Beveridge *et al.* 1993; Keshavanath *et al.* 1994) and periphytic cyanobacteria (Dempster *et al.* 1993). Here we provide a quantitative analysis of particle movement and entrapment in the buccopharyngeal cavity.

Materials and methods

Oreochromis niloticus (Linn.) were obtained from pure stock raised at an aquaculture company in the United States. Fish were held in 110 l aquaria at a temperature of 25–28 °C and maintained on a diet of Tetramin flakes and frozen adult brine shrimp. Endoscopy experiments were performed with four specimens (15.5–25.3 cm standard length, SL). Fish were anesthetized with MS-222 and a polyethylene cannula (2.15 mm i.d., 3.25 mm o.d., Intramedic PE 280) was implanted into the buccopharyngeal cavity through a hole drilled in the preopercular bone. The cannula fitted snugly into the hole, so that water could neither exit nor enter through the hole. A flange (approximately 1 mm wide) around the circumference of one end of the cannula lay almost flush with the tissue on the roof of the buccopharyngeal cavity. Externally, the cannula was threaded through a second flanged polyethylene cannula (2.5 cm long, 3.76 mm i.d., 4.82 mm o.d., Intramedic PE 360) that prevented it from slipping into the buccopharyngeal cavity. A piece of neoprene rubber (0.8 cm×0.8 cm) was placed between the second cannula and the skin, to reduce chafing. The fish was then returned to its aquarium.

A flexible fiberoptic endoscope (Olympus ultrathin fiberscope type 14, 1.4 mm o.d., 1.2 m working length, 75 ° field of view, 0.2–5.0 cm depth of field) was threaded through the cannula. The endoscope was attached to a CCD video camera (Canon Ci-20R) connected to a Hi-8 video player/recorder (Sony EVO-9700, 30 frames s^{-1}). A high-intensity light source (Olympus Helioid ALS-6250) provided light to the endoscope. Periodically during the experiments, the endoscopic image became obscured by a thin film of mucus on the endoscope lens. When this occurred, the endoscope was removed from the cannula and the tip was rinsed in fresh water.

During experiments on three specimens, external video tapes were taken using a hand-held Hi-8 camcorder (Sony CCD-TR81, 30 frames s^{-1}) for correlation with the endoscopic video tapes. The external and endoscopic video tapes were synchronized by recording externally and endoscopically while the high-intensity light source was turned on, off and on again at the beginning of each recording session. The light could be seen clearly in both the external and endoscopic video tapes.

To analyze the endoscopic and external video tapes, the video tapes were examined frame-by-frame using a Sony EVO-9700 player/recorder with a jog/shuttle. A RasterOps 24 STV color display board was used to digitize images for publication from the video tapes. The digitized endoscopic images were processed by convolving them with a mean kernel (7×7 pixels) using NIH Image 1.52. This process removed the fine honeycomb pattern that was caused by individual fibers in the fiberoptic bundle.

Data were recorded during feeding on whole Tetramin flakes (particles 3–10 mm in diameter), a slurry composed of finely crushed Tetramin flakes mixed with water (particles 0.1–1.0 mm in diameter) and frozen adult brine shrimp (*Artemia* sp., 4 mm long). Polystyrene microspheres (Bio-Rad Bio-Beads SM-2, 38–63 μm) and brine shrimp cysts (210–300 μm) were introduced as tracer particles alone and in combination with the above foods. Whole Tetramin flakes were placed in the aquarium by hand. The crushed Tetramin was added to the water above the fish through a short piece of tubing attached to a 30 ml syringe. *Artemia* sp., microspheres and brine shrimp cysts were also introduced to the aquarium using a 30 ml syringe. Prey were engulfed by the fish as they drifted down through the water column or lay on the bottom of the aquarium. The order in which prey types were added to the aquarium varied with each experiment so that each prey type was introduced first during at least one experiment.

By comparing video tapes taken prior to and following cannula implantation, we determined that the presence of the cannula did not substantially affect the sequence or duration of the kinematic events that occurred during feeding. Data were collected within 1–2 days of cannula implantation, during which time the fish remained healthy. At the conclusion of the experiment, the cannula was removed under anesthesia. The cannula insertion sites subsequently healed.

In addition to the experiments on live specimens, the endoscope was inserted into a dead specimen and an anesthetized specimen for confirmation of the identification of the buccopharyngeal structures that were visible through the endoscope. Manipulation of the dead and anesthetized specimens showed that opercular abduction during respiration and feeding resulted in an almost imperceptible ventral rotation of the field of view. This rotation did not interfere with the analysis of buccopharyngeal or particle movements.

Results

Feeding kinematics

From the preopercular insertion site, the endoscope entered

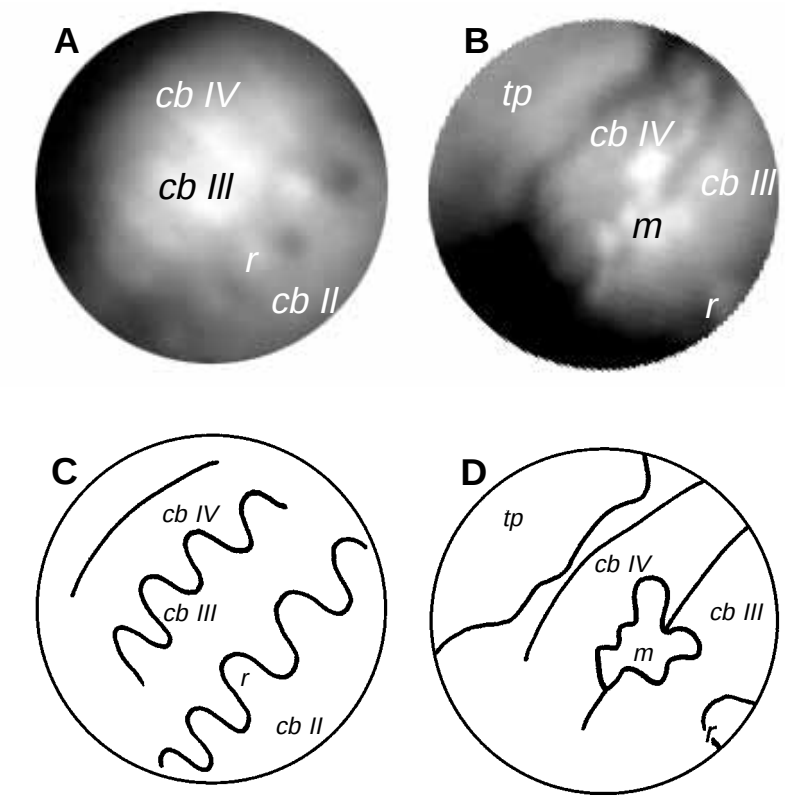

Fig. 1. Endoscopic images that have been digitized from Hi-8 video tapes and image-processed (top), with line drawings of the images showing major features (bottom). Anterior of the fish is to the left. (A,C) A row of gill rakers (*r*) on the second branchial arch (*cb II*) is visible in the foreground. The bases of these rakers are 0.5 mm wide. Light from the endoscope is reflecting from rakers on ceratobranchial III (*cb III*). The individual rakers on ceratobranchial IV (*cb IV*) cannot be discerned in this image. (B,D) A single raker from ceratobranchial II is visible in the foreground. Light is reflecting from particles that have been retained in a mucus aggregate (*m*). The mucus is resting on ceratobranchials III and IV. *tp*, tissue pad on the roof of the pharynx. (C) Line drawing of the image in A. (D) Line drawing of the image in B.

the buccopharynx immediately lateral to the left tissue pad located on the roof of the pharynx. This position was 4.0–4.8 cm posterior from the tip of the oral jaws, approximately 75 % of the distance between the oral jaws and the esophagus. The left ceratobranchials of arches II–IV could be seen clearly (Fig. 1). The left ceratobranchial of arch I could be seen intermittently. The gill rakers appeared as projections from the arches. The microbranchiospines (see Beveridge *et al.* 1988*a*,*b*) were obscured by the gill rakers and by the arches themselves. Occasionally, during feeding, the arches and interior of the operculum on the right side of the specimen could be viewed in the background.

O. niloticus suspension-fed on all three prey types by using a repetitive series of suctions (pump suspension feeding, see Lazzaro, 1987), during which water entered the mouth, continued posteriorly past the buccopharyngeal region and then exited from the opercular slits. This flow pattern was interrupted periodically by the generation of a flow from posterior to anterior. This 'backward' flow, which we term stage 1 of a reversal, occurred as the oral jaws were closed, the premaxillae were protruded, the hyoid was abducted and the opercula were adducted. A reversal was distinct from a cough or a spit (see Liem, 1984, and references therein) because water did not exit from the oral jaws.

A typical bout of suspension feeding involved 2–3 pumps at a rate of approximately 3 pumps s^{-1}, followed by one or two reversals and a resumption of pumping. This general pattern continued for 30–40 s and was followed by approximately 5 s of buccopharyngeal movements that were similar to the prey processing reported by Sanderson *et al.* (1991, 1994). The pattern of pumps and reversals differed with prey type (K. L. Ackermann and S. L. Sanderson, in preparation).

The oral and opercular movements observed during a pump (Fig. 2; Table 1) were similar to the kinematics described for the generation of slow inertial suction during particulate feeding by a number of non-suspension-feeding cichlid species (e.g. Liem, 1980). In the external video tapes, the mandible abducted, the premaxillae protruded and the hyoid abducted during a pump. Concurrently, the branchial arches were seen to abduct in the endoscopic video tapes. This branchial abduction increased the distance between the pharyngeal roof and the arches. Following opercular abduction, the mandible, premaxillae and hyoid were adducted. In the endoscopic video tapes, the branchial arches were observed to return to a position near the pharyngeal roof after the opercula had adducted. Particles were seen to flow posteriorly throughout the pump, except for a very slight anterior movement that occurred at the end of some pumps.

Frame-by-frame analysis of the external video tapes showed that a mean of 11 video frames (N=6, range 9–14 frames) elapsed between the onset of hyoid abduction at the beginning of a pump and the onset of hyoid adduction at the conclusion of a pump (Table 1). A similar analysis of the endoscopic video tapes taken synchronously with the external video tapes showed that the mean number of video frames that elapsed between the onset of branchial arch abduction at the beginning of a pump and the onset of branchial arch adduction at the end of a pump was 11 frames (N=6, range 7–14 frames).

Reversals were characterized by an abrupt change in kinematics, both internally and externally. A reversal could

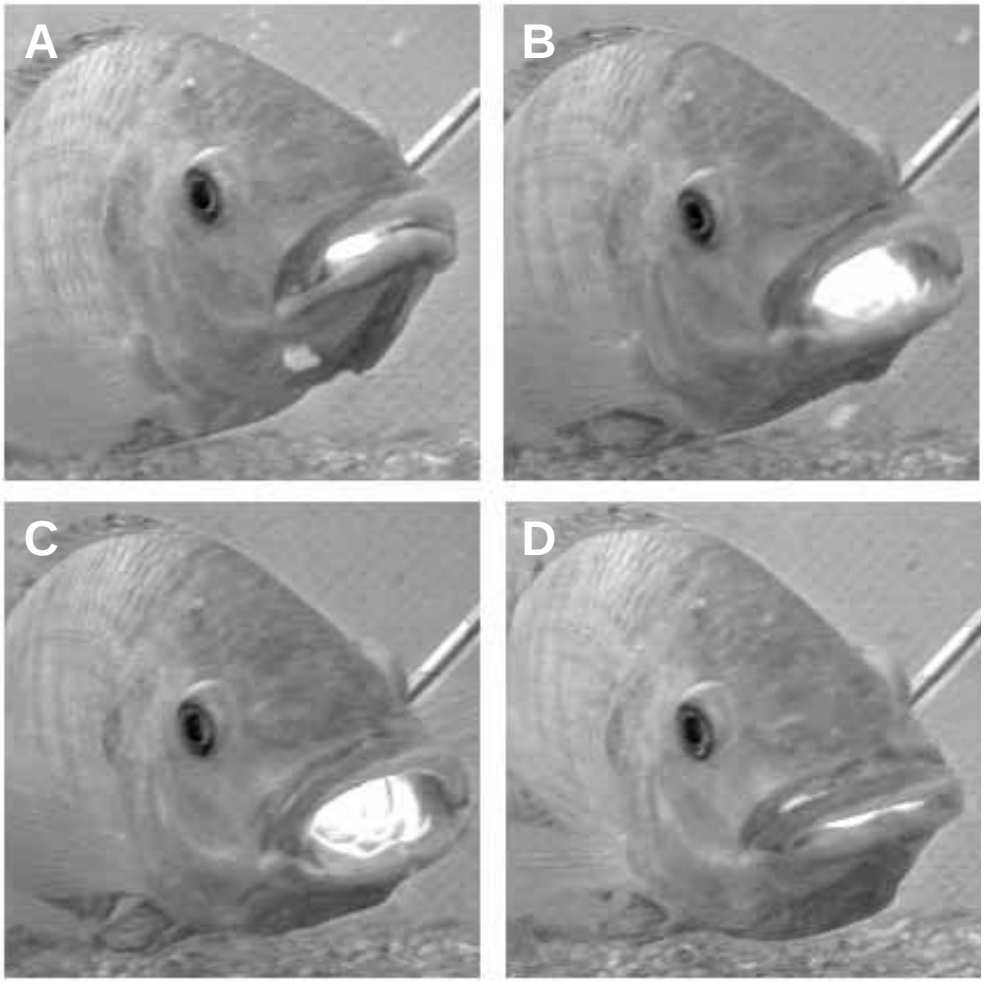

Fig. 2. Video images illustrating the sequence of movements observed during a typical pump (see Table 1). The cannula through which the endoscope is threaded can be seen at the upper right. Light from the endoscope is illuminating the interior of the buccopharynx. The duration of the sequence is 0.4 s. The fish is 20.5 cm SL.

Table 1. *The oral and opercular movements that were observed during a pump in* Oreochromis niloticus

External video tapes	Endoscopic video tapes	Particle flow
Mandible abducts Premaxillae protrude Hyoid abducts	Branchial arches abduct	From anterior to posterior
Opercula abduct	Mean duration of hyoid abduction = 11 frames (range 9–14) Mean duration of branchial abduction = 11 frames (range 7–14)	From anterior to posterior
Mandible adducts Premaxillae retract Hyoid adducts Opercula adduct	Branchial arches adduct	From anterior to posterior

The mean durations of hyoid and branchial abduction and the ranges of these durations are given in numbers of video frames (N=6). Recordings were made at 30 frames s^{-1}.

Particles were seen to flow posteriorly throughout a pump.

occur immediately following a pump or a previous reversal. In both cases, the opercula were abducted during the pre-reversal period. At this point, the branchial arches were adducted and the particle flow was in a posterior direction. During stage 1 of a reversal, the premaxillae protruded, the hyoid abducted and the opercula adducted (Fig. 3; Table 2). Internally, there was a pronounced abduction of the arches, and flow reversed so that particles were often observed to move in an anterior or

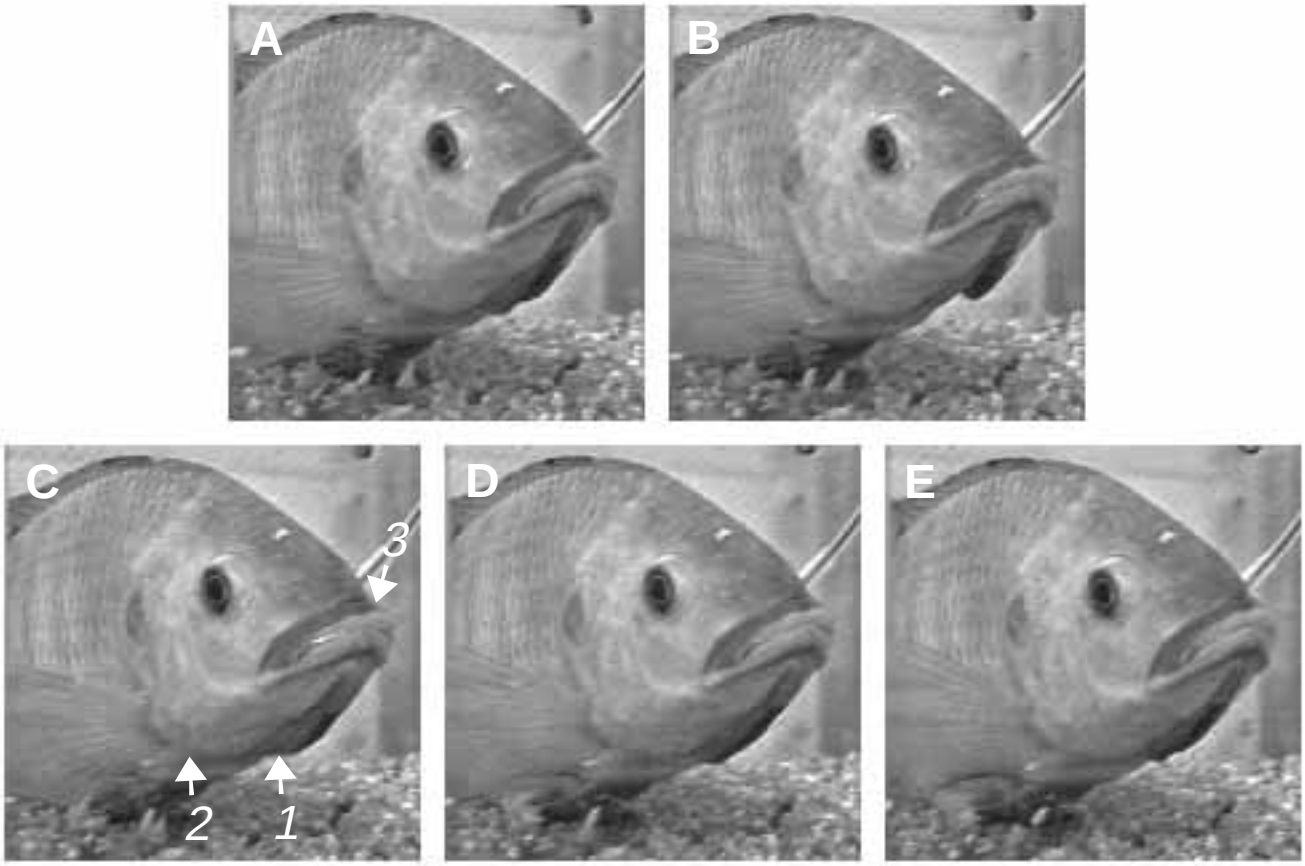

Fig. 3. Video images illustrating the sequence of movements observed during a typical reversal. Stage 1, during which the hyoid abducts, the opercula adduct and the premaxillae protrude, is shown in A, B and C. Arrows in C indicate (1) maximum hyoid abduction, (2) maximum opercular adduction and (3) maximum premaxillary protrusion. Stage 2, during which the hyoid adducts, the opercula abduct and the premaxillae retract, is shown in D and E. The duration of the sequence is 0.3 s. The fish is 20.5 cm SL.

Table 2. *The oral and opercular movements that were observed during a reversal in* Oreochromis niloticus

External video tapes	Endoscopic video tapes	Particle flow
Pre-reversal Mandible adducted Premaxillae retracted Hyoid adducted Opercula abducted	Branchial arches adducted	From anterior to posterior
Reversal stage 1 Mandible adducted Premaxillae protrude Hyoid abducts Opercula adduct	Branchial arches abduct	From posterior to anterior (flow reversal)
	Mean duration of hyoid abduction = 3 frames (range 2–4) Mean duration of branchial abduction = 3 frames (range 2–6)	
Reversal stage 2 Mandible adducted Premaxillae retract Hyoid adducts Opercula abduct	Branchial arches adduct	From anterior to posterior

The mean durations of hyoid and branchial abduction and the ranges of durations are given in numbers of video frames (N=14). Recordings were made at 30 frames s^{-1}.

During stage 1, particles reversed direction inside the buccopharyngeal cavity and flowed from posterior to anterior.

anterodorsal direction. During stage 2 of a reversal, the premaxillae retracted, the hyoid adducted and the opercula abducted. Internally, the arches were seen to adduct, and the flow resumed in a posterior or posteroventral direction.

Frame-by-frame analysis of the external video tapes showed that a mean of three video frames (N=14, range 2–4 frames) elapsed between the onset of hyoid abduction in stage 1 of a reversal and the onset of hyoid adduction in stage 2 (Table 2). Quantitative analysis of the endoscopic video tapes taken synchronously with the external video tapes showed that the mean number of video frames that elapsed between the onset of branchial abduction during stage 1 and the onset of branchial adduction during stage 2 was three frames (N=14, range 2–6 frames). Thus, reversals were significantly shorter in duration than pumps, in terms of external kinematics (one-way ANOVA; F=254.7; d.f.=1, 18; P<0.0001) as well as internal kinematics (one-way ANOVA; F=91.8; d.f.=1, 18; P<0.0001).

Origin and movement of mucus

As pointed out by Beninger *et al.* (1992), mucus is transparent and, therefore, a thin layer could adhere to the surface of structures without being apparent visually. During feeding in *O. niloticus*, however, a single strand of mucus or an irregularly shaped aggregate of mucus was often observed on the surfaces of the arches that form the pharyngeal floor (Fig. 1B,D). These strands and aggregates reflected light from the endoscope and appeared to be somewhat opaque.

Particles became entrapped in the mucus, as evidenced by the movement of multiple particles as a unit when water flow moved the mucus strands and aggregates. Numerous particles that were caught in the mucus maintained their spatial arrangement with respect to each other as the mucus slid along or lifted off the arches. In contrast, particles that were not entrapped in mucus moved independently of each other and of the mucus strands and aggregates. Mucus was not observed during respiration in the absence of food.

To examine the origins and fates of the mucus, video tapes of ten strands or aggregates for each of three individual fish and for each of two prey types (whole Tetramin flakes and finely crushed Tetramin flakes) were observed frame-by-frame. The locations where these 60 strands or aggregates were first observed through the endoscope are presented in Table 3. 50 % of the strands or aggregates originated on the left ceratobranchials of arches II–IV. The other 50 % originated anterior to the field of view of the endoscope and moved into view during a pump. Mucus was never observed to originate posterior to the field of view and move anteriorly into view. There were no obvious differences between strands and aggregates in site of origin, nor were there noticeable differences between the sites of origin of mucus that was observed during feeding on whole flakes *versus* finely crushed flakes (Table 3).

All but one of the 60 mucus strands or aggregates ultimately left the field of view by travelling in a posterior, posteroventral or posterodorsal direction during pumps and stage 2 of reversals. Presumably, this mucus moved to the esophagus and was swallowed, since mucus was never observed to enter the field of view from a posterior direction and was never observed to exit *via* the opercula. One mucus aggregate left the field of view while travelling in an anterior direction during stage 1 of a reversal and was not observed subsequently. This aggregate may then have travelled posteriorly on the right side of the buccopharyngeal cavity, as the right side could only rarely be seen through the endoscope.

38 (63 %) of the strands and aggregates lifted from the branchial arches prior to leaving the field of view in a posterior or posteroventral direction (Table 4). In contrast, 21 (35 %) of the strands and aggregates appeared to slide along the arch surfaces, without lifting, as they exited from the field of view in a posterior direction. In 33 of the 38 cases in which the mucus lifted off the branchial arches, this occurred during stage 1 of reversals. Pumps caused the mucus to lift from the arches in five cases only (Table 4).

To assess the roles of pumps and reversals in transporting the mucus, the action of the fish that occurred while the mucus moved out of the field of view was determined by viewing the video tapes frame-by-frame. Mucus was observed to leave the field of view during four actions: (1) a pump that followed a pump, (2) a pump that followed a reversal, (3) a reversal that followed a pump, and (4) a reversal that followed a reversal.

Table 3. *The locations where 60 mucus strands and aggregates were first observed through the endoscope during feeding of* Oreochromis niloticus *on whole or finely crushed Tetramin flakes*

Flake type	Form of mucus	Origin				Total
		Arch II	Arch III	Arch IV	Anterior	
Whole	Strand	1	1	3	11	16
	Aggregate	1	9	0	4	14
Crushed	Strand	2	2	3	12	19
	Aggregate	2	6	0	3	11
	Total	6	18	6	30	60

50 % of the strands or aggregates originated on the left ceratobranchials of arches II–IV. The other 50 % originated anterior to the endoscope's field of view and moved into view during a pump.

Table 4. *The position, with respect to the arches, of 59 mucus strands and aggregates as they were transported out of the field of view in a posterior or posteroventral direction during pumps and stage 2 of reversals in* Oreochromis niloticus

Action of fish	Position of mucus	
	Lifted off arch surfaces	Sliding along arch surfaces
Reversal	33	4
Pump	5	17
Total	38	21

Table 5. *The actions of the fish that were recorded as 59 mucus strands and aggregates moved out of the field of view during pumps and stage 2 of reversals that occurred in* Oreochromis niloticus *while feeding on whole and finely crushed Tetramin flakes*

		Action of fish			
Flake type	Form of mucus	Pump after a pump	Pump after a reversal	Reversal after a pump	Reversal after a reversal
Whole	Strand	4	1	7	4
	Aggregate	1	3	7	2
Crushed	Strand	6	3	7	3
	Aggregate	1	3	4	3
	Total	12	10	25	12

In general, when stage 2 of reversals was responsible for transporting the mucus out of the field of view, these reversals occurred immediately following a pump (25 of 37 cases, Table 5). Pumps that were responsible for transporting the mucus out of the field of view occurred with approximately equal frequency following a previous pump *versus* following a reversal (Table 5). The action by the fish that resulted in transport of the mucus out of the field of view did not seem to be related to the type of flake consumed (whole *versus* finely crushed) nor to the form of mucus (strand *versus* aggregate) (Table 5).

The time a mucus strand or aggregate stayed in the field of view was 1.0±1.0 s (mean ± S.D., range 0.2–4.9 s, *N*=60). The mucus often remained in view during one or more pumps or reversals, before exiting from view towards the posterior pharynx. Whereas Tables 4 and 5 summarize data on the mucus strands and aggregates as they were transported out of the field of view, Table 6 summarizes the movements of these strands and aggregates during all pumps and reversals prior to the transport of the mucus out of the field of view. During pumps that were not responsible for moving the mucus out of view, mucus usually either stayed in place on the arches or slid posteriorly along the arch surfaces in the field of view (Table 6). During reversals that did not transport the mucus out of view, mucus usually lifted from the arch surfaces and resettled on the arches further posteriorly or posteroventrally in the field of view (Table 6).

Endoscopic observations of particle movement

Not all particles were retained by the mucus strands and aggregates that were observed. During pumps, particles that were not caught in mucus travelled in a slightly convex or slightly concave path towards the posterior pharynx. Particles did not bounce off the roof, sides or floor of the buccopharynx.

We compared the percentage of finely crushed Tetramin flakes and microspheres that were retained in mucus with the percentage that moved as individual particles towards the posterior pharynx during the periods when mucus was observed through the endoscope. Each particle that was observed during a pump while a mucus strand or aggregate was present was classified as being retained in the mucus or as travelling independently. In this manner, we classified all of the particles that passed the endoscope (*N*=97) while a total of eight strands or aggregates were observed. 54 % of these particles were retained in mucus, while 46 % travelled independently towards the posterior pharynx.

Relationship between mucus presence and particle size

Endoscopic video tapes from three specimens were analyzed frame-by-frame to quantify the presence of mucus during feeding (Fig. 4). Although finely crushed flakes could be seen clearly through the endoscope, they were never observed to stick to the arches unless mucus was observed. In a total of 20 176 frames (672.5 s) of pumps and reversals recorded while the three fish were actively feeding on a slurry of finely crushed Tetramin flakes, mucus was observed in 5288 frames (176.3 s). In contrast, in 28 066 frames (935.5 s) of active feeding on whole Tetramin flakes, mucus was observed in only 838 frames (27.9 s). Thus, mucus was observed 26.2 % of the time during feeding on the finely crushed flakes, but only 3.0 % of the time during feeding on whole flakes.

The mucus that was observed during feeding on finely crushed flakes contained particles 97.9 % of the time. The mucus that was observed during feeding on whole flakes contained particles 90.9 % of the time. When mucus that

Table 6. *Net movements of 60 mucus strands and aggregates in the field of view during each pump and reversal that occurred prior to transport of the mucus out of the field of view in* Oreochromis niloticus

	Movement of mucus				
Action of fish	None	Slide posteriorly on arch surfaces	Lift, move posteriorly or posteroventrally	Lift, resettle in same place	Lift, move anteriorly
Pump	21	14	1	0	0
Reversal	6	1	28	6	3
Total	27	15	29	6	3

During pumps, mucus usually either stayed in place on the arches or slid posteriorly along the arch surfaces in the field of view. The net effect of stage 1 and stage 2 of reversals was usually the lifting of mucus from the arch surfaces and the resettling of the mucus on the arches further posteriorly or posteroventrally.

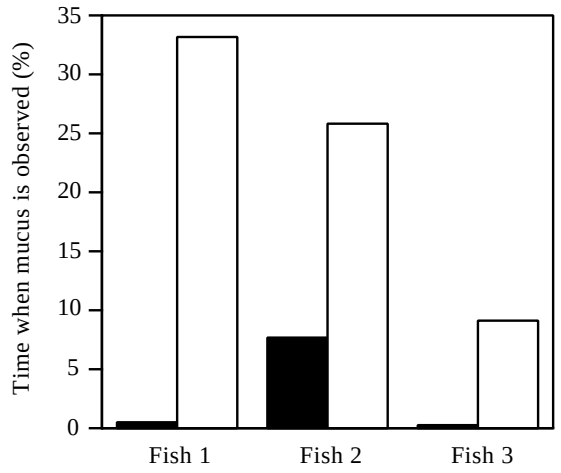

Fig. 4. Percentage of total observation time during which mucus was observed in endoscopic video tapes recorded from three *Oreochromis niloticus* during feeding on whole Tetramin flakes (filled columns) or finely crushed flakes (open columns).

contained particles was observed during feeding on whole flakes, the retained particles were usually small pieces of flakes (0.1–1.0 mm in diameter) that had broken off the whole flakes after they had been introduced to the aquarium. Whole flakes were seen attached to the mucus strands or aggregates only 4.5 % of the total time that mucus was observed with retained particles during feeding on whole flakes. However, whole flakes rested briefly on the arches without moving when no mucus was observable in 6315 frames (210.5 s, 22.5 % of the time during feeding on whole flakes). These whole flakes remained on the arches for approximately 0.07–0.5 s during one or more pumps.

When the fish were suspension-feeding on adult brine shrimp, more mucus was observed than when the fish were feeding on whole flakes, but less than when the fish were feeding on finely crushed flakes. The irregular outlines of the brine shrimp, as well as the appendages that had separated from the body, reflected light in a manner that hampered visualization of the mucus strands and aggregates through the endoscope. Consequently, the percentage of time during which mucus was present while the fish were feeding on brine shrimp could be determined only approximately. A conservative estimate is that mucus was observable in 117 frames (3.9 s) out of a total of 2838 frames (94.6 s) that were analyzed for one individual during feeding on adult brine shrimp. Mucus was therefore observed to be present approximately 4 % of the time during feeding on adult brine shrimp.

Discussion

Hypothesized particle retention mechanisms

Potential mechanisms for particle retention in suspension-feeding fishes involve sieving and/or a form of aerosol filtration. During sieving, filtering elements form a mesh that retains all particles larger than the pores of the mesh. In aerosol filtration, a number of fluid mechanical processes can result in contact between particles and a filtering element that has adhesive properties (Rubenstein and Koehl, 1977; LaBarbera, 1984; Shimeta and Jumars, 1991). Particles are then retained by adhesion to the sticky surfaces of the filter.

Hypothesized methods of sieving in suspension-feeding fishes include the retention of particles (1) between the lateral rakers on one arch and the medial rakers on an adjacent arch (sawtooth model: e.g. Sibbing, 1991; van den Berg *et al.* 1994*a*), (2) on the surfaces of two adjacent rakers on a single arch (comb model: e.g. Drenner *et al.* 1984*a*; Gibson, 1988; van den Berg *et al.* 1992), (3) in the channel between two adjacent rakers on a single arch (unreducible-channel model: e.g. Hoogenboezem *et al.* 1991; van den Berg *et al.* 1994*a*), (4) in the channel between two adjacent medial rakers on a single arch while a lateral raker from an adjacent arch moves, under muscular control, into the channel (reducible-channel model: e.g. Hoogenboezem *et al.* 1991, 1993; van den Berg *et al.* 1994*b*), (5) between secondary projections from the gill rakers, termed denticles or branchiospinules (e.g. de Ciechomski, 1967; Friedland, 1985) and (6) between the denticulate area of the pharyngobranchial organ and the gill rakers in mugilid fishes (e.g. Harrison and Howes, 1991). An additional hypothesized method of particle retention in fishes involves the capture of particles between the floor of the pharynx and local muscular bulges of the palatal organ in cyprinids (e.g. Sibbing and Uribe, 1985; Sibbing, 1988).

Aerosol filtration in suspension-feeding fishes, involving mucus entrapment of particles that are small enough to fit through the gaps between the filtering elements (Northcott and Beveridge, 1988) or mucus entrapment of particles on a non-porous sheet of tissue (Sanderson *et al.* 1991; Bauchot *et al.* 1993), has been proposed rarely. However, a number of researchers have suggested that mucus is used by fishes to aggregate and transport particles that have already been retained by sieving (e.g. Kuznetsov, 1977; Friedland, 1985; Harrison and Howes, 1991; Hoogenboezem and van den Boogaart, 1993).

Particle retention has been observed directly in two cyprinid species only. Using X-ray cinematography, Hoogenboezem *et al.* (1991) observed that zooplankters to which a small iron sphere (1 mm) had been glued were retained in the channels between the gill rakers of *Abramis brama*. Sanderson *et al.* (1991) used a fiberoptic endoscope to observe that the gill rakers of *Orthodon microlepidotus* served to guide particle-laden streams of water to the palatal organ on the roof of the pharyngeal cavity, where particles were retained in mucus aggregates. Particles were not retained on the gill rakers of *Orthodon microlepidotus*. Thus, the functions of gill rakers and mucus in suspension-feeding fishes have not been resolved. Interspecific and interfamilial differences in suspension-feeding mechanisms deserve further study.

Hypotheses for particle retention in tilapia

Both sieving and aerosol filtration mechanisms have been

proposed for suspension-feeding tilapia. Microbranchiospines are small protuberances located primarily in a single row along the lateral faces of branchial arches II–IV in many suspension-feeding and non-suspension-feeding cichlid species (Beveridge *et al.* 1988*a*,*b*). They have been hypothesized to comb mucus-bound particles from the medial face of the adjacent arch in suspension-feeding tilapia (Whitehead, 1959) or to act as a fine sieve while the gill rakers act as a coarse sieve (Gosse, 1956).

Owing to the presence of mucus cells in the oral and pharyngeal epithelium of suspension-feeding *Oreochromis esculentus*, Greenwood (1953) suggested that particles are entrapped by mucus into aggregates that are retained by a sieve formed from gill rakers. Northcott and Beveridge (1988) quantified the presence and types of mucus cells in the pharyngeal epithelium of *O. niloticus*. They proposed that mucus forms a net in the pores of the branchial sieve. Beveridge *et al.* (1988*a*) dissected specimens of the suspension-feeding tilapia *O. aureus* that had been placed in an aquarium with water-insoluble Sudan Black dye. While some individual dye particles (2–25 μm) and clumps of particles were found in mucus on the microbranchiospines, particles were retained primarily in mucus on the gill rakers of the dead specimens (Beveridge *et al.* 1988*a*). However, Drenner *et al.* (1987*b*) reported that surgical removal of the gill rakers and microbranchiospines from suspension-feeding *Sarotherodon galilaeus* (Cichlidae: Tilapiini) did not affect ingestion rates of zooplankton (>112 μm) or ingestion rates and size selectivity of synthetic microspheres (4.3–70.3 μm), indicating that these structures are not responsible for particle retention in this tilapia species.

Functions of pumps and reversals in Oreochromis niloticus

Pump suspension feeding by *O. niloticus* caused water that contained particles to be sucked into the buccopharyngeal cavity. During a sequence of pumps, individual particles as well as mucus strands and aggregates containing small particles moved towards the posterior pharynx. In general, pumps transported the mucus by causing it to slide along arch surfaces (Tables 4, 6). During stage 1 of a reversal, water flow in a posterior-to-anterior direction usually lifted the mucus from the branchial arches. During stage 2 of a reversal, the mucus was usually transported posteriorly or posteroventrally (Table 6). Lifting of the mucus during stage 1 may allow it to be moved more readily during stage 2 and/or lifting may prevent mucus from slipping through the spaces between adjacent arches.

The significantly longer durations of hyoid and branchial abduction during pumps relative to reversals (Tables 1, 2) may be related to the functions of pumps and reversals. Long pump durations involving substantial mandibular and hyoid depression are responsible for transporting massive volumes of water through the oral cavity for filtration. In contrast, abrupt movements of short duration function during reversals to lift mucus that contains food particles and transport it the short distance to the esophagus (Tables 4–6).

During pumps as well as during reversals, the close correspondence between the duration of hyoid abduction observed externally and the duration of branchial arch abduction observed endoscopically (Tables 1, 2) is due to the attachment of the ventral ends of the branchial arches to the hyoid apparatus. Branchial arch abduction is a component of the oral movements that result in oral cavity volume increases during pumps and reversals. The role of branchial arch abduction in regulating water velocity between the arches during filtration deserves further study.

Aerts *et al.* (1986) used X-ray cinematography of *O. niloticus* feeding on radio-opaque pellets to determine that engulfed food particles travelled directly posteriorly through the buccopharyngeal cavity and impacted on the pharyngeal jaws. They noted that, when particles occasionally shifted slightly laterally towards the opercular cavity, ‘a series of small and fast buccal and opercular abducting and adducting movements’ caused the particles to return to the midline of the pharynx between the upper and lower pharyngeal jaws. Our endoscopic observations are consistent with the reports of Aerts *et al.* (1986).

Movements similar to the reversals described here have been noted by Sibbing *et al.* (1986) in suspension-feeding and bottom-feeding carp (*Cyprinus carpio*, Cyprinidae). They reported the occurrence of ‘closed protrusion’, when the upper jaw was protruded and the opercula were adducted while the oral jaws remained closed, and suggested that this ‘back-washing’ served to resuspend food and inorganic particles during the process of the selective retention of food particles. During feeding on zooplankton, this positioning movement was thought to gather zooplankters from the branchial sieve and move them to the posteromedial portion of the pharynx (Sibbing *et al.* 1986). These closed protrusions in carp and reversals in tilapia may serve similar functions. In *O. niloticus*, however, dense inorganic particles (e.g. gravel from the bottom of the aquarium) were held immediately posterior to the lower jaw while reversals separated the organic from the inorganic particles by suspending the less dense organic particles only. Our endoscopic observations of particle retention in the buccopharynx did not indicate a mechanism for the separation of organic and inorganic particles that are of similar size and density.

Three surfperch species in the non-suspension-feeding family Embiotocidae engage in oral winnowing, which involves the generation of a posterior-to-anterior flow of water by simultaneous premaxillary protrusion, hyoid depression and opercular adduction (Drucker and Jensen, 1991). This prey-handling behavior is used to separate benthic prey items from non-digestible substratum material. Whereas winnowing is accompanied by a reduced oral gape that allows water to exit from the oral cavity (Drucker and Jensen, 1991), closed protrusion in carp (Sibbing *et al.* 1986) and reversals in *O. niloticus* are characterized by mandibular adduction that closes the oral jaws completely. This mandibular adduction may prevent the escape from the oral cavity of minute suspended food particles and mucus.

Aerosol filtration in Oreochromis niloticus

Larger particles, such as whole Tetramin flakes (3–10 mm in diameter) and adult brine shrimp (4 mm long), appeared to elicit limited secretion of mucus (Fig. 4). However, small, finely crushed flakes (0.1–1.0 mm in diameter) stimulated the secretion of mucus sufficiently to form strands and aggregates of mucus-bound particles on the branchial arches (Fig. 1B,D). We have limited evidence that the extent of mucus secretion may also be related to feeding motivation, since one individual, fish 3 (Fig. 4), did not feed as vigorously during the experiments as did the other two.

Our data suggest that *O. niloticus* may be able to adjust mucus secretion rates in response to particle size. Smaller prey (e.g. bacteria, resuspended benthic diatoms and phytoplankton) may elicit substantially more mucus secretion than larger prey (e.g. crustaceans and insect larvae). In our endoscopic observations, whole Tetramin flakes were rarely seen attached to mucus but appeared to be retained by sieving on the arches. Whereas the mucus that was observed during feeding on finely crushed flakes contained small food particles 97.9 % of the time, the mucus that was observed during feeding on whole flakes contained whole flakes 4.0 % of the time. Thus, larger prey may be retained primarily by sieving while smaller prey may be retained in mucus.

If whole Tetramin flakes were rarely observed to be retained in mucus, what was the function of the mucus strands and aggregates that were produced during feeding on whole flakes (Table 3; Fig. 4)? Even when whole flakes were the first prey type that was fed to the fish during an experiment, softening of the flakes in the aquarium and disturbance of the gravel substratum by the fish introduced small food particles into the water. These small particles were observed through the endoscope to be caught in mucus strands and aggregates while the fish fed on whole flakes. In fact, small food particles rather than whole flakes were retained in mucus during 86.9 % of the time that mucus was observed while the fish were feeding on whole flakes. Thus, although the drag on whole flakes appeared, in most cases, to be sufficient to prevent the adhesion of whole flakes to the mucus, mucus secretion may have been stimulated by the presence of small food particles in the water.

Mucus was observed to be present during 9–33 % of the total observation time when three fish specimens were feeding on finely crushed Tetramin flakes (Fig. 4). If mucus is used to retain small particles, why was mucus not present during most of the period of active feeding on small particles? A possible explanation is that the entire right side of the oral cavity, as well as the left ceratobranchial of arch I, were visible only infrequently through the endoscope, and the posterior pharynx and left epibranchials were never visible. The above percentages do not include times when mucus may have been present in those regions that were inaccessible to the endoscope.

In their histological study of *O. niloticus*, Northcott and Beveridge (1988) noted that small goblet-shaped mucus cells located primarily on the anterior face and sides of branchial arches I–IV secreted neutral glycoproteins or a mixture of neutral and acidic glycoproteins, whereas large clavate mucus cells located on the posterior trailing section of the gill rakers on the four anterior arches secreted acidic glycoproteins. They suggested that the more viscous acidic glycoproteins from the clavate cells served as a net in the pores of the branchial sieve, while the mucus from the goblet-shaped cells might be involved in transport of the retained particles to the posterior pharynx (Northcott and Beveridge, 1988). The exact sites on each arch where mucus originated could not be determined in our study, owing to the angle of view through the endoscope and to the movements of the branchial arches and the mucus. We do not know whether the glycoprotein composition of strands differs from that of aggregates. However, our data do not indicate separate functions for strands *versus* aggregates.

Mucus entrapment is a common method for particle retention and/or transport in a variety of vertebrate and invertebrate suspension feeders, including species of tadpoles, ammocoetes, ascidians, larvaceans, bivalves and polychaetes (e.g. Flood and Fiala-Médioni, 1981; Riisgård *et al.* 1992; Morris and Deibel, 1993; Ward *et al.* 1993; references in Sanderson and Wassersug, 1993). At an ultrastructural level, the mucus nets studied in invertebrate suspension feeders are a mesh consisting of regularly spaced longitudinal and transverse threads of mucus (e.g. Jørgensen *et al.* 1984). The pore dimensions reported for invertebrate mucus nets range from approximately 0.2 to 2.0 μm (e.g. Flood and Fiala-Médioni, 1981; Flood, 1991).

Owing to the rectangular-mesh arrangement of invertebrate mucus nets, researchers have suggested that sieving is occurring (e.g. Jørgensen *et al.* 1984; Flood *et al.* 1992), although ‘affinity binding’ to the mucus threads has also been proposed (Flood and Fiala-Médioni, 1982). The ultrastructure of the mucus observed in *Oreochromis niloticus* and *Orthodon microlepidotus* has not been examined. Irrespective of its ultrastructure, the mucus in *Oreochromis niloticus* is likely to serve as an aerosol filter, rather than a sieve, for a number of reasons. First, the mucus is in the form of strands and irregular aggregates that change shape frequently during pumps and reversals, rather than in the form of orderly sheets. Second, the mucus is located primarily on the branchial arches rather than in the gaps between the arches, so that water is unable to pass through most of the mucus. Third, the primary direction of water flow in the buccopharynx, as indicated by particle trajectories, is parallel to the mucus that is on the branchial arches, rather than through any pores that might be present in the mucus.

Particle encounter mechanisms and size selectivity

Of the five particle encounter mechanisms that may operate during aerosol filtration (Rubenstein and Koehl, 1977; Shimeta and Jumars, 1991), our data indicate that direct interception may be of the greatest importance in particle capture by *Oreochromis niloticus*. Particles may simply encounter a mucus strand or aggregate by direct interception when they pass within one particle radius of such mucus. In a second potential mechanism of particle encounter, termed inertial

impaction, the inertia of particles results in their deviation from streamlines and their subsequent encounter with the filter elements as water flows around the elements. Inertial impaction is likely to be less important than direct interception in *O. niloticus* because the predominant direction of flow through the buccopharyngeal cavity is parallel to the mucus strands and aggregates. Gravitational deposition, electrostatic attraction and diffusive deposition may not be as important as direct interception for particle capture in *O. niloticus*, since the flow velocity observed in the endoscopic video tapes did not appear to be low enough for these mechanisms to operate efficiently (S. L. Sanderson, in preparation). The efficiency of particle capture by these latter three mechanisms decreases as the flow velocity increases, whereas the efficiency of direct interception is not affected by flow velocity (Rubenstein and Koehl, 1977). A complete analysis of the importance of these mechanisms in *O. niloticus* will require calculations of encounter rates as well as efficiencies.

Tilapia are reported to be size-selective suspension feeders. In the presence of polystyrene microspheres (7–52 μm), *Oreochromis aureus* (4.3–18.7 cm SL) retained disproportionately more larger microspheres than smaller microspheres (Drenner *et al.* 1984*b*). The percentage of microspheres (4.3–70.3 μm) removed from the water by *Sarotherodon galilaeus* (3.9–6.0 cm SL) reached an asymptote at 20 μm (Drenner *et al.* 1987*b*), although larger specimens (12.6–14.3 cm SL) did not show size selectivity (Drenner *et al.* 1987*b*). There has been some question about whether a mucus entrapment system in tilapia would be capable of exhibiting such particle size selectivity (Fryer and Iles, 1972; Drenner *et al.* 1987*b*; Northcott *et al.* 1991). However, aerosol filtration theory predicts particle selectivity on the basis of particle size (e.g. Rubenstein and Koehl, 1977). For direct interception to take place, small particles have to be closer to the filtration surface than larger particles, in order to encounter that surface. Thus, small particles will encounter the filtration surface less frequently than larger particles at the same concentration, owing simply to their smaller radius. Consequently, disproportionately fewer small particles will be ingested. Similarly, if inertial impaction occurs during suspension feeding in *O. niloticus*, disproportionately fewer small particles will be ingested than larger particles of the same density (Rubenstein and Koehl, 1977).

During sieving, 100 % of the particles above a threshold size equivalent to the pore size of the sieve are predicted to be retained (Rubenstein and Koehl, 1977). Particle ingestion data (5.7–75.0 μm) for suspension-feeding silver carp (*Hypophthalmichthys molitrix*, Cyprinidae) are consistent with an aerosol filtration mechanism but not with sieving, since substantially less than 100 % of the particles greater than the reported mesh size of the gill rakers were retained (Smith, 1989). Particles (40.1–75.0 μm) that were 2–3 times larger than the distance between gill rakers (12–26 μm) were retained at more than twice the rate of particles (26.5 μm) that were slightly larger than the maximum distance between gill rakers (Smith, 1989), indicating that the gill rakers were not functioning as a sieve.

Table 7. *Advantages of aerosol filtration by suspension-feeding fishes compared with sieving*

Aerosol filtration by suspension-feeding fish	Sieving by suspension-feeding fish
Extraction of small particles (approximately 5–50 μm) involves lower drag	Extraction of small particles involves higher drag
Wide range of particle sizes retained	Few particles below threshold size retained
Filters less prone to clogging	Filters more prone to clogging
Particles already bound in mucus for transport to esophagus	Separate process required to prepare particles for transport to esophagus

Advantages of aerosol filtration by suspension-feeding fishes

There are at least 56 suspension-feeding fish species in 16 families for which the sites and mechanisms of particle retention are unknown (Sanderson and Wassersug, 1993; S. L. Sanderson, unpublished data). Of the two species in which the filtration mechanism has been identified previously, one uses gill rakers for sieving (*Abramis brama*, Cyprinidae; Hoogenboezem *et al.* 1991) whereas the other uses mucus entrapment on the pharyngeal roof for aerosol filtration (*Orthodon microlepidotus*, Cyprinidae; Sanderson *et al.* 1991). We have determined that *Oreochromis niloticus* uses mucus entrapment on the branchial arches for aerosol filtration. We propose that aerosol filtration by suspension-feeding fishes has a number of advantages compared with sieving (Table 7), particularly at the lower end of the size spectrum of particles consumed by suspension-feeding fishes.

When a suspension feeder moves water actively between filter elements, the drag force on the filter imposes an energetic cost (Fenchel, 1980; LaBarbera, 1981). The clearance rate (volume of water cleared of particles per unit time) is predicted to decrease with decreasing porosity of the filter (Fenchel, 1980). Thus, a suspension-feeding fish using a sieve with a mesh size fine enough to retain small particles (approximately 5–50 μm) is expected to incur a higher energetic cost for a given clearance rate than one using an aerosol filter, because an aerosol filter is capable of retaining small particles with widely spaced filter elements or with filter elements that the flow passes over rather than through. A second advantage of an aerosol filter is that a wide range of particle sizes may be retained. In fact, aerosol filters can retain small particles by aerosol filtration and large particles by sieving. In contrast, sieves are predicted to retain 0 % of the particles that are smaller than the spaces between filter elements (Rubenstein and Koehl, 1977; LaBarbera, 1984). A third advantage of aerosol filters is that, although they can saturate with particles, they are less prone to clogging than are sieves because water does not have to pass through an aerosol filter for particle retention to occur. For example, aerosol filtration can occur on a non-porous surface (e.g. Sanderson *et al.* 1991). Finally, an advantage of aerosol filtration involving mucus entrapment by

suspension-feeding fishes is that the particles are already bound in mucus for transport (Sanderson *et al.* 1991; present study). Particles that are retained on a sieve must then be removed from the filtration surface and transported to the esophagus (e.g. Hoogenboezem and van den Boogaart, 1993). This transport is one of the most problematic and least understood processes involved in vertebrate suspension feeding (Sanderson and Wassersug, 1993).

Given the advantages listed in Table 7, we predict that many cichlid and cyprinid suspension feeders that retain bacteria and phytoplankton use mucus entrapment for aerosol filtration, rather than sieving. Further research using fiberoptic endoscopy is needed to test this hypothesis.

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