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Functional Morphology of the Branchial Basket Structures Associated with Feeding in the Atlantic Menhaden, *Brevoortia tyrannus* (Pisces: Clupeidae)

KEVIN D. FRIEDLAND

Structures of the branchial basket associated with filter-feeding in Atlantic menhaden, *Brevoortia tyrannus* were studied with light and scanning electron microscopy. Surface ultrastructure, epithelial organization and gross morphology were analyzed with respect to food-particle capture, transport of food from point of capture to point of ingestion and potential gustatory reception. Predictions of the fluid dynamics involved in particle capture and handling were based on histological characterization of the mucous glycoproteins produced in the epithelium of the feeding structures. Branchiospinules, the sites of small-particle capture, lack mucous cells, suggesting that food is captured primarily by mechanical sieving. Particles probably move down the length of the raker blade by two methods: (1) one side of the raker has mucous cells and particles apparently are held in dynamic balance as they are transported the length of the blade, either over, or complexed with, a mucous layer; (2) the other side of the raker lacks mucous cells and particles apparently move down the blade in a vortex formed in a recessed groove. The arch sections where most filtration takes place have a cutaneous fold over the mesial raker elements. The epithelium on the lateral surface of the cutaneous fold is rich in mucous cells. The positioning of this surface relative to the base of the filtering raker suggests that particles coming off the raker blades are held in a dynamic balance and are transported back into the buccal cavity over, or complexed with, a mucous layer. Particles apparently cascade to the more interior arches via the epi-ceratobranchial joint. The mucus associated with the higher energy filtering environments was more viscous. Taste buds were found in two locations in the buccal cavity: those on the glossohyal probably are mechanoreceptors, while those on the crest of the fifth branchial arch probably are chemoreceptors.

ATLANTIC menhaden, *Brevoortia tyrannus* (Latrobe), are microphagous planktivores in the estuaries and coastal waters of the eastern United States. Although they play a important ecological role because of their ability to filter-feed on extremely small planktonic organisms (Durbin and Durbin, 1975; Friedland et al., 1984), relatively little information exists on their feeding mechanics. In this paper I describe the ultrastructure and other morphological aspects of the filter-feeding apparatus. From these observations I propose a number of hypotheses for food particle capture and transport.

The exact mechanism of particle capture by menhaden is not understood. The early work of Peck (1893) suggests that the secondary projections off the gill rakers, the branchiospinules (terminology after Monod, 1961), are the principal site of particle capture. Copious mucus production associated with the branchial basket, in which the rakers reside, led Peck to conjecture that mucus plays a role in food particle capture. Since models of aerosol feeding, retention of particles smaller than the apertures of the capture structure, rely on mucus covered filter elements, the particle retention strategies proposed for marine sedimentary and filter-feeders may be applicable to particle capture strategies in menhaden (Rubenstein and Koehl, 1977).

Food particles retained at various positions on the gill rakers must be transported to the base of the raker blade before they can be passed farther back in the buccal cavity for ingestion. Particles larger than the spaces between the raker blades can simply tumble along the leading edges of the rakers to the base. But particles smaller than the spaces between the blades, but nonetheless filterable (Durbin and Durbin, 1975; Friedland et al., 1984), cannot utilize this meth-

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od of transport. As yet, no one has described how these particles reach the base of the rakers.

From the base of the gill rakers, food particles must traverse part of the axis of the branchial arches before reaching the epi-ceratobranchial joint. Opposite the base of the lateral rakers, which perform the filtering, is a structure composed of the much smaller, non-filtering mesial rakers and a soft-tissue extension of these rakers called the cutaneous fold. This arrangement is present in the hypobranchial and ceratobranchial arch sections, the sections where most of the filtration takes place. Peck (1893) originally hypothesized that the lateral surface of the fold was a ciliated membrane where particles collected by the rakers could be moved farther back into the buccal cavity. In many cases sedimentary feeders, which feed on food particles of similar size to those fed on by menhaden, rely on ciliated tracts to transport particles (Jorgensen, 1983). Most workers continued to assume that menhaden used this type of transport (Gunter and Christmas, 1960), until Gusev (1964) examined the surface of the fold and found no cilia. The only alternative mechanism for moving fine particles over a nonciliated surface is one that relies on hydrodynamics, of which there are few precedents in biological systems (Wassersug, 1972).

The feeding process in menhaden is considered passively selective (Durbin, 1979), a result of anatomical characteristics of the feeding apparatus. Selection on a chemoreceptive criterion, in the case of menhaden detecting and feeding in an area of high phytoplankton productivity and biomass as opposed to less productive conditions, has not yet been demonstrated. Selective feeding based on olfactory reception would appear to be at least physiologically possible in menhaden since the fish have well developed nasal rosettes. Gustatory receptors have not been described in menhaden.

Materials and Methods

Specimens of menhaden used for scanning electron microscopy (SEM) preparations were obtained from pound-net fishermen of the York River, Virginia. Tissues were immediately dissected and individually fixed in 3% gluteraldehyde in 0.1 M sodium cacodylate for one hour. Fixation was followed by three rinses in 0.1 M sodium cacodylate in 0.15 M NaCl and held in this buffer at 5 C. Tissue used for SEM was sent through two mucus stripping procedures. First, successive 24 h baths of 16% glycerol were followed by a bath of 20% ethanol as suggested for marine teleosts by Dobbs (1972). Second, the tissue was bathed in Cleland's reagent (tradename Sputolysin). The cleaned tissue was then dehydrated through a graded ethanol series and transferred to acetone for critical point drying. Dry specimens were coated with gold palladium for viewing with either an AMR-1000 or an ISI-40 scanning electron microscope.

Specimens used for light microscopy were obtained from purse-seine fishermen in North Carolina. Individual tissue was carefully dissected and fixed for 48 h in Boulin-Hollande solution (Solanki and Benjamin, 1982). The tissue was then transferred to 70% alcohol before decalcification in 5% formic acid in 80% alcohol for 7 days. Decalcified tissue was dehydrated through a graded alcohol series, cleared in terpenol for 40 h and embedded in paraffin wax at 50 C. All sections were 7 μm in thickness.

Sections were stained with hematoxylin-eosin (H-E) for structural analysis or alcian blue PAS for identification of epithelial glycoproteins. Sections for H-E staining were dewaxed, hydrated through a graded alcohol series, stained with hematoxylin, then dehydrated with alcohol. At this point the eosin stain was applied and the sections were cleared in xylene and mounted in Permount. Sections for alcian blue PAS were stained according to the methods outlined in Jones and Reid (1973). Mucous cells stained with the alcian blue PAS were classified by color after Fletcher et al. (1976). Cells were scored as red (R), red with a trace of blue (RB), blue with a trace of red (BR), or blue (B). Acid glycoproteins stain blue at pH 2.6 whereas neutral glycoproteins stain red. Cuticle-secreting cells, indistinguishable in histological sections, were not enumerated.

Results

The gill arches and rakers of menhaden collectively form a mesh through which water must pass while the fish is feeding. The outer edge of the mesh is sealed by the abutment of the rakers of the first arch against the inner surface of the opercle apparatus. Each successive inner arch abuts the cutaneous fold of the next outer arch. The fourth and fifth arch articulate to form a channel that is confluent with the epibranchial organs and in succession the esophagus (Fig. 1A). The arrangement of surfaces suggests that food particles collected at various

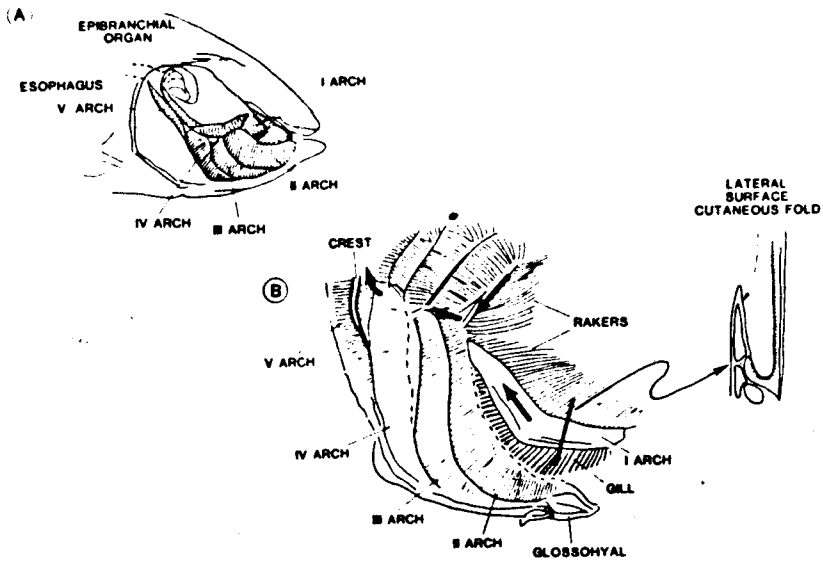

Fig. 1. A) Relative position of left side gill arches, epibranchial organ and esophagus in the buccal cavity of Atlantic menhaden, *Brevoortia tyrannus*. B) Gill arches of the left side of the branchial basket. Arrows represent proposed path followed by food particles captured on the first arch.

positions along the rakers travel toward and along the branchial arch axis, eventually converging at the epi-ceratobranchial joint (Fig. 1B). When the rakers are splayed to the spatial arrangement that would be held while feeding, a groove formed by each epi-ceratobranchial joint fits into the like structure of the next inner arch.

The branchiospinules, the smallest elements of the filtering mesh, consist of a central bony element overlaid by a thin layer of epithelial cells that is devoid of mucous cells (Fig. 2A). Surface ultrastructure of the branchiospinules (Fig. 2B) reveals a mosaic of cells identified as cuticle-secreting cells based on the distinct pattern of surface convolutions typical of cuticle-secreting cells of marine teleosts and related groups (Hossler et al., 1979; Crespo, 1982; Karlsson, 1983). The lateral edges of the branchiospinules of all arches are serrated.

The leading-edge keel of the gill raker is asymmetric in structure and the two sides apparently are subjected to different flow stresses. The raker is oriented such that one side of the keel faces anteriorly and the other faces posteriorly. The anterior side is oriented towards the prevailing direction of water flow in the buccal cavity, whereas the posterior side is in the lee of these flows. These surfaces shall be referred to as the anterior and posterior transport zones, respectively.

The anterior transport zone is a convex surface the epithelium of which is richly populated with mucous cells. The surface of the transport zone is composed of cuticle-secreting cells similar to those on the branchiospinules (Fig. 2C). Occasionally the surface manifestation of a mucous cell is observed between the cell junctions of cuticle-secreting cells (Fig. 2D). Asymmetry in the distribution of mucous cells between anterior and posterior transport zones is revealed in histological cross-section (Fig. 2A). The rich supply of mucous cells on the anterior side of the raker and the paucity on the posterior side is a consistent feature of all arches.

The anterior transport zones of the different gill arches produce different quality mucus as indicated by the results of alcian blue PAS staining of the mucous cells. The higher proportion of blue stained cells (Fig. 3) for arch I than for arch IV indicates that the glycoproteins of arch I have a higher proportion of acidic groups.

The posterior transport zone of each raker forms a groove (Fig. 2A). This groove extends along the full length of the longitudinal axis of the raker blade (Fig. 2E). As with the anterior transport zone the surface of the posterior zone is composed of cuticle-secreting cells.

The lateral and mesial raker elements form a continuous tract which abruptly terminates at the transition to the lateral surface of the cu-

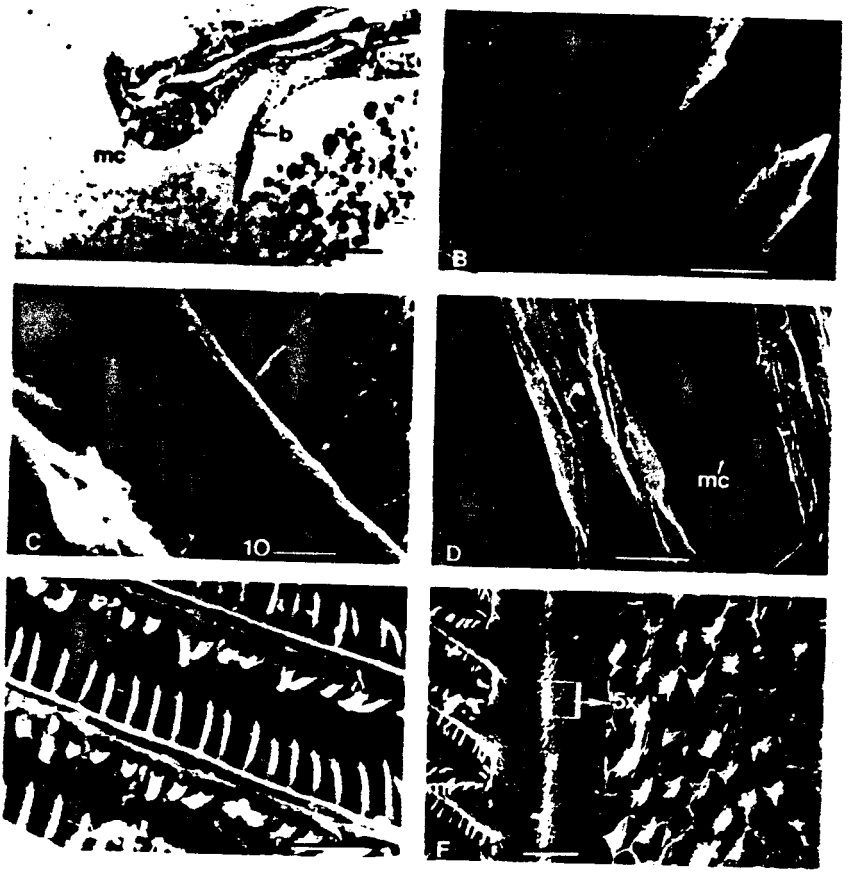

Fig. 2. A) Histological cross-sections of lateral gill raker. B) SEM of branchiospinule. C) SEM oblique view of anterior transport zone of gill raker. D) SEM of the surface ultrastructure of anterior transport zone. E) SEM side view of gill rakers showing groove of posterior transport zone. F) Split-screen SEM, left side shows junction of mesial rakers and lateral surface of the cutaneous fold, right side shows 5× enlargement of the lateral surface as demarked by box on left side. All scale bars are in microns. Key: b, branchiospinule; mc, mucus cell; cs, cuticle-secreting cell; ptz, posterior transport zone; lf, lateral surface of cutaneous fold; mr, mesial raker.

taneous fold. The lateral and the mesial raker elements differ in size and morphology (Fig. 4). The arrangement indicates that the lateral raker elements collect food whereas the mesial rakers, being capped with a cutaneous fold, do not. The mucous cells of the epithelium of the lateral surface of the cutaneous fold are larger and more densely packed than mucous cells of epithelium in other locations of the branchial basket. Surface ultrastructure, dominated by cuticle-secreting cells, is essentially flat in small (150 mm) fish (Fig. 2F), with an occasional mucous cell breaking through the cell junctions (Fig. 5B). The analogous surface had a pitted appearance in large (230 mm) fish (Fig. 5A and 5C). No evidence of glandular organization could be found in histological sections of small (Fig. 5D) or large fish (Fig. 5E).

The mucus produced in different portions of the lateral surface of the cutaneous fold varied in chemical composition. Results of alcian blue PAS staining showed glycoproteins produced in the epithelium become less acid from the anterior to the posterior portion of the lateral surface (Fig. 6).

Taste buds were observed in two locations along the presumed path that food travels as it moves through the branchial basket. One group of taste buds occur anteriorly in the branchial basket on the glossohyal. The glossohyal is covered with papillae arranged in periodic rows (Fig. 5F). Each papilla had a patch of microvilli

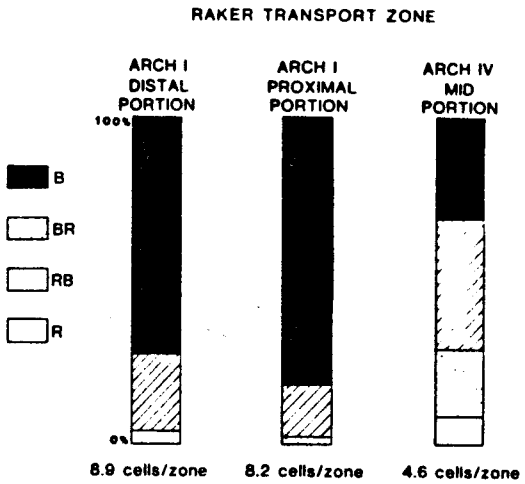

Fig. 3. Cell count scores of alcian blue PAS staining of anterior transport zone of Arch I and Arch IV at pH 2.6.

(Figs. 7A and 7B) typical of taste buds in teleosts and related groups (Ono, 1980; Ezeasor, 1982). Histological cross sections confirmed that taste buds occur in these structures (Fig. 7C).

A second group of taste buds occurs farther back in the buccal cavity. A crest of soft-tissue occurs where the right and left fifth branchial arches articulate. Rows of concave papillae occur on both sides of this crest (Fig. 7D). The center of each papilla has a patch of microvilli (Fig. 7E), which is the surface manifestation of a taste bud (Fig. 7F).

Discussion

Menhaden appear to capture food particles by mechanical sieving as opposed to aerosol entrapment mechanisms. The morphology of menhaden gill rakers does not meet the necessary criteria for the application of aerosol feeding models. Aerosol particle capture requires that the filter elements themselves be "sticky"; thus, in menhaden the elements should produce mucus (Rubenstein and Koehl, 1977). In addition, particle capture by aerosol mechanisms such as adhesion, electrostatic attraction, or inertial impaction can only take place when there is a laminar flow regime around the filter element (Koehl and Strickler, 1981).

The surface of the branchiospinule should be relatively "dry" or devoid of mucus. The only potential source of mucus on the branchiospinules is the exudate of the cuticle-secreting cells. These cells produce a very thin protective coat-

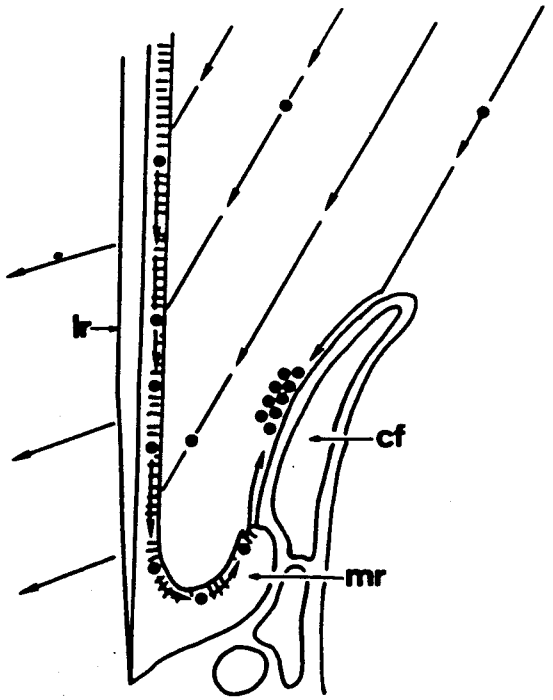

Fig. 4. Cross-section of branchial arch illustrating proposed particle movements and water flows. Key: lr, lateral raker; mr, mesial raker; cf, cutaneous fold.

ing, a cuticle, of predominantly acid glycoproteins (Whitear, 1970). The cuticle is typically 1 μm or less in thickness and has been found to be more viscous than secretions from epithelial mucous cells. Thus, the branchiospinules probably are covered with this thin, relatively stable coating.

Based on the Reynolds numbers for the most appropriate model system (i.e., flow around a cylindrical structure) the flow regime around the branchiospinules is probably in a transitional state to turbulence. A conservative estimate for menhaden (15 cm Fork Length) over the range of probable feeding velocities (1.5–2.5 body lengths s^{-1}), the Reynolds numbers associated with the flow around the branchiospinules would be 2–3 as given by the equation:

$$Re = \frac{\rho v L}{\mu}$$

where ρ is the density of the fluid (1.025×10^{-3} kg m^{-3} for seawater 33‰ at 20 C), v is the velocity of the fluid, μ is the dynamic viscosity of the fluid (1.1×10^{-3} kg m^{-1} s^{-1}) and L is the linear dimension of the object—in this case the cross width of the branchiospinule (10 μm).

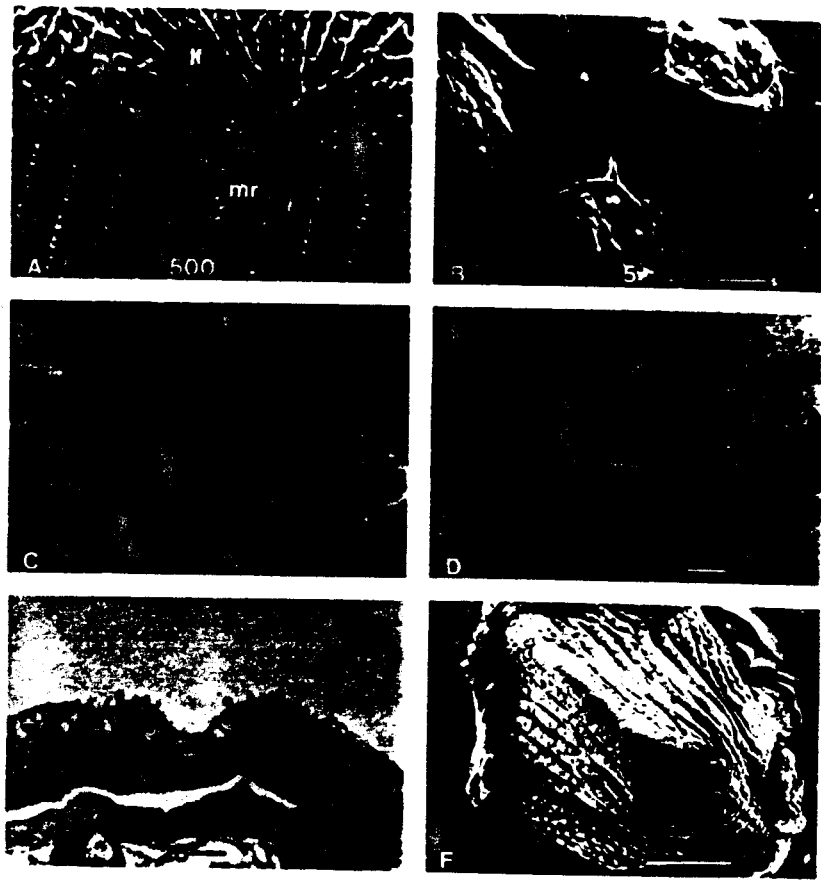

Fig. 5. A) SEM of junction between mesial rakers and lateral surface of the cutaneous fold. B) SEM of lateral surface of the cutaneous fold. C) SEM of lateral surface of the cutaneous fold. D) Histological cross-section of the lateral surface of the cutaneous fold. E) Histological cross-section of the lateral surface of the cutaneous fold. F) SEM of glossohyal. All scale bars are in microns. Key: lf, lateral surface of cutaneous fold; mc, mucus cell.

Reynolds numbers (Re) less than 1 are considered representative of laminar conditions, where backflow turbulence appears at Re values of 40 (Blake and Sleigh, 1974; Blake, 1983).

The dimensions of the serrations on the margins of the branchiospinules considered in light of the characteristics of menhaden prey items suggests these structures have little to do with prey handling, but instead may improve flow around the structures. The points formed by the serrations on the margins seem too small to impale or disable a zooplankton prey in order to ensure capture. Any damage done to phytoplankton by the serrations would be counterproductive as cell contents would be carried away by seawater flushing out the buccal cavity. The fish process huge amounts of water through an extremely small mesh. These serrations, by channelling flow through the raker gaps, may improve filtration efficiency.

Two mechanisms are proposed for the transport of particles down the length of the raker blades. The raker blade has a complex orientation to the fluid flowing through the buccal cavity. One transport zone is anterior to the origin of the flow, thus directly impacted by it. The transport zone on the other side of the raker is posterior, or in the lee of the flow. The structural asymmetry of blade morphology exploits this orientation. The anterior zone utilizes a mucous assisted transport, whereas the posterior zone utilizes flow discontinuities.

The proposed transport mechanism on the anterior side of the blade depends on the creation of a null zone superior to the mucous rich epithelium of the anterior transport zone. A

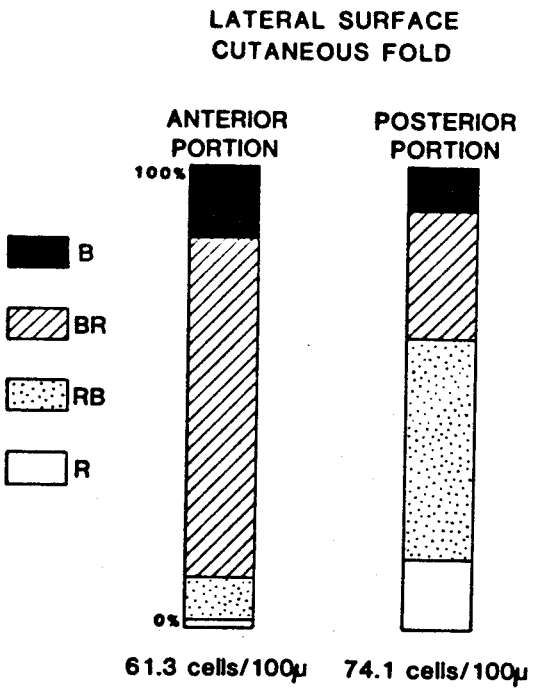

Fig. 6. Cell count scores of alcian blue PAS staining of anterior and posterior portions of the lateral surface of the cutaneous fold of Arch I at pH 2.6.

flow that carries captured food particles should be induced by fluid diverted by the branchiospinules. Particles and water diverted toward the sagittal plane represent the first step in initiating transport down the length of the raker. The flow should travel into the crotch between the branchiospinule and the raker and follow the contour up the face of the transport zone (Fig. 8). A flow counter to this should be created by fluid diverted by the leading edge of the blade. With these flows in balance the resultant vector should drive the food material down the blade, since the longitudinal axis of the blade is also oriented into the fluid flowing through the buccal cavity.

It is not clear whether mucus on the anterior transport zone serves as a lubricant-conveyor or actually complexes with food particles. The forces at work would have tended to compact the food particles against the surface of the zone. Irregularly shaped particles could either ride over an easily displaced mucous surface, or could mix with the mucus to form a more easily movable particle-fluid complex. Physiologic economy would be served by the former since the fish would not have to replenish mucus at such a high rate.

The behavior of these fluid systems may depend on the type of glycoproteins contributing to the mucus found on the various branchial basket structures. The relative contribution of acid and neutral groups confer a number of different physiologic and rheotactic characteristics to the mucus (Solanki and Benjamin, 1982). In mammalian systems, viscosity increases as the acidic glycoprotein content of the mucus increases (Jones et al., 1973; Iravani and Melville, 1974). Since fish mucus is chemically similar to mammalian mucus, its viscosity probably varies accordingly (Solanki and Benjamin, 1982).

The type of mucus produced by the rakers of an arch appears to be related to the size of the particles the arch can filter. Results of the alcian blue PAS staining of mucous cells of the anterior transport zone suggest rakers of the inner gill arches operate differently than rakers of the outer arches. Preliminary examination of the gap distance between the branchiospinules (Friedland, unpubl.) suggests that the gill arches become progressively better at filtering small particles from exterior to interior. The transport zones of the outer arches produce more acidic glycoprotein, thus more viscous mucus and move larger food particles. The zones of the inner arches exhibit the opposite: they transport smaller food particles, produce more neutral glycoproteins and function with less viscous mucus.

Less viscous mucus production in the arches that capture small particles and higher viscosity mucus in the arches that capture large particles may reflect particle handling requirements of the respective arches. Though mucus may not play a role in particle capture it may be critically important in controlling particles once they are captured. The difference in viscosity associated with the capture of different sized particles may reflect the degree in which the mucus interacts and complexes with captured particles. Small, fragile phytoplankton cells could disperse or lyse when they enter the transport zone. A less viscous mucus may be better at controlling or complexing cells and cell contents, thus the food benefits are not lost. Large cells that resist breakage, like diatoms, could be transported with less mucus interaction in order to transmit food benefit.

The proposed transport mechanism on the posterior side of the blade depends on the creation of a vortex within the confines of the

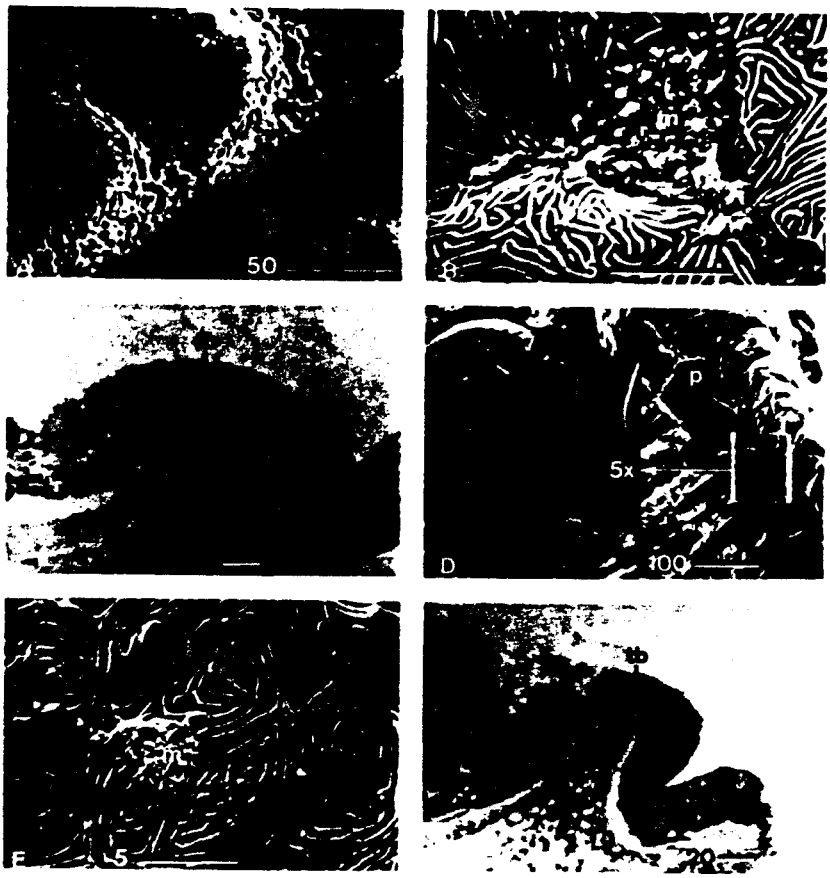

Fig. 7. A) SEM of papillae on the surface of the glossahyal. B) SEM of microvilli on papillae of glossohyal. C) Histological cross-sections of papillae of the glossohyal. D) Split-screen SEM, right side shows papillae on articulation of right and left branchial arches, left side is 5× enlargement of papillae as demarked by box on right side. E) SEM of microvilli of papillae of the articulation of the fifth arch. F) Histologial cross-section of papillae of articulation of the fifth branchial arch. All scale bars are in microns. Key: m, microvilli; tb, taste bud; p, papillae.

groove that runs along the longitudinal axis. Fluid flowing over the leading edge of the raker would be expected to sweep over the groove in a curved trajectory (Fig. 8). Fluid diverted by the branchiospinules should also create a flow in the same manner as the anterior side. It should travel into the crotch between the branchiospinules and the raker and then follow the contour up the face of the transport zone. The two flows should create a null zone away from the surface of the raker which has a net movement down the length of the raker. Particles deposited in the zone could be carried to the base of the raker without the need of a lubricant.

Food particle transport along the branchial axis of the principal filtration arches may be similar to that proposed for the anterior transport zone of the raker blades. The potential for a null zone to form over the lateral surface of the cutaneous fold in concert with a mucus-mediated transport of plankton particles is suggested by the spatial arrangements of the raker elements. Food particles collected on the lateral raker elements may be swept toward a groove formed by the confluent base of the lateral and mesial raker elements. I propose that the rakers act as raceways to guide particles into the groove along the transport zones of the rakers and then out of the groove onto the mesial side, where they are deposited on the lateral surface of the cutaneous fold (Fig. 4). Since lateral raker elements are not articulated by hard or soft struc-

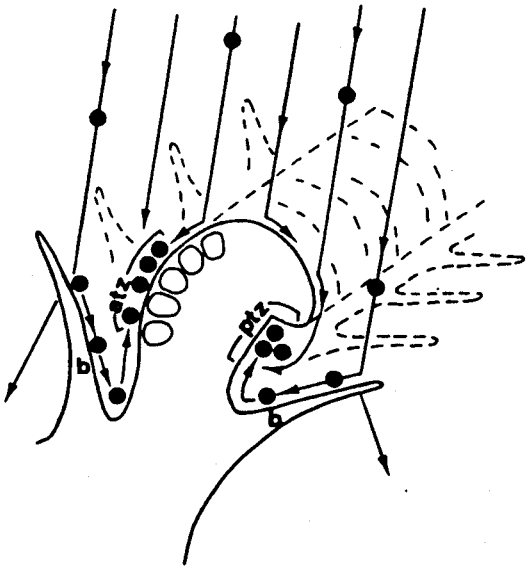

Fig. 8. Cross-section of gill raker illustrating proposed particle movement and water flows. Key: b, branchiospinule; atz, anterior transport zone; ptz, posterior transport zone.

tures, fluid is free to pass out of the groove all along the lateral side, making transport along the bottom of the groove unlikely. Particles deposited on the lateral surface of the cutaneous fold could be held in balance by the flow that has been diverted by the extremities of the fold itself (Fig. 4). A null zone should exist in the transverse plane with resultant flow along the longitudinal axis due to the orientation of the branchial arch into the prevailing flow in the buccal cavity.

The large number of mucous cells in the epithelium of the lateral surface of the cutaneous fold suggests that they play a role in food particle transport. Mucus is probably involved in the transport of food particles along the surface of the cutaneous fold, but its exact role is unclear. Food particles appear to travel, as on the anterior transport zone of the rakers blades, over or complexed with a mucous layer. The mucous layer in this region is difficult to speculate about due to variability in the types of mucus produced. Glycoproteins produced in the epithelium become less acid from the anterior to the posterior portion of the transport zone and in addition to the possibilities of a stationary or moving mucous layer, this poses the question of whether the mucus of different qualities becomes misible or flows in a bilayered arrangement. Prediction of the behavior of this fluid system would require direct experimental observation or fluid dynamic modeling.

The role mucus plays in the transport system of the lateral surface of the cutaneous fold may vary with the size of the fish. The pitting of the lateral surface in larger fish serves to raise the relative number of mucous cells per unit area, thus increasing the potential for mucus production. The differences in feeding repertoire of large vs small fish may be reflected in different food-particle transport requirements. The higher proportion of zooplankton in the diet of large menhaden may dictate the need for a deeper mucous layer to control more active prey than found in the diet of smaller fish.

Feeding behavior and the orientation of glossohyal taste buds suggests that these taste buds assay suspended particles for physical rather than chemical information, and thereby fulfill a mechanoreceptive role (Reutter, 1982). As menhaden encounter particles in the water, they sample the water by "gulping" at it (Durbin and Durbin, 1975). The motion involves rapid movement of their lower jaw. Their taste buds, which are on the tip of the lower jaw, would have a perpendicular trajectory to particles in the water. During feeding there is no jaw movement, the taste buds on the glossohyal are not impacted by particles in the water, as water would have a parallel trajectory to the surface of the glossohyal. Both food and non-food particles incite "gulping" and in turn initiate feeding. If the particles are usable food, feeding is sustained. In contrast, if the particles are not usable food, feeding may be initiated but will be quickly aborted (Friedland, unpubl.).

The positioning of taste buds on the fifth branchial arch could enable the fish to sense successfully filtered food particles that have been transported to the back of the branchial basket and are ready for ingestion. Food particles captured on the rakers apparently cascade to a channel formed by the fourth and fifth arch. This channel is confluent with the cavities of the epibranchial organs. A slurry of food particles and possibly mucus sloshing around in this area would undoubtedly contact the taste buds of the fifth arch.

Chemical gustation by the taste buds of the fifth arch would fit behavioral patterns of the fish. Menhaden encountering non-food particles might begin to feed on them based on information from the glossohyal taste buds which are sensing the presence of filterable particles. But when these particles arrive at the back of the branchial basket and are found to be gus-

tatorially unsuitable by the taste buds of the fifth branchial arch, inhibition of feeding would be expected. Gustation seems to proceed as a two-stage process.

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Literature Cited

Blake, J. R., and M. A. Sleigh. 1974. Mechanics of ciliary locomotion. Biol. Rev. 49:85–125.

Blake, R. W. 1983. Fish locomotion. Cambridge University Press, New York.

Crespo, S. 1982. Surface morphology of dogfish (*Syliorhinus canicula*) gill epithelium, and surface morphological changes following treatment with zinc sulfate: a scanning electron microscope study. Mar. Biol. 67:159–166.

Dobbs, D. H. 1972. A method for preservation of soft tissues of marine teleosts for scanning electron microscopy. Tissue & Cell 4:687–690.

Durbin, A. G. 1979. Food selection by plankton feeding fish, p. 203–218. *In:* Predator-prey systems in fisheries management. H. Clepper (ed.). Sport Fishing Institute, Washington, D.C.

———, and E. G. Durbin. 1975. Grazing rates of the Atlantic menhaden, *Brevoortia tyrannus* as a function of particle size and concentration. Mar. Biol. 33:265–277.

Ezeasor, D. N. 1982. Distribution and ultrastructure of taste buds in the oropharyngeal cavity of the rainbow trout, *Salmo gairdneri* Richardson. J. Fish Biol. 20:53–68.

Fletcher, T. C., R. Jones and L. Reid. 1976. Identification of glycoproteins of plaice (*Pleuronectes platessa* L.), flounder (*Platichthys flesus* (L.)) and rainbow trout (*Salmo gairdneri* Richardson). Histochem. J. 8:597–608.

Friedland, K. D., L. W. Haas and J. V. Merriner. 1984. Filtering rates of juvenile menhaden, *Brevoortia tyrannus* (Pisces: Clupeidae), with consideration of the effects of detritus and swimming speed. Mar. Biol. 84:109–117.

Gunter, G., and J. Y. Christmas. 1960. A review of literature on menhaden with special reference to the Gulf of Mexico menhaden, *Brevoortia tyrannus* Goode. U.S. Fish and Wildlife Serv., Spec. Sci. Rep.-Fisheries No. 363.

Gusev, E. E. 1964. Some peculiarities in menhaden morphology—*Brevoortia tyrannus* (Latrobe). Contribution to Commercial Fisheries Research of the Arctic Basin 2:13–16.

Hossler, F. E., J. R. Ruby and T. D. McIlwain. 1979. The gill arch of the mullet, *Mugil cephalus* I. surface ultrastructure. J. Exp. Zool. 208:379–398.

Iravani, J., and G. N. Melville. 1974. Long-term effect of cigarette smoke on mucociliary function in animals. Respiration 31:358–366.

Jones, R., and L. Reid. 1973. The effect of pH on alcian blue staining of epithelial glycoproteins. I. Sialomucins and sulphomucins (singly or in combinations). Histochem. J. 5:9–18.

———, P. Bulduc and L. Reid. 1973. Goblet cell glycoprotein and tracheal gland hypertrophy in rat airways: the effect of tobacco smoke with or without the anti-inflammatory agent phenylmethyloxadiazole. Br. J. Exp. Path. 54:229–239.

Jorgensen, C. B. 1983. Fluid mechanical aspects of suspension feeding. Mar. Ecol. Prog. Ser. 11:89–103.

Karlsson, L. 1983. Gill morphology in the zebrafish, *Brachydanio rerio* (Hamilton-Buchanan). J. Fish Biol. 23:511–524.

Koehl, M. A. R., and J. R. Strickler. 1981. Copepod feeding currents: food capture at low Reynolds number. Limnol. Oceangr. 26:1062–1073.

Monod, T. 1961. Brevoortia Gill 1861 and Ethmalosa Regan 1971. Bull. de l'Inst. Francais d'Afrique Noire. 23:506–547.

Ono, R. D. 1980. Fine structure and distribution of epidermal projections associated with taste buds on the oral papillae in some Loricariid catfishes (Siluroidei: Loricariidae). J. Morph. 164:139–159.

Peck, J. I. 1893. On the food of the menhaden. Bull. U.S. Fish. Comm. 13:113–126.

Reutter, K. 1982. Taste organ in the barbel of the bullhead, p. 87–88. *In:* Chemoreception in fish. T. J. Hara (ed.). Elsevier Scientific Pub. Co., New York.

Rubenstein, D. I., and M. A. R. Koehl. 1977. The mechanisms of filter feeding: some theoretical considerations. Am. Nat. 111:981–994.

Solanki, T. G., and M. Benjamin. 1982. Changes in the mucous cells of the gills, buccal cavity and epidermis of the nine-spined stickleback, *Pungitius pungitius* L., induced by transferring the fish to sea water. J. Fish Biol. 21:563–573.

Wassersug, R. 1972. The mechanism of ultraplanktonic entrapment in anuran larvae. J. Morph. 137: 279–288.

Whitear, M. 1970. The skin surface of bony fish. J. Zool. Lond. 160:437–454.

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