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Particle Ingestion by *Tilapia galilaea* Is Not Affected by Removal of Gill Rakers and Microbranchiospines

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Abstract.—Particle ingestion by filter-feeding Galilee Saint Peter's fish *Tilapia galilaea* increased as a function of particle size, leveling off when particle diameter exceeded 20 μm. Ingestion rates by this cichlid also increased with particle concentration, asymptotically approaching maxima of 4,785 and 84,746 particles·fish^{-1}·min^{-1} for small (3.9–6.0 cm standard length, SL) and large (12.6–14.3 cm SL) fish, respectively. Surgical removal of gill rakers and microbranchiospines did not affect particle ingestion rates or selectivity.

Based on anatomical studies by Greenwood (1953) and Gosse (1956), we hypothesized that planktivorous cichlids collect particles by a double-filtration system in which large particles such as zooplankton are strained by gill rakers and small particles such as phytoplankton are strained by microbranchiospines. Microbranchiospines are small mucus-covered structures which bear fine lateral spines and occur in a single row posterior to the gill rakers on the second, third, and fourth gill arches (Figure 1A). In this study, we tested our hypothesis by examining the effects of surgical removal of gill rakers and microbranchiospines on particle ingestion by Galilee Saint Peter's fish *Tilapia galilaea,* a filter-feeding cichlid (Drenner et al. 1982).

Methods

Tilapia galilaea were obtained from the kibbutz Mevo Hamma fish ponds or by castnetting from Lake Kinneret, Israel, during March and April. They were acclimated at the Yigal Allon Kinneret Limnological Laboratory for at least 1 month in 60-L plastic tubs which were continually supplied with fresh lake water containing natural lake plankton. Particle ingestion by fish was examined during feeding trials by monitoring declines in densities of synthetic microspheres and zooplankton in tubs as fish fed.

To examine the roles of gill rakers and microbranchiospines in selective particle ingestion, we conducted a factorial experiment of 2 × 2 design consisting of four treatment combinations having the following number and size ranges of fish (cm standard length, SL): (1) gill rakers removed, five fish, 13.0–13.4; (2) microbranchiospines removed, five fish, 13.8–14.2; (3) gill rakers and microbranchiospines removed, four fish, 11.9–13.1; and (4) untreated, four fish, 13.8–14.2. We also used a sham-operated fish treatment (five fish, 12.6–14.3) and a small-fish treatment (two groups of 50 fish, 3.9–6.0). Each treatment was replicated six times.

The rows of gill rakers and microbranchiospines of fish anesthetized with tricaine were surgically stripped from the gill arches with microforceps. During the operations (mean duration, 22.7 ± 1.5 min), performed on each side of the head, fish were placed in a plastic pan and periodically moistened with water containing tricaine. Follow-up operations (12.7 ± 1.1 min) were performed to assure that all structures had been removed. Sham

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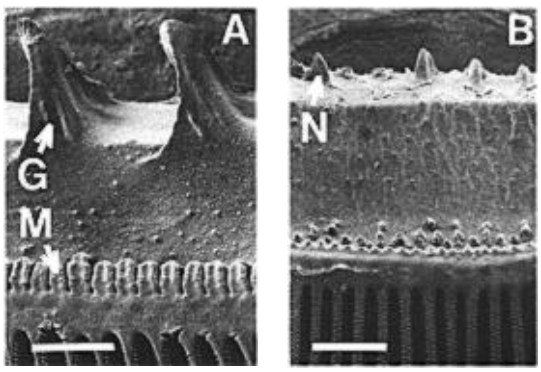

FIGURE 1.—Scanning electron photomicrographs of gill rakers (G), microbranchiospines (M), and gill raker nubs (N) of the anteriolateral surfaces of the second gill arches of *Tilapia galilaea*. (**A**) An untreated fish of 14.1 cm standard length. (**B**) A fish (12.4 cm) whose gill rakers and microbranchiospines had been removed surgically. Bars = 0.5 mm.

TABLE 1.—Gill raker and microbranchiospine characteristics of experimental *Tilapea galilaea*. Treatments: U = untreated; GR = gill rakers removed; MR = microbranchiospines removed; GR + MR = gill rakers and microbranchiospines removed. Nubs are partially regenerated gill rakers.

	Gill rakers		Microbranchiospines	
Treatment	Number·cm^{-1}	Nubs·cm^{-1}	Number·mm^{-1}	Mean height (μm)
U	29.9±0.4	0	7.6±0.2	238±9
GR	2.6±0.8	19.7±3.2	7.0±0.2	220±8
MR	30.6±0.2	0	10.8±0.7	103±9
GR+MR	2.6±0.4	25.4±2.4	10.4±1.5	93±13

operations and follow-up operations (22.6 ± 0.8 min and 17.6 ± 1.6 min, respectively) consisted of anesthetizing a fish, placing it into a pan, and opening its operculum to expose the gill arches. To prevent infection, fish were placed in water containing malachite green for 1 d after the operations and then moved to tubs with continual inflow of lake water. Fish began to feed within a day of the operations, as evidenced by feces production, and had no infections prior to the feeding trials. To allow fish to recover fully from the trauma of surgery, we began the feeding experiments in late July, approximately 2 weeks after surgery. After all feeding trials were concluded, fish were sacrificed, and branchial baskets were removed and preserved in 10% formalin. Gill rakers were counted on all gill arches, and microbranchiospine numbers were estimated by counting them on three 1.35-mm sections of the second, third, and fourth arches. Partial regeneration of gill rakers and microbranchiospines occurred during the period of experimentation, but the regeneration was incomplete and the structures were abnormal in size, number, and position on the gill arch (Figure 1; Table 1).

Microspheres used in the size-selective ingestion trials ranged from 4.3 to 70.3 μm in diameter and were mixtures of 0.5 g Sephadex G-25, 0.5 g Bio-Rad Bio-beads S-X3-400, 0.1 g Ionics 10–20 μm, and 0.1 g Ionics 20–30 μm. Because Bio-Rad Bio-beads are hydrophobic and both Sephadex and Bio-Rad Bio-beads swell in water, all particles were soaked in dilute soap solutions for at least 24 h prior to being used in experiments. For each range of particle sizes, the mean (±SE) initial numbers of particles per milliliter were as follows: 4.3–6.4-μm-diameter spheres (69.1 ± 3.5); 8.5–12.8 μm (106.0 ± 5.9); 14.9–19.2 μm (97.1 ± 4.7); 21.3–32.0 μm (185.0 ± 6.4); 34.1–44.7 μm (308.1 ± 8.7); 46.9–57.5 μm (173.4 ± 6.1); and 59.6–70.3 μm (101.3 ± 6.1).

We also examined the effect of particle concentration on ingestion rates of fish from five of the groups used in the size-selective ingestion experiments (gill rakers removed, microbranchiospines removed, untreated, sham-operated, and small fish). In these experiments, microspheres were 50:50 mixtures of Sephadex G-25 and Bio-Rad Bio-beads S-X3 200–400 which were added to tubs at densities ranging from 75 to 1,900 microspheres·mL^{-1}. These particles ranged from 20 to 60 μm in diameter, sizes which the selective ingestion experiments indicated would be ingested at maximum rates.

Before an experiment, fish were moved to tubs containing filtered lake water and allowed to acclimate for 1 h. Feces were siphoned out, and water samples were taken from well-stirred tubs at 0 and 1 h to check for egestion of microspheres which had been ingested by fish in previous trials. We detected no meaningful addition of microspheres to the tubs from fish egestion. An experiment began with the addition of microspheres and heat-killed zooplankton to the tubs. Zooplankton were larger than 112 μm and included *Keratella* sp., *Mesocyclops* sp. nauplii and copepods, *Bosmina* sp., and *Ceriodaphnia* sp. at densities of 156–2,196 organisms·L^{-1}. Duplicate water samples were taken from well-stirred tubs when the microspheres and zooplankton were added and 40–60 min after the start of the experiment. Water samples were taken by quickly lowering a Plexiglas

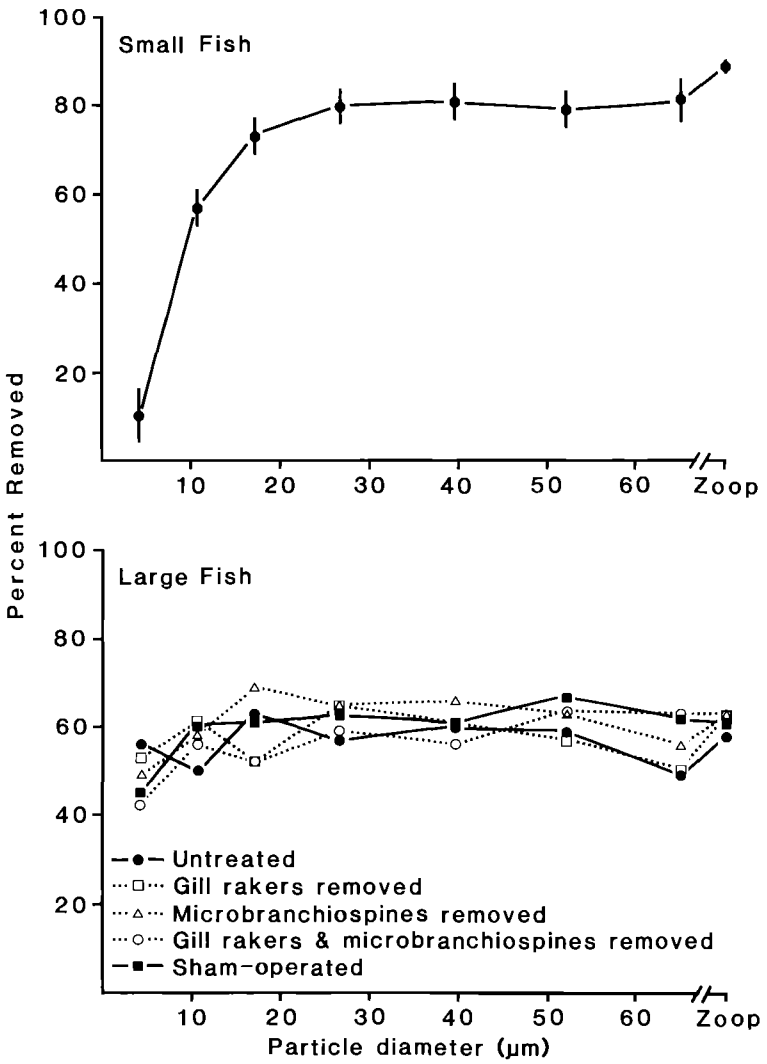

FIGURE 2.—Removal rates of microspheres and zooplankton by small (3.9–6.0 cm standard length) and large (11.9–14.3 cm) *Tilapia galilaea* as functions of particle size. Zoop = heat-killed zooplankton.

tube (6.3 cm in diameter) onto a randomly placed rubber stopper lying on the tub bottom. Zooplankton were strained from one of the samples through a 63-μm-mesh sieve and preserved in 5% formalin; 125 mL of unfiltered water from the second sample were preserved in 1% Lugol's solution for microsphere enumeration. Zooplankton and microspheres were counted and measured under dissecting and inverted compound microscopes, respectively. We controlled for particle loss due to unknown factors by monitoring the loss of microspheres and zooplankton in fishless control tubs.

Particles were kept in suspension by air bubbles from an airstone, movement of the fish, and stirring every 10 min. Feeding trials were conducted at 28.8 ± 0.1°C under fluorescent lighting and natural sunlight from a window and an open doorway. After completion of each trial, fish were transferred to clean tubs containing a continual flow of fresh plankton. Fish were held in tubs for 24–48 h before being used in another experiment.

The chronology of the experiments may have influenced the feeding rates of the fish. During the size-selective ingestion experiments (24 July–5 August), small fish readily consumed microspheres and zooplankton, but the feeding activity of large fish, which were slow to adapt to experimental conditions, was more prone to being in-

terrupted when tubs were sampled and stirred. Therefore, the particle-removal rates of the fish in these experiments should be viewed as relative rates for a given size of fish for different sizes of particles. In the experiments examining the effect of particle concentration on fish feeding (2 August–1 September), the fish were more acclimated to experimental conditions and their feeding rates were nearer to maximum. So that fish acclimation would not be a factor in the particle concentration experiments, the feeding trials with different microsphere densities were conducted in random order.

Results

Ingestion rates for small *Tilapia galilaea* increased as a function of particle size, leveling off when particle diameter exceeded 20 μm (Figure 2). Although large fish were more efficient grazers of small microspheres, they were selective particle grazers (Figure 2). Analysis of variance of the treatments of large fish revealed a significant effect of particle size ($P = 0.01$) but detected no significant effects of gill rakers ($P = 0.72$) and microbranchiospines ($P = 0.65$), or their interaction ($P = 0.52$).

Ingestion rates of small and large fish (untreated and sham-operated) increased with particle concentration, asymptotically reaching maximal ingestion rates of 4,785 and 84,746 microspheres·fish^{-1}·min^{-1}, respectively (Figure 3). Although the number of feeding trials of fish without gill rakers or microbranchiospines was not adequate for curve fitting, ingestion rates of these fish did not appear to differ from ingestion rates of untreated or sham-operated fish.

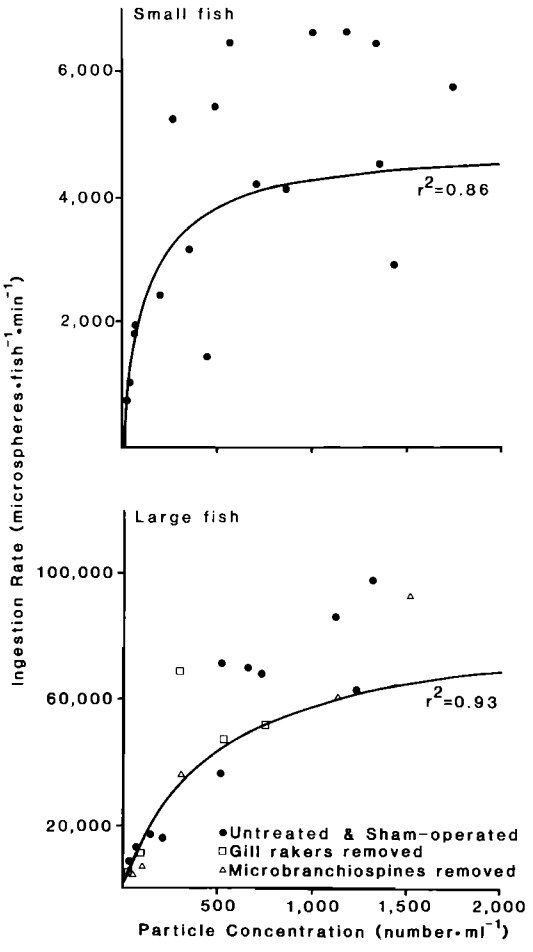

FIGURE 3.—Ingestion rates of microspheres by small (3.9–6.0 cm standard length) and large (12.6–14.3 cm) *Tilapia galilaea* as functions of microsphere concentration. Curves show ingestion rates predicted by the Michaelis–Menten model: $I = I_{max}C/K_{½} + C$, where I_{max} is the maximum feeding rate, $K_{½}$ is the half-saturation constant, and C is microsphere concentration calculated as $C = C_f - C_i/\log_e(C_f/C_i)$, where C_f and C_i are final and initial microsphere concentrations, respectively (Seale and Beckvar 1980). The curve for large fish refers only to untreated and sham-operated animals. The I_{max} values were determined from linear regressions of the inverses of microsphere ingestion rates versus the inverses of microsphere concentrations (Lehninger 1982). For small and large fish, I_{max} values were 4,785 and 84,746 and $K_{½}$ values were 122.5 and 462.7, respectively.

Discussion

Size-selective particle ingestion by freshwater filter-feeding fish has been studied for gizzard shad *Dorosoma cepedianum* and blue tilapia *Tilapia aurea* (Taylor 1984; Drenner et al. 1984a, 1984b, 1986; Mummert and Drenner 1986). Gizzard shad and blue tilapia ingestion rates increased as functions of particle size, leveling off above 60 and 25 μm, respectively. Although the particle-size-dependent ingestion rates of gizzard shad were consistent with a mechanical-sieve model of filtering efficiency based on the cumulative frequency of interraker distances of gill rakers, the role of gill rakers in particle selection by cichlids has not been tested.

Because ingestion rates of normal and surgically altered large fish were similar, we reject our double-filtration hypothesis that gill rakers of fish of this size strain large particles and microbranchiospines strain small particles. It is unlikely that failure to detect significant treatment effects is explained by partial regeneration of gill rakers and microbranchiospines. If gill rakers and micro-

branchiospines function as mechanical sieves, we would expect that differences in spacing and position of regenerated structures versus normal structures would produce different size-selection patterns.

Although we did not determine the mechanism used by *Tilapia galilaea* for particle capture, Greenwood (1953) and Fryer and Iles (1972) suggest that cichlids may collect small particles by entrapping them in mucus to form food–mucus aggregates. Other fish such as larval lamprey *Petromyzon marinus* (Mallatt 1981) and spined loach *Cobitis taenia* (Robotham 1982) collect food by mucus entrapment of particles. Although Fryer and Iles (1972) suggest that a mucus-entrapment mechanism would not be selective, filter-feeding anurans which use mucus for particle collection may be selective grazers (Seale and Wassersug 1979; but see Seale and Beckvar 1980).

We do not know the function of gill rakers and microbranchiospines in *T. galilaea*. Perhaps the function of gill rakers is to retain eggs and fry in the buccal cavity during mouth brooding. The function of microbranchiospines may be to protect gill filaments from abrasion by fine particles, possibly explaining the occurrence of microbranchiospines in cichlids which do not feed on phytoplankton (Fryer and Iles 1972).

Acknowledgments

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