The Feeding Mechanics of the Gizzard Shad (Dorosoma Cepedianum)

by Ray W. Drenner

1977

Submitted to the Department of Systematics and Ecology and the Faculty of the Graduate School of the University of Kansas in partial fulfillment of the requirements for the degree of Doctor of Philosophy

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ABSTRACT

Field studies have shown that young gizzard shad (Dorosoma cepedianum) are carnivores, visually feeding on individual zooplankton. Shad larger than 30 mm are omnivores, feeding predominantly as filter-feeders on both phytoplankton and zooplankton. This study experimentally identified and quantified the causal mechanisms determining the feeding selectivity and feeding rate of filter-feeding gizzard shad.

Laboratory observations found shad to filter-feed by inhaling water and food through expansion of the buccal and opercular cavities. Shad did not visually select and attack individual zooplankter prey items, but swam through the water inhaling water containing prey with a rapid series of undirected suctions. Shad filtering rate, the volume of water inhaled per minute, was equal to the multiple of the volume of the expanded buccal cavity and the pumping rate.

I determined buccal volume by making plaster of Paris molds of the expanded buccal cavity. The volume of the expanded buccal cavity increased as a power function of shad length. Pumping rate, measured by high speed movie films and visual observation, decreased with shad length. Filtering rate increased as a power function of shad length with

shad 17 cm in standard length filtering over one liter of water per minute.

The actual rate that particles were inhaled and ingested was determined by the shad's capture efficiency and filtering efficiency. Capture efficiency is a function of both the shad's capture and the prey's escape mechanisms. A shad's suction pump mechanism creates a flow into the mouth similar to flow into a pipe.

I simulated a fishlike suction intake using a siphon system which afforded control over the three variables of fish suction intakes; mouth opening size, buccal volume, and buccal expansion rate. The simulated suction inhaled 10 ml into a tube 1.0 cm in diameter in 0.4 sec. The capture probability of the simulated suction for zooplankter prey was highest for the cladocerans _Ceriodaphnia_ _reticulata_ (P = .96), _Daphnia_ _galeata_ _mendotae_ (P = .92), and _Daphnia_ _pulex_ (P = .76); intermediate for cyclopoid copepods (mostly _Cyclops_ sp. and _Mesocyclops_ sp.) (P = .28) and _Cyclops_ _scutifer_ (P = .24); and lowest for the calanoid copepod _Diaptomus_ _pallidus_ (P = .07).

To test the results of the capture experiments, the relative feeding rates of gizzard shad on a mixture of different zooplankton were determined in laboratory experiments and compared to predictions based on the capture probabilities. Shad feeding rate constants, k (liters/hr), were lowest on _Diaptomus_ spp. ($\bar{x}$k = .67), intermediate on cyclopoid copepods ($\bar{x}k = 1.37$) and highest on *D. galeata mendotae* ($\bar{x}k = 3.60$), *C. reticulata* ($\bar{x}k = 3.00$) and copepod nauplii ($\bar{x}k = 4.01$). These experiments show that differential capture probabilities of nonvisual-feeding planktivores result in an apparent feeding selectivity for zooplankton which have poor escape ability.

Particles inhaled into the mouth are filtered from the water by the gill rakers. The shad's filtering efficiency was determined by measuring the interraker spaces. Cumulative frequencies of interraker distances weighted for raker length show that filtering efficiency for particles 1 to 70 microns was a hyperbolic function of particle size with particles 70 microns or larger filtered with 100% efficiency. This filtering efficiency would result in an apparent feeding selectivity for large algae versus small algae.

The feeding rate of filter-feeding gizzard shad on a particular prey type was equal to the multiple of 4 factors: (1) prey density, (2) shad filtering rate, (3) shad capture efficiency, and (4) shad filtering efficiency. This feeding rate model was confirmed in an experiment which compared computer simulated to observed shad feeding rates.

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INTRODUCTION

Classically, limnologists have viewed the interactions between components of lake ecosystems as being a unidirectional flow of influence passing from the physical and chemical factors to the phytoplankton to the zooplankton and finally to the fish (Straskraba, 1965). The dynamics of lake biota were treated primarily as a problem of energy transfer (Lindeman, 1942). It was not until the studies by Hrbacek et al. (1961), Hrbacek (1962, 1964), Straskraba (1965) and Brooks and Dodson (1965) that the reverse influence of planktivorous fish on zooplankton and phytoplankton communities was recognized. Their studies showed that zooplankton communities in ponds or lakes containing visual-feeding planktivorous fish were composed of smaller bodied zooplankton species than zooplankton communities in lakes without planktivores. Other studies have shown similar zooplankton community structure when fish were present (Wells, 1970; Hutchinson, 1971; Warshaw, 1972) although some lake community structure can be an exception (O'Brien et al., in prep.).

Brooks and Dodson (1965) used the size-efficiency hypothesis to explain the shift in dominance from large zooplankton such as *Daphnia* in fishless lakes to dominance by small zooplankton such as Bosmina in fish lakes. They hypothesized that an increase in feeding efficiency with increase in body size gave a competitive advantage to the larger zooplankton which allowed them to be dominant in fishless lakes. The large body size became disadvantageous when visual-feeding planktivores were present. The higher mortality rates imposed on the large zooplankton by planktivore predation allowed the smaller zooplankton species to be dominant in fish lakes.

Brooks and Dodson's (1965) hypothesis of a size-related feeding efficiency has not been confirmed by zooplankton feeding studies (Burns, 1969; Egloff and Palmer, 1971) and needs further investigation (Hall et al., 1976). Instead, Dodson (1974) found that large body size was advantageous in avoidance of invertebrate predation. Invertebrate predators, present in fishless lakes, feed selectively on small zooplankton. Such size-selective invertebrate predation causes the large-bodied zooplankton species to be dominant in fishless lakes.

Studies of the feeding mechanics of visual-feeding planktivores have substantiated Brooks and Dodson's (1965) hypothesis of the role of fish predation in causing small-bodied zooplankton to be dominant in lakes containing planktivores. These planktivores selectively feed on large-bodied zooplankton because they have greater probabilities of encountering and attacking large versus small zooplankton

(Werner and Hall, 1974; Confer and Blades, 1975; O'Brien et al. 1976). The resulting small-bodied zooplankton community has had variable effects on the phytoplankton community. Increases in small algae biomass have been associated with Bosmina dominance (Hrbacek et al., 1961). Hrbacek et al. (1961) also found large algae such as diatoms and Dinobryon to increase with Bosmina dominance, but decreases in the large bluegreen alga Aphanizomenon were associated with a decrease in zooplankter size (Hrbacek, 1964). Such variable results reflect the indirectness of the cause and show the significance of other factors in phytoplankton community structure such as nutrient limitation and interspecific competition of algae (Hutchinson, 1967). These studies do show that phytoplankton and zooplankton communities can be influenced by the feeding of planktivorous fish.

Although the feeding of the planktivorous gizzard shad (Dorosoma cepedianum) has great potential for affecting phytoplankton and zooplankton communities, its feeding mechanics have not been studied. The gizzard shad and its congener, the threadfin shad (Dorosoma petenense), are almost unique in North American waters in their ability to use both phytoplankton and zooplankton food resources as adult fish. Also, the gizzard shad is a numerically significant fish in the freshwaters of North America. It is distributed over most of the eastern half of the United States from North Dakota (Carufel and Witt, 1963), eastward through the

Great Lakes to southern New York, southward throughout the Mississippi River system and along the Atlantic slope [except the Appalachian Mountains (Pflieger, 1975)] to the Gulf coast of the United States and to the basin of the Rio Panuco in eastern Mexico (Miller, 1960). Shad can become very abundant with densities of young shad of over 7000 individuals per acre (Rose, 1957). Gizzard shad often account for more than 50% of fish biomass in a lake (Martin and Campbell, 1953; Schoonover and Thompson, 1954; and Jenkins, 1955, 1967).

Knowledge of the feeding of gizzard shad has come from field studies of shad stomach contents. Although shad stomach contents have included macroinvertebrates such as insects, mollusks, spiders, and water mites (Forbes, 1888; Forbes and Richardson, 1920; Rice, 1942; Bodola, 1966; Jude, 1973), their dominant mode of feeding is planktivory. Young gizzard shad, < 20 mm in total length, are carnivores feeding on protozoan, rotiferan and crustacean zooplankton (Bodola, 1966; Cramer and Marzolf, 1970). Shad begin to switch to omnivory at $\geq$ 25 mm in total length and feed predominantly on detritus, phytoplankton and zooplankton for the rest of their lives (Tiffany, 1921a, b, 1922; Ewers and Boesel, 1936; Rice, 1942; Kutkuhn, 1957; Darnell, 1961; Bodola, 1966; Cramer and Marzolf, 1970; Baker and Schmitz, 1971; Jester and Jensen, 1972). The shift from carnivory to omnivory suggests a change in feeding mechanics. Carnivorous small shad probably feed by visually selecting individual prey items whereas omnivorous large shad feed predominantly as a type of filter-feeder.

Although such shad diet studies as well as studies of phytoplankton or zooplankton community structure with shad presence (Stavn, 1975) provide insight into the influence of shad on plankton communities, their results are often site specific and difficult to use in predictive management. Furthermore, the shad stomachs contain food items from a community composition that their feeding has potentially created. They are in effect eating leftovers. Therefore, such stomach content studies cannot completely reveal the long term effects of fish feeding on plankton communities.

I feel that an understanding of the effects of any predator on a prey population or a grazer on a plant population can only come from studies of the mechanisms determining food selectivity and feeding rate. As will be shown, the feeding mechanisms of a shad preying on zooplankton is mechanically similar to its grazing on phytoplankton, with the exception of one functional component, the prey's escape ability. Although much of shad feeding as a grazer and predator has been analyzed simultaneously, this study focused on the mechanically more complex interaction, predation.

A predator-prey interaction can be broken down into four sequential events: encounter, attack, capture and ingestion (Gerritsen and Strickler, 1977). The probability of some individual of a prey type being eaten is the multiple of the probabilities of those four events (P1 x P2 x P3 x P4). Evaluation of these probabilities reveals each event's role in selective feeding. Although these four events occur in most predator-prey interactions, the mechanical components vary from predator to predator.

I have used a synthesis of Holling's (1959) experimental component analysis and Gerritsen and Strickler's (1977) probabilistic analysis to examine the feeding mechanics of omnivorous gizzard shad. This study experimentally identifies and quantifies the causal mechanisms that determine the feeding selectivity and feeding rate of filter-feeding gizzard shad.

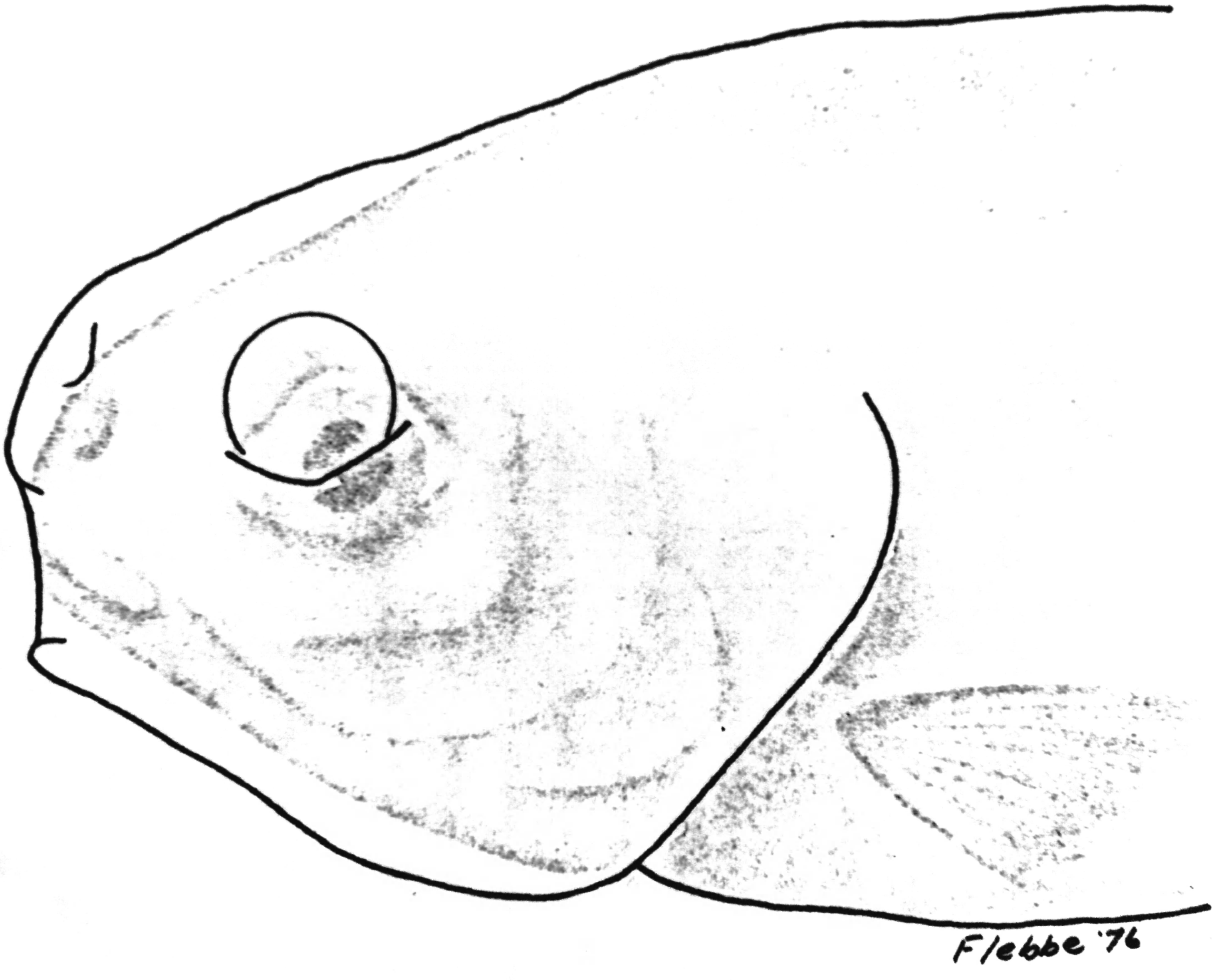
MATERIALS AND METHODS

Feeding mechanics

My study of the feeding of omnivorous gizzard shad began by observing shad 5.3 to 17.5 cm in standard length feeding on zooplankton and phytoplankton in a 30 gallon aquarium at water temperatures from 19 to 20°C. Standard length, SL, is the length of a fish from the tip of the snout to the structural base of the caudal fin (Hubbs and Lagler, 1947). Shad were filmed with a 16 mm Bolex Rex H16 movie camera at 64 frames/sec. Analysis of these films showed that the shad fed by inhaling water and food through expansion of the buccal and opercular cavities (Fig. 1). Shad did not visually select and attack individual zooplankter prey items, but swam slowly through the water inhaling water containing prey with a rapid series of suctions. Because the suctions are not visually directed at individual food items, this is a type of filter-feeding.

These observations show that the encounter and attack events do not play a role in determining the shad's feeding selectivity on zooplankton prey when shad feed in this manner. A predator is said to have fed selectively when the ratio of prey it ingests is different from the ratio of

Figure 1. Change in head contour of a feeding shad 8.28 cm in standard length. The shaded area is the shape of the head while the buccal cavity is collapsed. The dark outline is the head contour 0.09 sec later while buccal and opercular cavities are expanded to inhale food into the mouth and draw water through the gill rakers.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potential prey found in the environment (Ivlev, 1961). Filter-feeding shad encounter and attack prey in proportion to their densities, and therefore the encounter and attack events cannot cause selectivity.

The rate that filter-feeding shad encounter and attack prey is determined by their filtering rate and the prey density. The filtering rate, the volume of water inhaled per minute, should be equal to the multiple of the volume of the expanded buccal cavity and the rate of filling and emptying of the buccal cavity or the pumping rate.

Previous studies of fish feeding have estimated buccal volume by filming a feeding fish's head from two directions (Nyberg, 1971) or by taking photographs of dead specimens whose buccal cavities had been expanded by pulling appropriate muscles (Alexander, 1967b). These pictures were then used to calculate volume changes. Such estimates are costly in time and money and Alexander (1967b) felt his estimates might be wrong by as much as 30%.

I determined buccal volume by making plaster of paris molds of the expanded buccal cavity. Because the buccal cavity is surrounded by bony elements, its maximum volume is rigidly restricted and can be measured using plaster injections. The plaster solutions were dense enough to expand the cavity but dilute enough to allow bubbles to ascend to the surface and escape. The plaster was injected into the shad's mouth using 15 cm long tubes made from glass tubing 2.5 cm in diameter. A series of tubes was constructed to fit a variety of mouth sizes. Tube ends were drawn into a funnel shape having end diameters ranging from 3 to 15 mm. A squeeze bulb was inserted on the other end.

To examine the plaster technique, molds were made of the buccal cavities of three planktivore species, gizzard shad, white crappie (Pomoxis annularis) and bluegill sunfish (Lepomis macrochirus). Only buccal volumes of the gizzard shad were determined as a function of fish length. Fish used in buccal cavity measurements were killed by pithing and positioned vertically between foam rubber cushions. The plaster was then injected into the mouth of the fish using a tube having an end diameter slightly smaller than the inside diameter of the fish's open mouth. The plaster was injected with enough pressure to expand the cavity, depress the tongue and cause plaster flow out of the gill slits. After the plaster became firm, usually within 20 minutes, any plaster protruding out of the mouth was trimmed even with the external edge of the mouth. The mold was then removed by severing the mandible at the isthmus and peeling the shad's head away from the mold. Plaster in the opercular cavity which was attached to the buccal mold was also trimmed away. The opercular cavity is used to draw water through the gill rakers as the mouth closes. This cavity acts as a separate pump (Hughes and Shelton,

1958) and its volume should not be considered as buccal volume. The expansion of the opercular cavity does decrease the potential of backflush caused by mouth closure. An oral valve also reduces the potential backflush. Therefore the entire buccal mold including the area inside the mouth was used to determine buccal volume.

The volume of the mold was determined by weight using standards of known volume. Following each injection into a fish, plaster was also placed into a 5 ml disposable micro beaker (Curtin Matheson Scientific, Inc.). The beakers actually contained 6.7 ml when full of water. Once the plaster set up, the beaker was cut away. Both standards and buccal molds were placed into an oven and dried. Then buccal and standard molds were weighed on a Christian Becker Model EA2 balance and the buccal volume calculated.

The pumping rate of individual shad was obtained from the 16 mm movie films and visual timing using a stop watch. The film was analyzed using a microfilm reader. A shad's filtering rate could then be calculated by multiplying its pumping rate times its buccal volume.

Capture efficiency

The actual rate particles are inhaled is determined by the shad's capture efficiency which is a function of both the predator's capture and the prey's escape mechanisms. The shad's suction pump mechanism creates a velocity of water entering the mouth as well as a flow field in front of the mouth depending on the size of the mouth opening, the volume of the buccal cavity, and the rate of buccal cavity expansion (Nyberg, 1971). The flow of water into a fish's mouth is similar to the flow into a pipe (Alexander, 1967a).

I simulated a fishlike suction intake using a siphon system. The siphon system afforded control over the three variables of fish suction intakes; suction time, suction volume and mouth opening size. The suction time was set using a timed valve. The volume was regulated by siphon head. For example, increases in the siphon head increase the volume siphoned with suction time constant. The end of the tube into which the water was siphoned can correspond to mouth shape and size. The interaction of suction time, volume and mouth size then produce fishlike intake velocities and flow fields.

Rather than specifically mimic the intake of one fish species, I constructed a hypothetical yet ecologically meaningful fish suction, based on the results of my studies as well as other studies on fish feeding mechanics. Buccal volumes usually range from 5 to 8 ml/100 gram body weight (Alexander, 1970). The rate of buccal cavity expansion can be measured as the time between mouth opening and mouth closure. Studies have found it to be 0.06 sec for *Hoplias malabaricus* (Lauder, 1976), 0.04 sec for *Micropterus salmoides* (Nyberg, 1971) and 0.85 sec for *Helostoma temmincki* (Liem, 1967).

The siphon system that I constructed (Fig. 2) consisted of a glass tube 1.2 cm O.D. and 1.0 cm I.D. whose intake end was horizontally mounted in the center of a 20 gal aquarium. The round end of the tube corresponds to the rounded, not notched, open mouths of planktivores such as bluegill sunfish, white crappie, and gizzard shad.

Water was siphoned into the tube, through a vibration damper loop, down 100 cm of glass tubing, and through a solenoid valve (Fig. 3). The valve consisted of two 6 mm brass plates which had a brass sliding plate between them. The external plates had a 1 mm deep groove, 33 mm in width, routed in them to contain the sliding plate. A hole, 8 mm in diameter in the center of the plate, allowed flow through the valve. Two cm long sections of brass tubing, 1.5 cm in diameter, were used as an entrance and exit to the valve. O-rings, seated in circular grooves surrounding the inside of the valve entrance and exit, sealed the flow through the valve. The valve was opened by activation of a Guardian Electric solenoid which pulled the sliding plate to an open position where the hole lined up with the entrance and exit tubes. It was closed by a spring which pulled the sliding plate to a closed position when the solenoid was deactivated. The length of time the solenoid held the valve open was controlled by an Industrial Solid State Controls timer. The simulated suction used in these experiments inhaled 10 ml of water in 0.40 sec using a siphon head of 50 cm.

Figure 2. Siphon system used to simulate fish suction intake. See text for explanation.

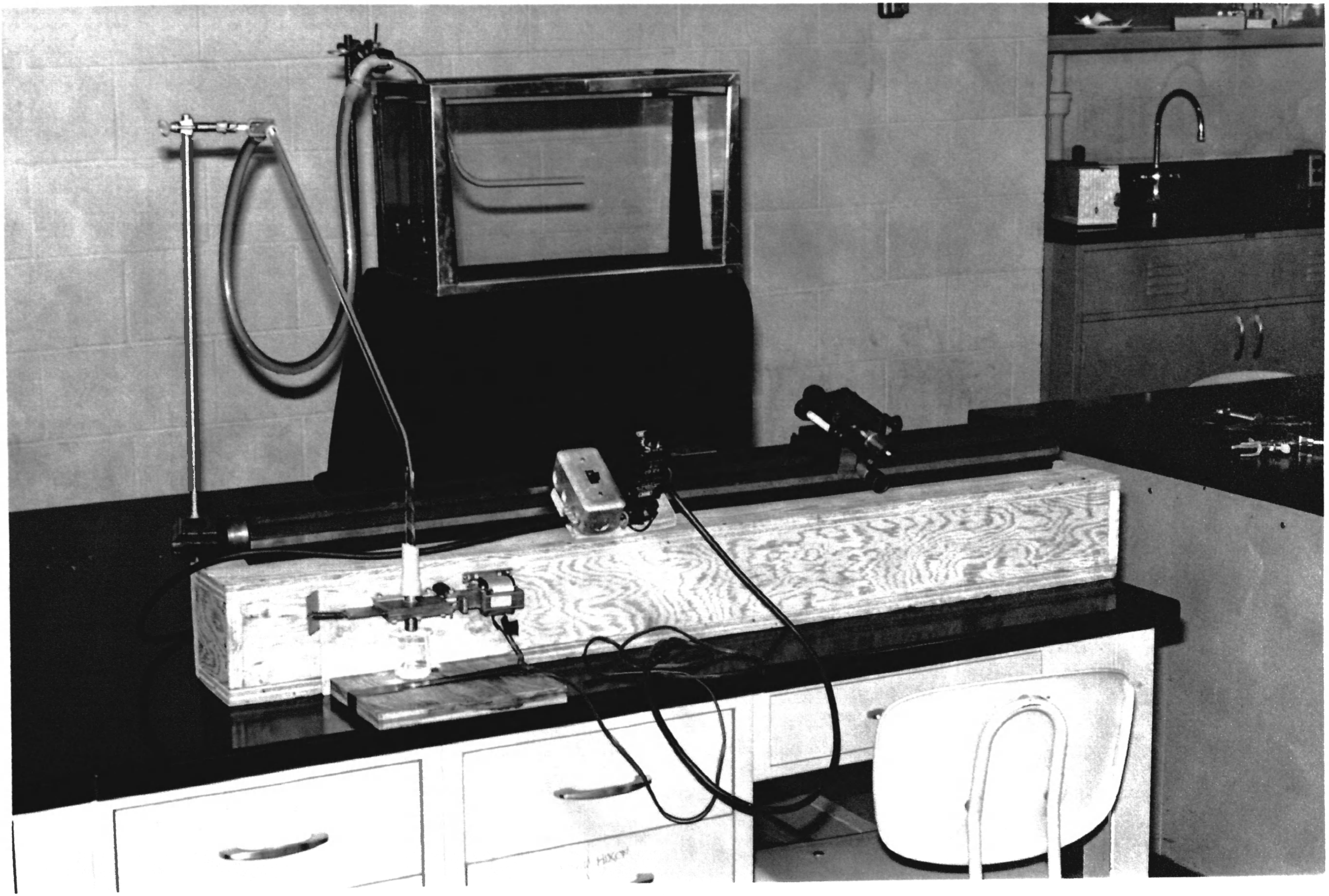
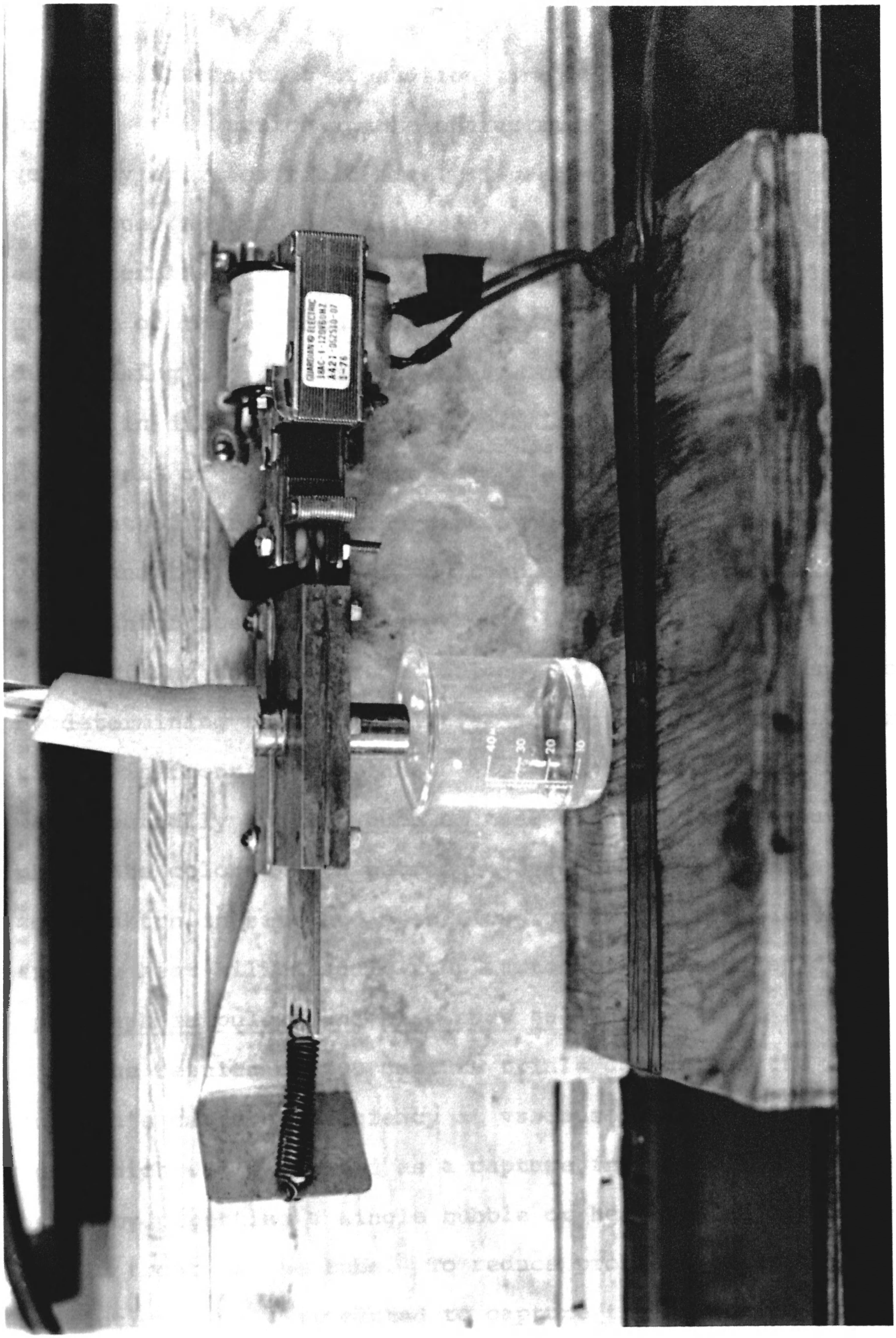


Figure 3. Solenoid valve in closed position. See text for explanation.



The interaction of suction time, volume and mouth size produces the suction intake characteristics such as water velocity and flow field size. I used the hydrogen bubble technique (Schraub et al., 1965) to observe the flow field and determine water speed in front of the tube as well as the contour of the suction volume. Hydrogen bubbles were produced using a platinum wire as the cathode. The wire was .08 mm in diameter and suspended below the suction tube. Hydrolysis of the water produced a curtain of hydrogen bubbles in front of the tube. The siphon system could then be activated and the movement of the bubbles into the tube filmed with a high speed movie camera.

I found the capture efficiency of the simulated suction by determining the probabilities of capturing nonmotile particles in front of the tube. The nonmotile particles used were neutrally buoyant bubbles made of xylene and n-butyl phthalate colored with petroleum dye which were similar to zooplankton in size and specific gravity. I also used freshly heat-killed adult zooplankton of the species *Chaoborus* sp., *Daphnia pulex*, and *Diaptomus pallidus*.

The results of 200 capture trials determined the suction's capture efficiency at various distances from the tube which was expressed as a capture frequency. Each trial began by pipetting a single bubble or heat-killed zooplankter in front of the tube. To reduce problems of spatial resolution I only attempted to capture the nonmotile particles and zooplankton when they were directly in front of the tube and along the axis of the tube (Fig. 9). Once a particle was positioned along the axis, I measured the distance between the opening of the tube and the center of the particle using a horizontal cathetometer (Fisher Scientific) (Fig. 2). The siphon system was then activated and the capture success observed.

I determined the capture probabilities for live zooplankton using zooplankton recently obtained from local lakes. *Cyclops scutifer*, *D. pulex* and *Chaoborus* sp. were captured in Fullers Pond, Conn. while *Ceriodaphnia reticulata*, cyclopoid copepods (mostly *Cyclops* sp. and *Mesocyclops* sp.), *D. galeata mendotae* and *Diaptomus pallidus* came from reservoirs or ponds near Lawrence, Kansas. Capture trials always used zooplankton within 3 days of capture from the lake. Water temperature ranged from 19 to 21°C. A diffuse light source consisted of a 75 watt bulb suspended in a 20 liter plastic jug. The jug contained 5 cm of water which absorbed heat and provided low heat illumination.

Trials were conducted with zooplankton swimming freely in the aquarium. A second person sat behind and somewhat above the tube to give depth of field. When a zooplankter swam within 2 mm of the axis (Fig. 9), the cross hairs of the cathetometer eyepiece were aligned with the center of the body and the siphon system was activated. I then determined whether the capture trial was concluded successfully or unsuccessfully by observing whether the animal was in the tube or had escaped capture.

To test the results of the capture experiments, the relative feeding rates of gizzard shad on a mixture of different zooplankton were determined in laboratory experiments and compared to predictions based on the capture probabilities obtained from the capture experiments. For each experiment 31 to 38 gizzard shad were placed in a plastic swimming pool containing 120 to 150 liters of water. Invertebrate predation and other effects were monitored in a control pool of the same volume without shad. An experiment began when freshly caught zooplankton were poured into the pools. Following a thorough mixing of the pools, zooplankton were sampled by quickly lowering a clear plexiglass tube, 6.9 cm in diameter, onto a rubber stopper which had been randomly placed on the pool bottom. The tube, which now contained a column of water, was removed from the pool, column height recorded, and the contents preserved in 10% formalin. One to three such samples were made at each sampling time. A tube was used because it is an effective method of capturing zooplankters. Szlauer (1964) found that a transparent tube lowered quickly caught *Daphnia* most effectively. Janssen (1976b) found that a tube with nylon netting on one end captured *Diaptomus oregonensis* more efficiently than a suction mechanism. Initial total zooplankton concentrations ranged from 13.5 to 376.0 org/liter. Five trials were conducted in room lighting and three in the dark.

Filtering efficiency

Particles inhaled into the shad's mouth must be strained from the water by the gill rakers. The gill rakers are comblike structures lying along the gill arches. The gill arches of Dorosoma seem to be one of the most highly specialized of clupeid fishes, with the absence of teeth, the presence of well developed epibranchial organs and numerous gill rakers (Nelson, 1967b). These specializations are indicative of microphagous feeding habits (Nelson, 1967a). Other studies have also used gill raker number as an indicator of feeding habits (Fryer, 1959). However, it is the interraker distances, the distances between gill rakers, that determine the size filtering efficiency of fish.

Interraker distance was measured on the gill rakers from shad which had been preserved in a 10% formalin solution. All of the shad had been captured using an electrofishing unit and immediately preserved to reduce mucous discharge. To measure interraker distance, the gill arches were wet dissected from the opercular cavity. The row of rakers was removed by stripping the fiberlike base from the gill arch. The row of rakers was then placed on a microscope slide. Water was gently dropped on the rakers to eliminate dessication as well as suspend rakers in an unrestricted position.

Gill raker spacing must be weighted by raker length to compute filtering efficiency. For example, the short rakers at the ends of a gill arch contribute less to filtering because their filtering surface area is smaller. Therefore, the raker rows were broken up into a series of trapezoids. The formula for trapezoid surface area is:

$$1/2(a + b)h$$

where a & b are the length of the sides and h is the length of the base.

Gill raker measurements were made on an inverted microscope. Measurement began by measuring the length of a; moving laterally 745u and measuring two interraker spaces; then moving laterally 745u and measuring b. Each trapezoid section of rakers would then have a base h of 1490u. The gill rakers of a shad could then be expressed as a series of filtering surface areas, each area having a filtering effectiveness represented by the mean of the two interraker spaces in its center.

Feeding rate

The results from the previous observations and experiments can be tested by using them to predict the feeding rate of omnivorous shad. The feeding rate should be equal to the multiple of four variables: (1) food density, (2) filtering rate, (3) capture probability for that food item, and (4) filtering probability for that food item. The feeding rate calculated from the above equation was used in a computer simulation of the changes in zooplankton density occurring in an aquarium containing a feeding shad. To test the validity of the feeding rate model, this simulation was then compared to observed changes in zooplankton densities caused by a shad's feeding. The experiment was performed in an aquarium so that the shad's pumping rate could be monitored.

The feeding rate experiment began by pouring freshly captured zooplankton into a 20 gal aquarium containing a gizzard shad. Zooplankton density was monitored using a clear plexiglass tube in a similar manner used in the capture efficiency pool experiments. Filtering rate was calculated by multiplying the buccal volume of the shad times the pumping rate which was determined using a stopwatch and a counter. Capture and filtering probabilities associated with each prey type were obtained from results of the previous capture efficiency experiments and gill raker spaces measurements. Changes in zooplankton density were simulated by calculating the number of prey captured by a suction, subtracting these prey from the total number in the aquarium and recomputing the prey density. This sequential computation began using the initial observed density and was repeated for the number of suctions occurring through some time interval. The simulated densities could then be compared to actual prey densities observed in the aquarium at the same time.

RESULTS AND DISCUSSION

Feeding mechanics

Fish can capture prey in three ways (Alexander, 1967a). (1) The fish can swim up to the food with an open mouth. The mouth just encloses the food. The anchovy *Engraulis* feeds in this manner in dense plankton (Gunther, 1962). Other method 1 type feeders are *Euthynnus* (Walters, 1966) and *Lepisosteus* (Alexander, 1967a). (2) A stationary fish can suck food into its mouth by enlarging its buccal and opercular cavities. In addition to Alexander's (1967a) examples of method 2 feeding [the angelfish (*Pterophyllum*), the orfe (*Idus*) and the sea horse (*Hippocarpus*)] I have observed that bluegill sunfish and white crappie feed using method 2. (3) A fish can use a combination of (1) and (2). The fish swims toward the food and sucks at the same time. A pike is an example of method 3 (Alexander, 1967a).

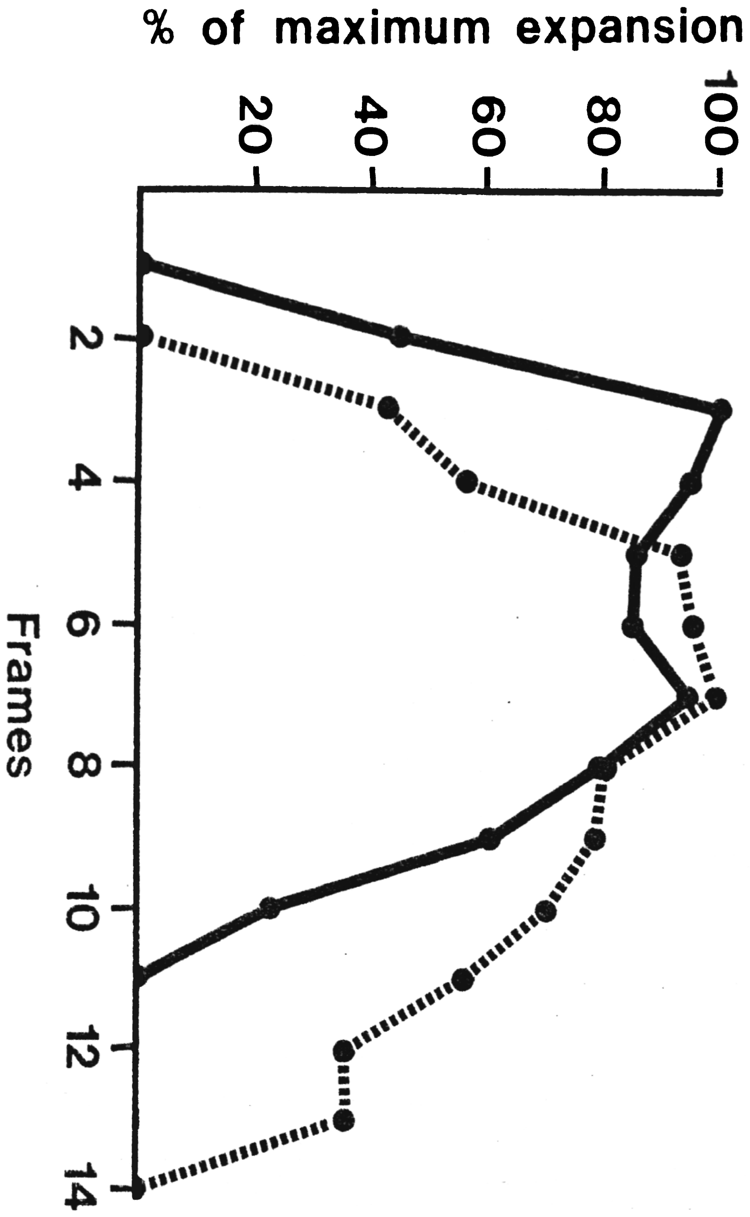
Tiffany (1921a) incorrectly hypothesized that shad filter-fed by method 1 or like a living "townet". My filmed laboratory observations showed shad to feed by swimming through the water, capturing food using a series of rapid suctions that were not visually directed toward individual food items. Because their swimming is slow and undirected, I feel that swimming is an insignificant component of their capture of prey, and that their filter-feeding is mechanically most similar to method 2.

Films of changes in the profile of the shad's head while feeding showed that the suction was created by a two pump system mechanically similar to the systems used by other teleosts in feeding (Alexander, 1967a; Nyberg, 1971; Liem, 1967) and respiration (Hughes and Shelton, 1958; Osse, 1969; Ballintijn and Hughes, 1965). Figure 4 shows the sequential relationship of the two pumps. First the mouth opens and the buccal cavity expands. This is accomplished by (1) contraction of the levator operculi muscle which depresses the mandible and (2) contraction of the dorsal musculature which lifts the head (Liem, 1967). These movements create a low pressure area which inhales water into the buccal cavity. Secondly the branchiostegal membrane spreads and opercles flair moving the low pressure area posteriorly and drawing water through the gill rakers.

Closing is not the reverse of opening as suggested by Schaeffer and Rosen (1961). A reversal of the movements would force water out of the mouth. In fact a reversal of movements is used by fish to reject prey after the prey have been captured (Nyberg, 1971).

Mouth closure begins while the opercular cavity is still expanding (Fig. 4), reducing potential backflushing. Alexander (1967a) felt that backflushing might occur in

Figure 4. Sequential relationship of the buccal and opercular pumps of a feeding gizzard shad, 8.28 cm in standard length. The vertical opening or expansion of the mouth associated with the inhaling of water using the buccal cavity pump is represented by the solid curve. The ventral expansion of branchiostegal rays associated with the drawing of water through the gill rakers by the opercular pump is shown by the broken curve. Data was obtained by analyzing films taken at 64 frames/sec of the side of a feeding shad's head as shown in Fig. 1.

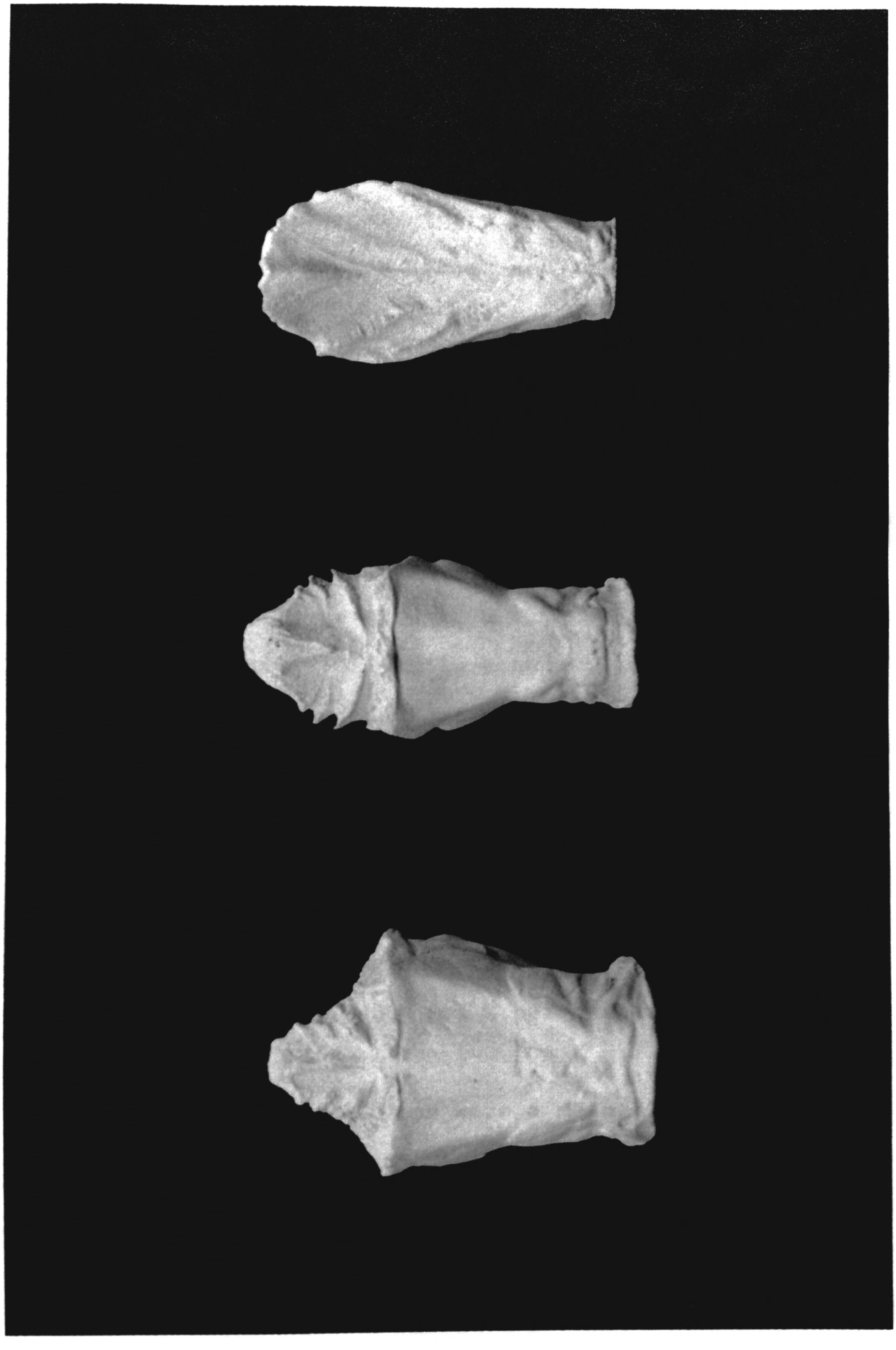

% of maximum expansion
100
80
60
40
20
2
4
6
8
10
12
14
Frames

species without protrusible mouths such as the gizzard shad and result in a loss of buccal volume. I have occasionally observed small backflushes in front of gizzard shad feeding along a silt covered aquarium bottom. However these backflushes appeared to be very small. I feel that two-pump system creates a posteriorly directed momentum which reduces such backflushes to volumes that are insignificant in relation to overall filtering volumes.

The morphology and volume of the expanded buccal cavities of the three planktivores were different (Fig. 5). The protrusible upper jaws of the crappie and sunfish are responsible for the anterior tubelike extensions of the buccal cavity. This jaw protrusibility is found in about half the living species of teleosts (Gosline, 1961; Marshall, 1965) and reflects an advanced state of mouth evolution (Alexander, 1967a) which increases suction effectiveness by getting the mouth opening close to the food (Alexander, 1967b) and by permitting a greater expanded buccal volume during mouth closure (Alexander, 1966, 1967b).

The open mouths of the three planktivores were rounded. The roundness is achieved by the depression of the jaw causing the maxilla to swing forward and fill in the corner of the open mouth, making it round. Round mouths are much more efficient than notched mouths in capturing food. Fish with round mouths can capture prey at a greater distance with a faster intake velocity (Lauder, 1976).

Figure 5. Plaster molds of expanded buccal cavities of three planktivores. From left to right, a 11.2 cm SL white crappie, a 10.5 cm SL bluegill, and a 14.3 cm SL gizzard shad.

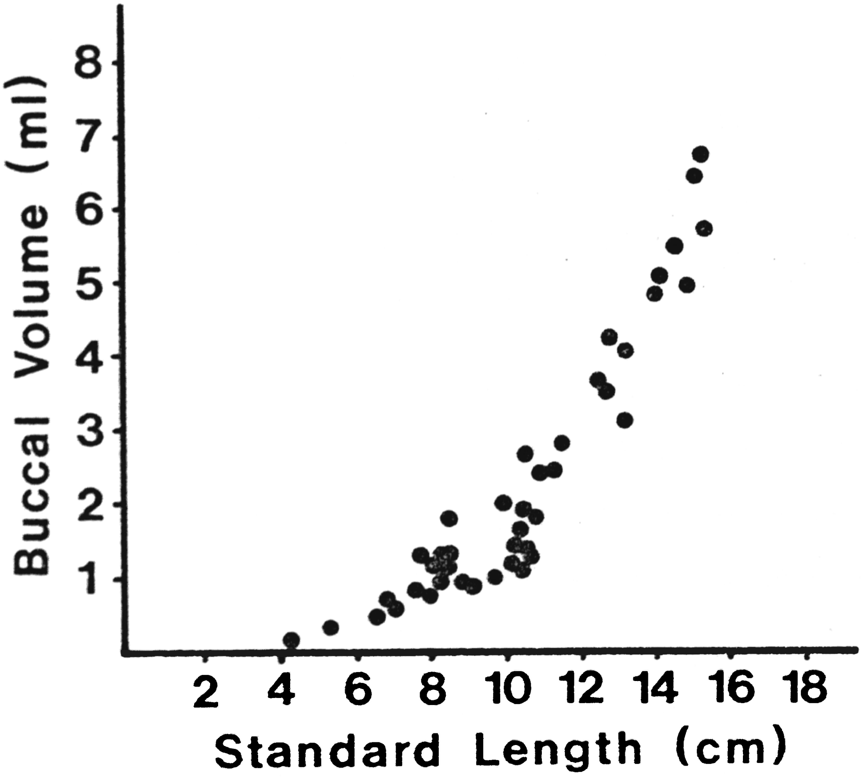


The area of the open shad's mouth was smaller than the other two planktivores. This may reflect the fact that shad are obligate planktivores while crappie and bluegills are facultative planktivores. The size of fish mouths has been correlated with food size (Keast and Webb, 1966). Mouth size limits the size of prey taken into the mouth (Alexander, 1967a). The size of the mouth is also significant in terms of the flow field characteristics (Alexander, 1967a; Nyberg, 1971). The smaller the diameter of the mouth the faster the speed of water entering the mouth. Decrease in mouth diameter increases the maximum distance from which prey can be sucked into the mouth. These effects would be advantageous for a fish suction-feeding on mobile prey such as zooplankton.

The buccal molds of different sized shad showed that the volume of the expanded buccal cavity increased as a power function of shad standard length (Fig. 6). The function, fitted by the Hewlett Packard Stat Pac 124A, was represented by the equation $Y = (3.52 \times 10^{-6})X^{2.8185}$ and had a coefficient of determination of 0.82 with Y being buccal cavity volume in ml and X being shad standard length in mm.

The shad buccal volumes were a mean 3.84 ml/100 gram body weight ± .92 standard deviation. Body weight was calculated from total length measurements using Schneider's (1969) equation for shad body weight as a function of length: $\log W = 4.09229 + 2.71712 \times \log L$. Expanded buccal volumes

Figure 6. The volume of the expanded buccal cavity versus shad standard length.


Buccal Volume (ml)
1
2
3
4
5
6
7
8
2
4
6
8
10
12
14
16
18
Standard Length (cm)

generally range from 5 to 8 ml/100 gram body weight although Anguilla has a buccal volume of 2.3 ml/100 g (Alexander, 1970). Hughes found a maximum respiratory stroke volume of 5.0 ml/100 g for Callionymus lyra and 5.0 ml/100 g for Salmo gairdneri (personal communication to Alexander, 1970).

As shad increase in length their pumping rate decreases (Fig. 7). This decrease is probably due to the longer distances the skeletal elements must move. The curve was fitted best by the linear function $Y = 461.74 + -1.87X$ and had a coefficient of determination of 0.96 with Y representing pumping rate in pumps/min and X representing shad SL in mm.

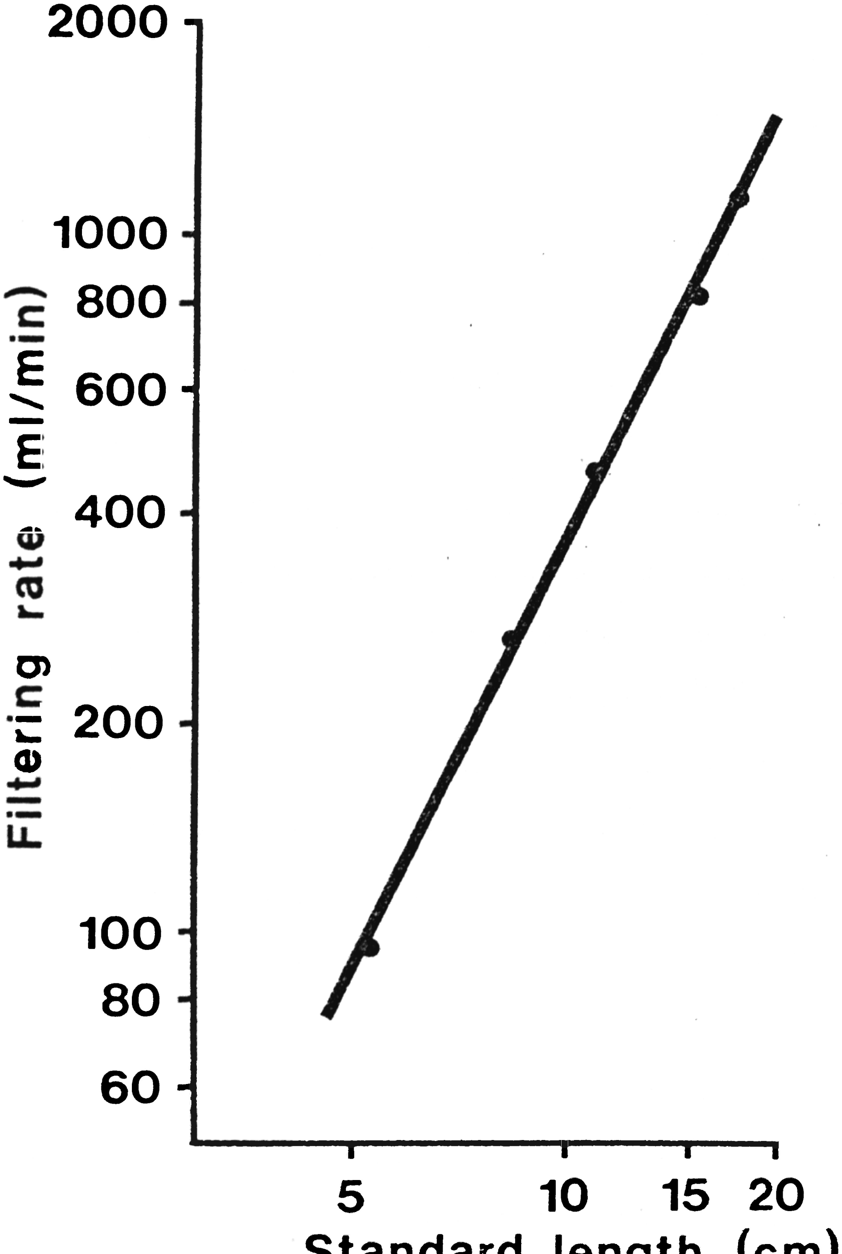
A shad's filtering rate, the volume of water inhaled per minute, was then calculated by multiplying the observed pumping rate times the buccal volume computed from the power curve for buccal volume as a function of standard length. The calculated filtering rate increases as a power function of shad standard length with shad of 17 cm SL filtering over one liter of water per minute (Fig. 8). The function was described by the equation $Y = .031X^{2.041}$ and had a coefficient of determination of .997. This filtering rate is a maximum rate because it is calculated based on maximum expansion of the buccal cavity and pumping rates associated with warm water temperature.

Capture efficiency

As expected from fluid mechanics models of water flow

Figure 7. The pumping rate of feeding shad versus shad standard length.

Figure 8. Maximum filtering rate versus shad standard length. Filtering rate was calculated by multiplying maximum buccal cavity volume (obtained using the function of buccal volume and standard length) times the observed pumping rates.


2000
1000
800
600
400
200
100
80
60
Filtering rate (ml/min)
5
10
15
20
Standard length (cm)

into a pipe (Bird, Stewart and Lightfoot, 1960), the hydrogen bubble technique showed that the flow field in front of the siphon tube was axial symmetric (Fig. 9). The pathlines, the paths the hydrogen bubbles traveled into the tube, were straight along the center axis of the tube and became curved for bubbles off the axis. This flow field is similar to the flow field in front of a fish's mouth (Alexander, 1967a).

The speed of water was measured on the pathlines along the center axis and is shown in Fig. 10. The speed decreased with distance away from the tube. Speed increased during the 0.4 second long suction. At 0.04 sec the speed of water as an exponential function of distance from the tube was represented by the equation: $Y = 201.67e^{-9.84}X$. At 0.32 sec the water speed was represented by the equation: $Y = 2161.39e^{-10.21}X$ with Y in cm/sec and X in mm.

The capture experiments consisted of attempts to capture particles or organisms with the siphon system's simulated fish suction. Only particles or organisms along the center axis of the tube (Fig. 9) were considered in the capture experiments. The results of these trials are shown in Figure 11. The capture frequency of the neutrally buoyant bubbles was identical to the capture frequency of the heat-killed zooplankton. This shows that particle shape is not important in evasion of the flow field.

I then determined the capture frequency for live

Figure 9. The flow field around the end of the siphon tube. The symbols are: C, intake contour; A, center axis of the tube; and T, tube. The figure was created by superimposing 4 successive frames of movie film.

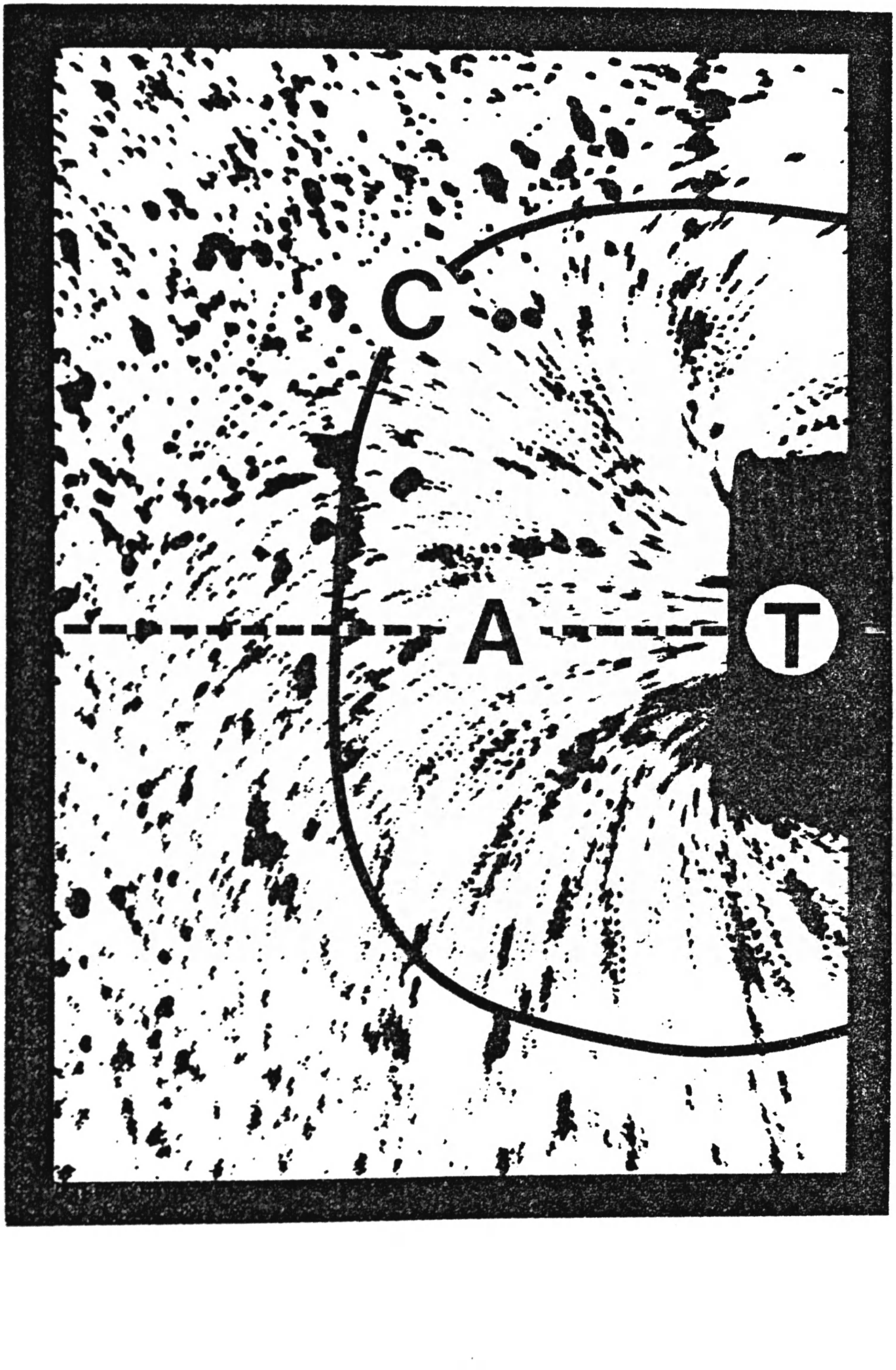
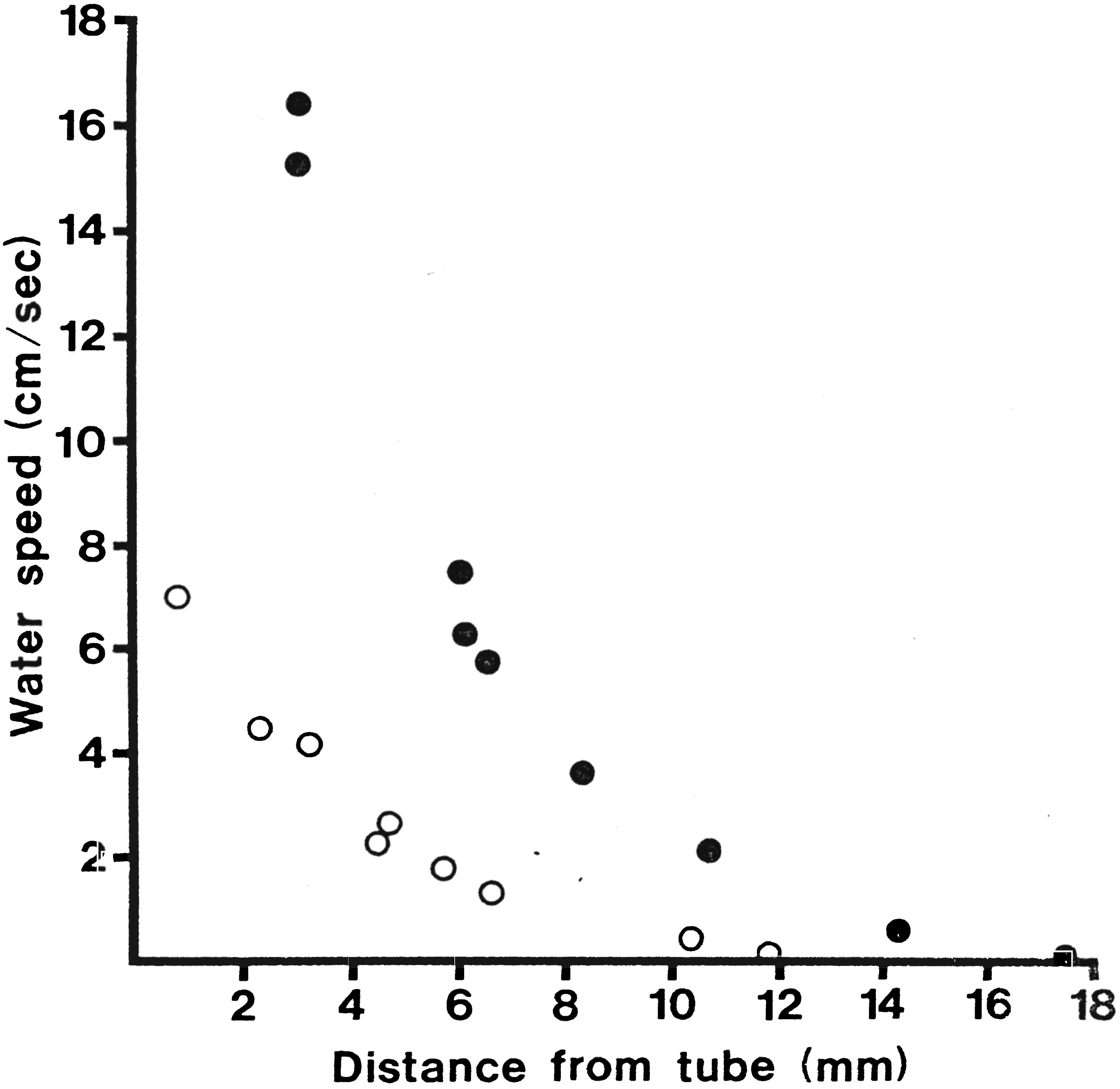

C
A
T

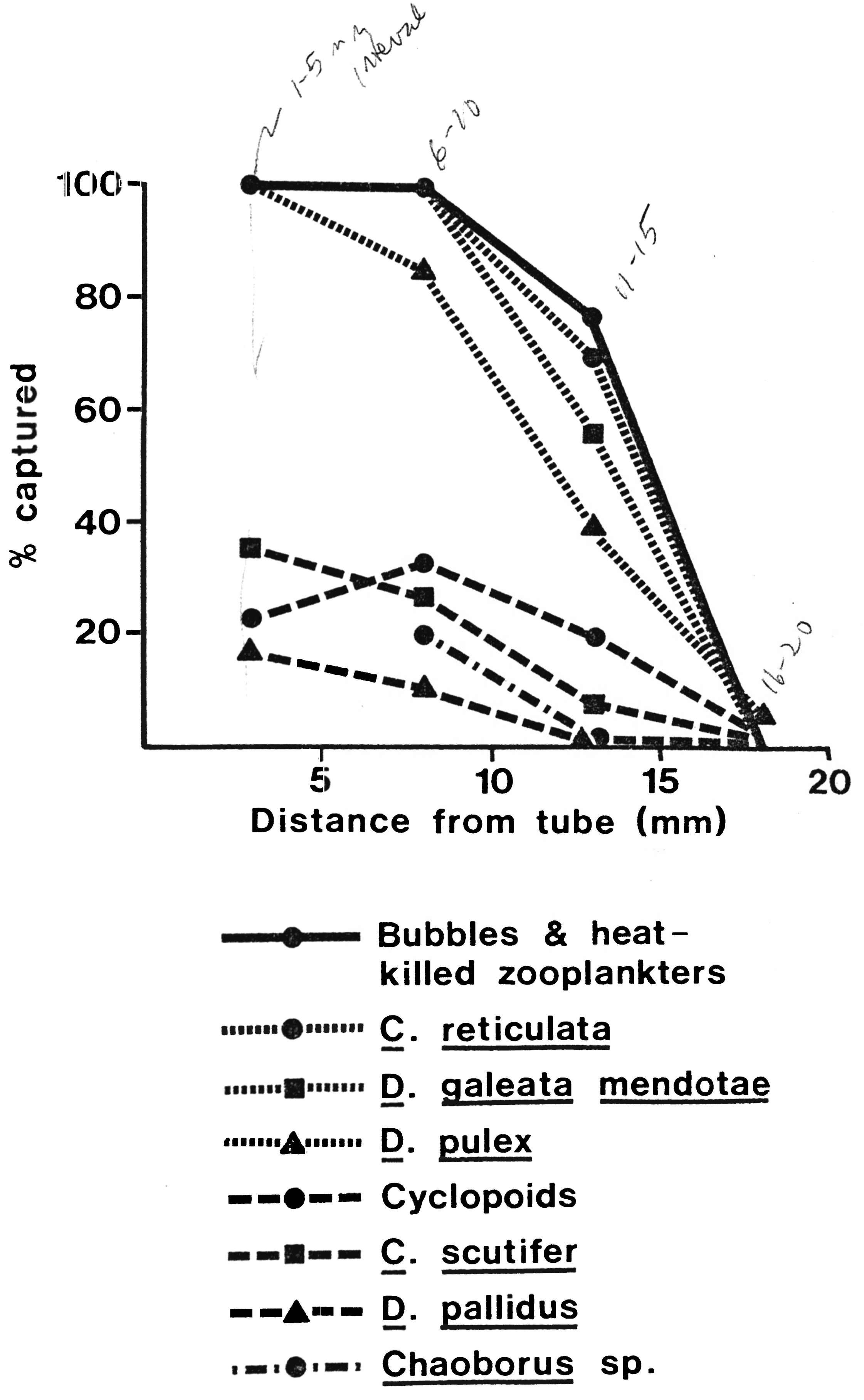
Figure 10. The speed of water along the tube axis versus distance from the tube. Light points represent speeds occurring 0.04 sec after the suction began. Dark points represent speeds occurring 0.32 sec after suction began.


18
16
14
12
10
8
6
4
2
Water speed (cm/sec)
2
4
6
8
10
12
14
16
18
Distance from tube (mm)

zooplankton swimming freely in front of the siphon tube. The capture frequencies of the small cladocerans _C. reticulata_ and _D. galeata mendotae_ (Fig. 11) were not significantly different than the capture frequency for dead zooplankton using a G-test (Sokal and Rohlf, 1969). The larger cladoceran, _D. pulex_, could escape significantly better ($P < .05$). These cladoceran capture frequencies reflect the importance of body size in zooplankter escape. Rosenthal (1972) found that zooplankter cruising speeds increased with zooplankter size. Higher cruising speeds decrease cladoceran capture probabilities by offsetting the slow reaction times and escape speeds of cladocerans. Cushing (1955) found that _Daphnia_ could swim at speeds up to 6 cm/sec.

Cruising speed is less significant in copepod escape which relies on faster reaction times and escape speeds. Copepods perceive the hydrodynamic disturbances with their mechanoreceptors and react very quickly (Strickler, 1975). _Cyclops_ can gain a speed of 8 cm/sec in ten milliseconds and reach speeds of 30 to 50 cm/sec (Strickler, 1975) while _Diaptomus_ can swim at speeds up to 147 cm/sec (Swift and Fedorenko, 1975). Comparison of cladoceran and copepod swimming speeds with the intake water speed of the siphon system (Fig. 10) reveals the significance of reaction time and escape speed in avoiding capture and explains why the cyclopoid copepods, _C. scutifer_, and _Diaptomus pallidus_ could escape significantly better than the cladoceran

Figure 11. Percent of particles and organisms captured by siphon system versus their distance from the tube. The points plotted at distances 3, 8, 13 and 18 mm represent averages of capture success within the intervals of 1 to 5 mm, 6 to 10 mm, 11 to 15 mm, and 16 to 20 mm, respectively.


1-5 mm interval
6-10
11-15
16-20
% captured
100
80
60
40
20
5
10
15
20
Distance from tube (mm)
Bubbles & heat-killed zooplankters
C. reticulata
D. galeata mendotae
D. pulex
Cyclopoids
C. scutifer
D. pallidus
Chaoborus sp.

zooplankters ($P < .005$). Water speed quickly accelerated so that the speed close to the tube was above cladoceran escape speeds. Therefore, the siphon system captured 100% of the cladocerans close to the tube. Copepod escape speeds were faster than the water speeds, enabling a large percentage of copepods to escape even the fastest intake speeds.

The capture frequency of the cyclopoid copepods (*Cyclops* sp. and *Mesocyclops* sp.) was significantly different than the *Diaptomus pallidus* frequency (Fig. 11) ($P < .01$). The difference in the capture frequencies of the cyclopoid and calanoid copepods is not only due to swimming speed but also reaction direction. Cyclopoids facing the tube must first turn to swim away, whereas the calanoids can escape with a flip of the first antennae (Strickler, personal communication).

I then define 100% capture probability as the area under the capture frequency curve for nonmotile particles and dead zooplankters (Fig. 11). The capture probability of live animals is the ratio of the area under the animal's capture frequency curve divided by the area under the 100% capture frequency curve (Fig. 11). These calculated capture probabilities were highest for the cladocerans *C. reticulata* ($P = 0.96$), *D. galeata mendotae* ($P = 0.92$) and *D. pulex* ($P = 0.76$); intermediate for cyclopoid copepods (*Cyclops* sp. and *Mesocyclops* sp.) ($P = 0.28$) and *Cyclops scutifer* ($P = 0.24$); and lowest for *Diaptomus pallidus* ($P = 0.07$) and *Chaoborus* sp. ($P = 0.09$).

Several other studies have found capture probabilities to vary with prey types. Herring larva (Clupea harengus) captured Artemia nauplii 100% of attempts but captured Artemia metanauplii 96.5% (Rosenthal, 1969). This decrease in capture probabilities with increase in age found in copepods has also been found in other predator-prey interactions (summarized in Curio, 1976). The 95% capture probability of wild dogs for Thomson's gazelles less than 2 months old decreased to 49% for Thomson's gazelles older than 2 months. Cheetahs had a 100% capture probability for Thomson's gazelle fawns and only a 54% capture probability for Thomson's gazelle adults.

How significant differential capture probabilities are in fish feeding depends on the type of planktivore. For those fish that do not visually select individual prey, such as filter-feeders feeding at night, capture probability is a major component of selection. Such fish attack and encounter prey in proportion to prey densities. Because the probability of ingestion after capture (filtering efficiency) is determined by the relative size of the prey and the interraker distance, ingestion probability is similar for all prey of similar size and all prey larger than the 100% filtering efficiency size. Thus the diet of filter-feeders on similar sized prey will be determined primarily by differential capture probabilities.

The results of the shad feeding experiments support these conclusions. While the zooplankton densities did not change in the control pools, the densities did decrease in the shad pools as predicted from the capture probabilities (Fig. 12). Cladoceran densities decreased more rapidly than copepod densities. All zooplankton were larger than the 100% filtering efficiency size and therefore changes in zooplankter density were due to differential capture probabilities.

Shad feeding rate constants (k) were calculated using Dodson's (1975) procedure with the dimensions of k being liters/hour. Shad feeding rate constants were lowest on *Diaptomus* spp. ($\bar{x}k = 0.67$), intermediate on cyclopoid copepods ($\bar{x}k = 1.37$), and highest on *D. galeata mendotae* and *C. reticulata* ($\bar{x}k = 3.60$ and 3.00, respectively). The feeding rate on copepod nauplii was also high ($\bar{x}k = 4.01$). A multiple comparison by STP test (Sokal and Rohlf, 1969) of the feeding rate constants on all zooplankton species showed the feeding rate constant for *Diaptomus* spp. to be lower ($P < 0.05$) than the feeding rate constants for *C. reticulata*, *D. galeata mendotae* and copepod nauplii.

Fig. 13 shows the mean shad feeding rate constants for zooplankton prey plotted against the zooplankton capture probabilities. Feeding rate constants were a linear function of capture probability. The regression line was $Y = .44 + 3.23X$ which had a coefficient of determination of .94 with Y representing mean feeding rate constant (liters/hr) and X representing capture probability. As shown in Fig. 13, I

Figure 12. Density of zooplankton as a percent of initial density in the control and fish pools versus time.

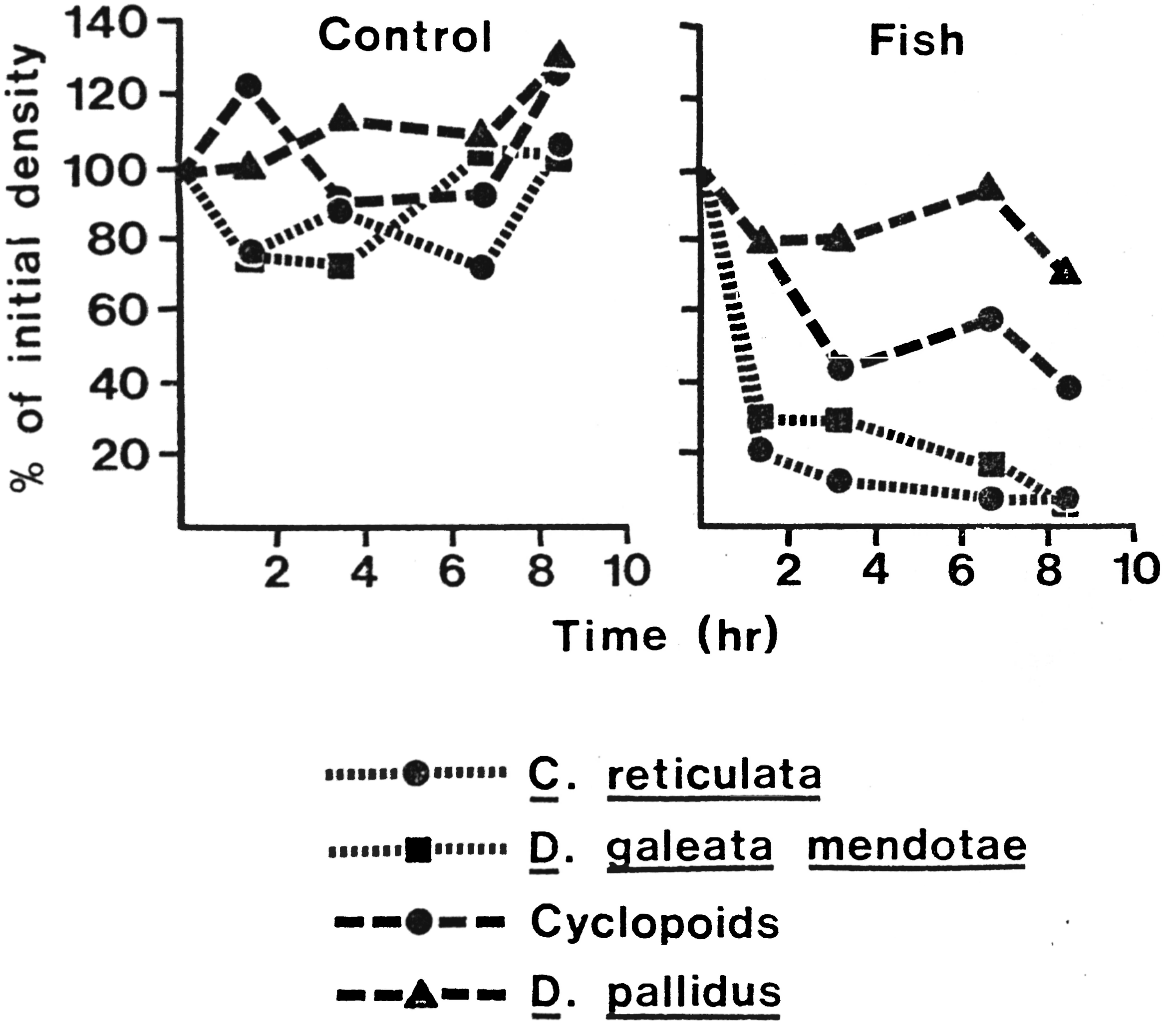
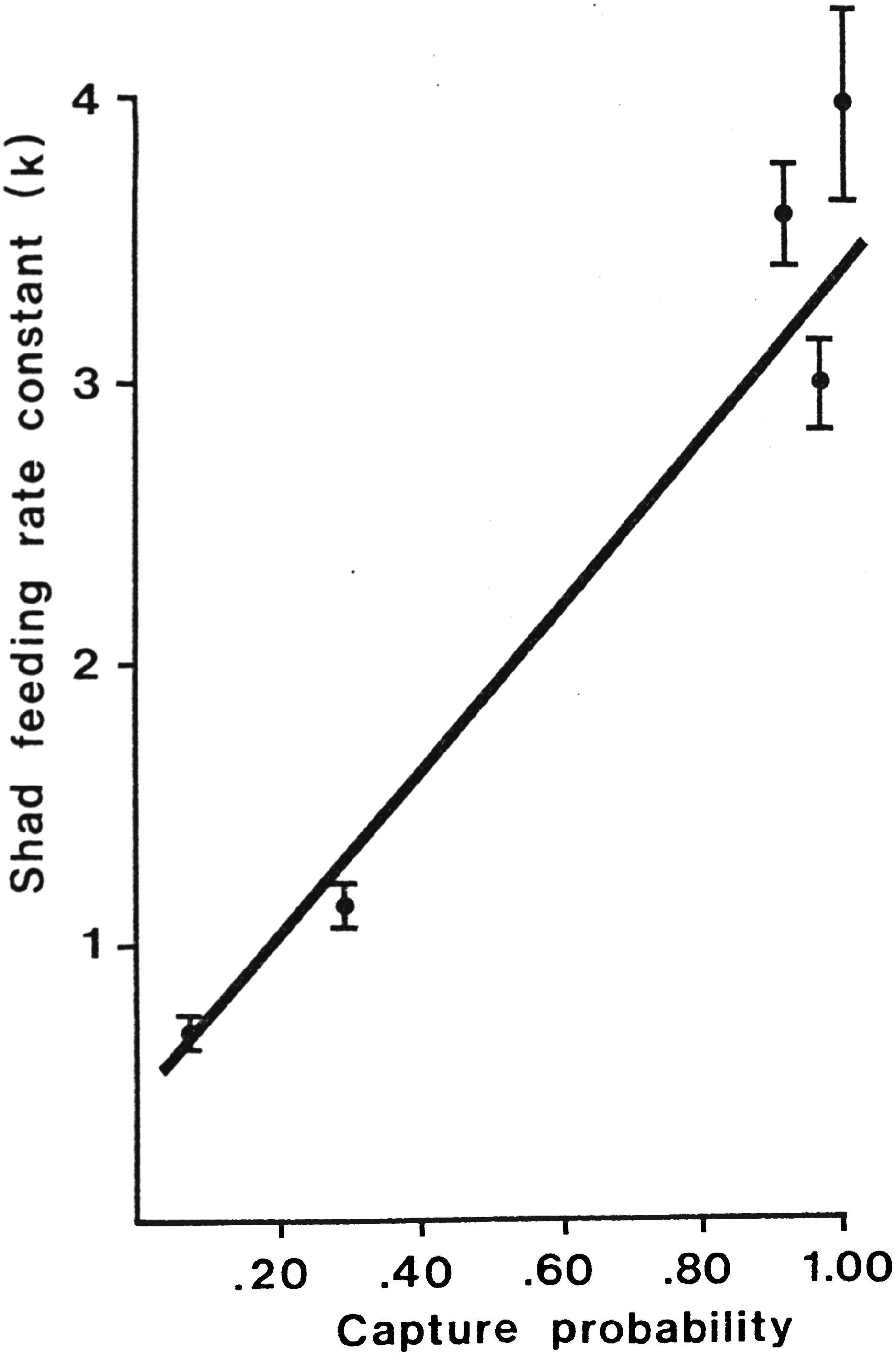

Control
Fish
% of initial density
140
120
100
80
60
40
20
2
4
6
8
10
Time (hr)
C. reticulata
D. galeata mendotae
Cyclopoids
D. pallidus

Figure 13. Mean shad feeding rate constants for zooplankton prey versus the capture probabilities of the simulated suction for zooplankton. From left to right, points represent *Diaptomus* spp., cyclopoid copepods, *D. galeata mendotae*, *C. reticulata* and copepod nauplii. The 100% capture probability used for copepod nauplii was obtained from Rosenthal (1969). Bars represent ± 1 standard error.



4
3
2
1
Shad feeding rate constant (k)
.20
.40
.60
.80
1.00
Capture probability

did not find zooplankton with intermediate capture probabilities. The absence of prey with intermediate escape abilities may be due to the small sample size or may reflect the ecological differences in copepod and cladoceran zooplankton (Allan, 1976).

These differential feeding rates have been reflected in shad stomach contents as apparent selectivities for copepod nauplii and cladocerans. Smith (1971) found nauplii and cladocerans but no adult copepods in shad stomachs although adult copepods were present in the lake. Cramer and Marzolf (1970) suspected zooplankton escape ability as a factor when they found that omnivorous gizzard shad stomachs had a lower proportion of *Diaptomus* than the lake samples.

Results of field studies substantiate the role of zooplankton escape in the apparent selectivity of filter-feeders. Begg (1976) found that the sardine (*Limnothrissa miodon*) selected *Bosmina longirostris* over *Mesocyclops leuckartii* at night. The alewife (*Alosa pseudoharengus*), which feeds either visually or by filter-feeding (Janssen, 1976a), selected *Bosmina* over cyclopoid copepods (Hutchinson, 1971).

The influence of zooplankton escape on the feeding of bigmouth buffalo (*Ictiobus cyprinellus*) was recognized by Starostka and Applegate (1970). They used Ivlev's (1961) electivity index to describe the feeding selectivity of adult bigmouth buffalo. Electivity is an index of the selectivity in a predator's diet. It does not distinguish between selectivity caused by predator selection versus apparent selectivity resulting from prey or environmental influences. The electivity value just reflects the difference in proportion of prey types in a predator's stomach to the proportion of prey in the environment. Therefore, electivity is an index of apparent feeding selectivity, not active selectivity by the predator. Positive values represent higher proportions in the stomach than in the environment and negative values represent lower proportions in the stomach than the environment.

In agreement with the results of my study, the buffalo had a positive electivity for adult D. pulex and a negative electivity for calanoid copepods. Cyclopoid copepods were fed on with a slightly positive electivity. The deviation of cyclopoid copepods from an expected negative electivity may be due to sampler electivity. A water core plankton sampler (Applegate et al., 1968) and a metered Miller sampler (Miller, 1961) were used to sample the lake plankton populations. These types of samplers have electivities (Langford, 1953; Fleminger and Clutter, 1965) and therefore may obscure the actual feeding electivities of the planktivore.

Zooplankton escape plays a less significant role in determining the feeding selectivity of visual-feeding planktivores. Their selectivity is also a function of differential encounter and attack probabilities (Werner and Hall, 1974; Confer and Blades, 1975; O'Brien, Slade, and Vinyard, 1976). Ingestion probabilities (filtering efficiencies) are probably not a significant determinant of the selectivity of visual-feeding planktivores (Gailbraith, 1967).

Capture probabilities may affect the feeding of visual planktivores indirectly as well as directly. The fish may learn to eat prey with limited escape ability by forming a search image (Beukema, 1968). Or the planktivore may learn to recognize prey with good escape ability and change the mechanics of its attack. The fish can change the intensity of its suction by expanding its buccal cavity more rapidly or by keeping its mouth opening smaller. It can also position its mouth closer to the prey which would increase the capture probability (Fig. 11). Such modifications of attack behavior may play a role in determining the capture probabilities of the sight-feeding pumpkinseed sunfish (*Lepomis gibbosus*) for zooplankton prey (Confer and Blades, 1975). The pumpkinseed's capture success, the ratio of the number of prey ingested to the number of prey pursued, was 100% for several species of *Daphnia*. The capture success for copepods was a function of fish learning, being initially low for fish which had been fed on *Daphnia* for several days. Experienced sunfish had a capture success of 79% for *Diaptomus sicilis* and 39% for *Diaptomus ashlandi*. Such learning time and capture probabilities may explain why Brooks (1968) found that *Daphnia* disappeared before *Epischura* from experimental pools containing visual-feeding Alosa.

Capture probability is significant in the effects of visual-feeding planktivores on lake zooplankton. Copepods can remain higher than cladocerans in the water column (Langford, 1953), where predation by visual-feeding planktivores is most intense. In deep lakes containing fish, copepods are often larger than cladocerans (Brooks and Dodson, 1965; Hutchinson, 1971) again showing that low capture probabilities can offset high attack probabilities associated with large zooplankton size.

Filtering efficiency

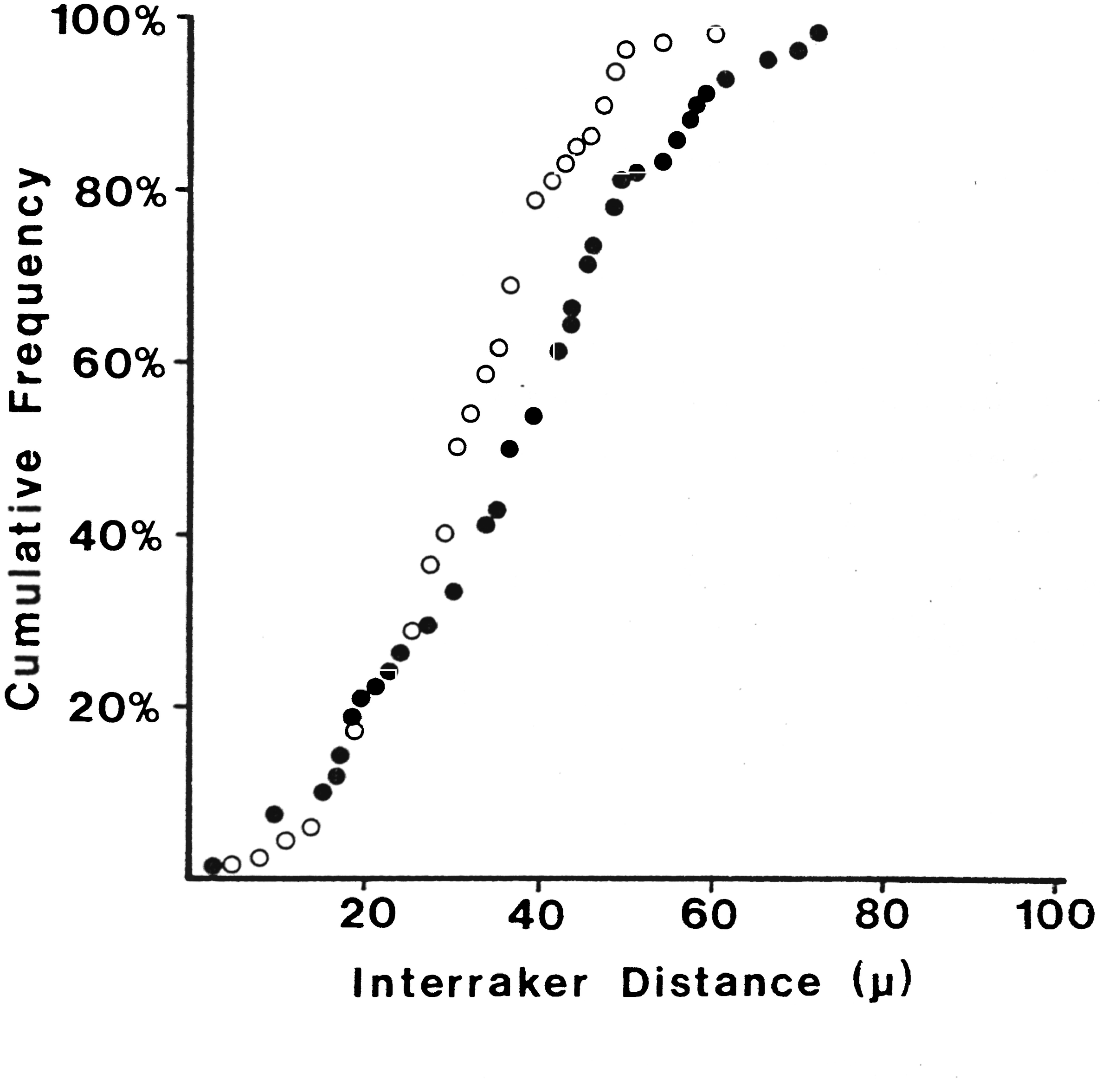
Following the capture of food items into their mouths, shad strain the items from the water with their gill rakers. The particles are incorporated into a mucous strand and passed into the epibranchial organs or the esophagus. The epibranchial organs consist of a paired dorsal diverticulum at the posterior limit of the pharynx and lying above the branchial arches (Nelson, 1967a; Miller, 1969). Although its development is correlated with microphagus feeding, studies have not determined its exact role in feeding. In this study I assume that it does not contribute significantly to feeding selectivity.

Kutkuhn (1957) measured the distance between the proximal ends of adjacent gill rakers in yearling gizzard shad. He found interraker spaces as fine as 14 microns, showing that shad's gill rakers could retain minute particles. However, he attributed their feeding selectivity to visual selection of individual plankton. It is unlikely that large shad visually select phytoplankton. Shad may reject algae based on taste, but this has not been observed. I feel that the selection of algae by shad is probably an apparent selectivity mechanically similar to the selection of algae by filter-feeding copepods (Boyd, 1976). The sievelike copepod mouthparts passively select for the larger particles out of an array of particle sizes because the larger particles are filtered with greater efficiency.

I used an analysis similar to Boyd's (1976) to examine shad filtering efficiency. I measured the distances between gill rakers and then constructed a cumulative frequency of interraker spaces, weighted for raker length, for a 76 and 129 mm SL shad (Fig. 14). The two frequencies were not significantly different according to the Smirnov test (Conover, 1971). The frequencies show that the filtering efficiency for particles 1 to 70 microns is a hyperbolic function of particle size with shad being able to filter particles 70 microns or larger with about 100% efficiency. This filtering efficiency would result in an apparent feeding selectivity for large algae versus small algae because large algae would be filtered more efficiently.

Substantiation of this hypothesis using the results of field studies is difficult. Shad may have been feeding in

Figure 14. Cumulative frequency of shad interraker spaces, weighted for raker length. Closed circles represent a 76 mm SL shad and open circles represent a 129 mm SL shad.


100%
80%
60%
40%
20%
Cumulative Frequency
20
40
60
80
100
Interraker Distance (μ)

a different area in the lake than the phytoplankton samples were taken. Kutkuhn (1957) presented only part of his results and therefore a comprehensive analysis is not possible. The algae that were selected by the shad (Kutkuhn, 1957) and their approximate sizes (estimated from Prescott, 1962) included the filamentous bluegreen *Anabaena spiroides* (> 100µ long), the colonial bluegreen *Microcystis aeruginosa* (> 80µ in diameter) and the green algae *Golenkinia radiata* (> 60µ including spines). These algae were larger or close to the shad's 100% filtering efficiency.

It is difficult to accurately assess Smith's (1971) results because he does not report species names. He found shad to selectively feed on *Glenodinium* sp. and *Dinobryon* sp. which are both usually larger than the shad's 50% filtering efficiency. Although roughly confirming my hypothesis, more quantitative field and laboratory studies are needed.

The filtering efficiency of bigmouth buffalo also results in an apparent selectivity for large algae (Starostka and Applegate, 1970). They found the interraker spaces of buffalo to be from 0.2 to 0.3 mm for fish ranging from 145 to 609 mm total length. The algal components of buffalo diet were the colonial bluegreen algae *Anacystis* sp. and the colonial green algae *Pediastrum* sp. which are both large algae.

Filtering efficiency also determined the feeding selectivity of two cichlid species (*Lethrinops* sp.). Fryer

(1959) found that some cichlids living in Lake Nyasa fed by filling their mouths with sand which was then discharged through the opercular cleft. The gill rakers strained out burrowing invertebrates. The dominant food of species which have widely spaced gill rakers was chironomid larvae, while ostracods were the main food of a species with more closely spaced rakers.

Feeding rate

The feeding rate of filter-feeding gizzard shad on a particular prey type is equal to the multiple of 4 factors: (1) prey density, (2) shad filtering rate, (3) shad capture efficiency for that particular prey type, and (4) shad filtering efficiency for that size of prey. The validity of this hypothesis and these results was tested by comparing computer simulated to observed feeding rates of a shad on five zooplankton prey types. Feeding rate was converted into changes in prey density for comparison.

As in the pool experiments, shad feeding rates were greatest on prey with poor escape abilities. The shad's observed feeding rates, presented as a change in prey density, were highest on *Asplanchna* sp. (Fig. 15), copepod nauplii (Fig. 16), and *Daphnia ambigua* (Fig. 17), intermediate on *Cyclops* sp. (Fig. 18), and lowest on *Diaptomus* sp. (Fig. 19). Simulated changes in densities closely approximated observed changes for the prey with

Figure 15. Observed and simulated changes in *Asplanchna* sp. density in an aquarium with a filter-feeding shad.

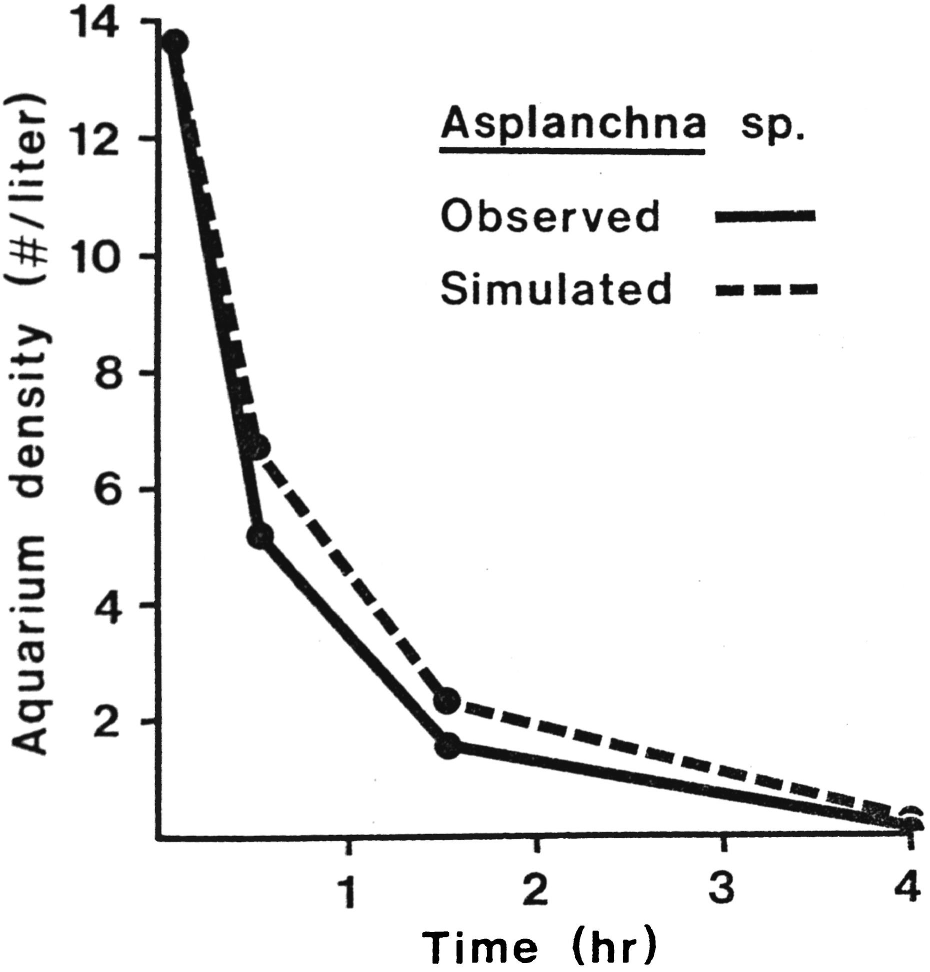

Asplanchna sp.
Observed
Simulated
Aquarium density (#/liter)
14
12
10
8
6
4
2
1
2
3
4
Time (hr)

Figure 16. Observed and simulated changes in copepod nauplii density in an aquarium containing a filter-feeding shad.

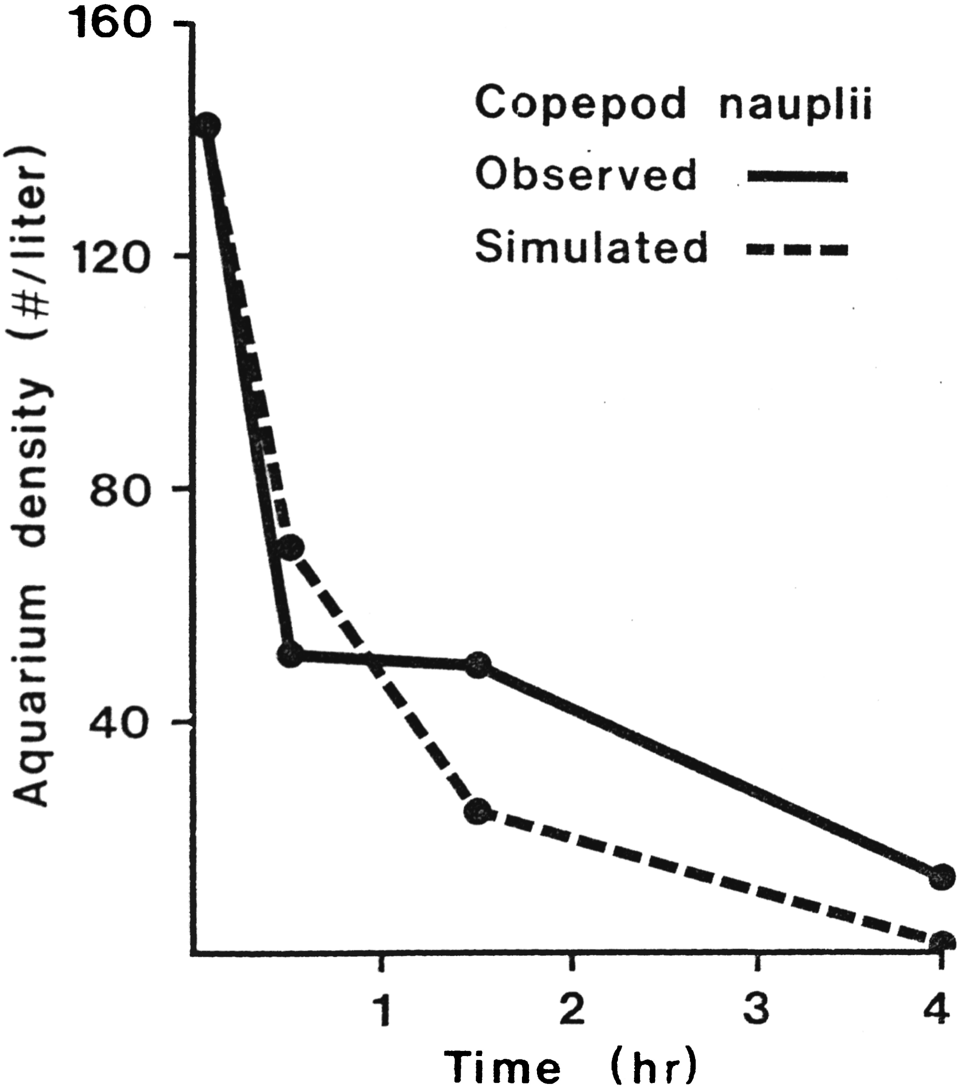

160
120
80
40
Aquarium density (#/liter)
Copepod nauplii
Observed
Simulated
1
2
3
4
Time (hr)

Figure 17. Observed and simulated changes in *Daphnia ambigua* density in an aquarium containing a filter-feeding shad.

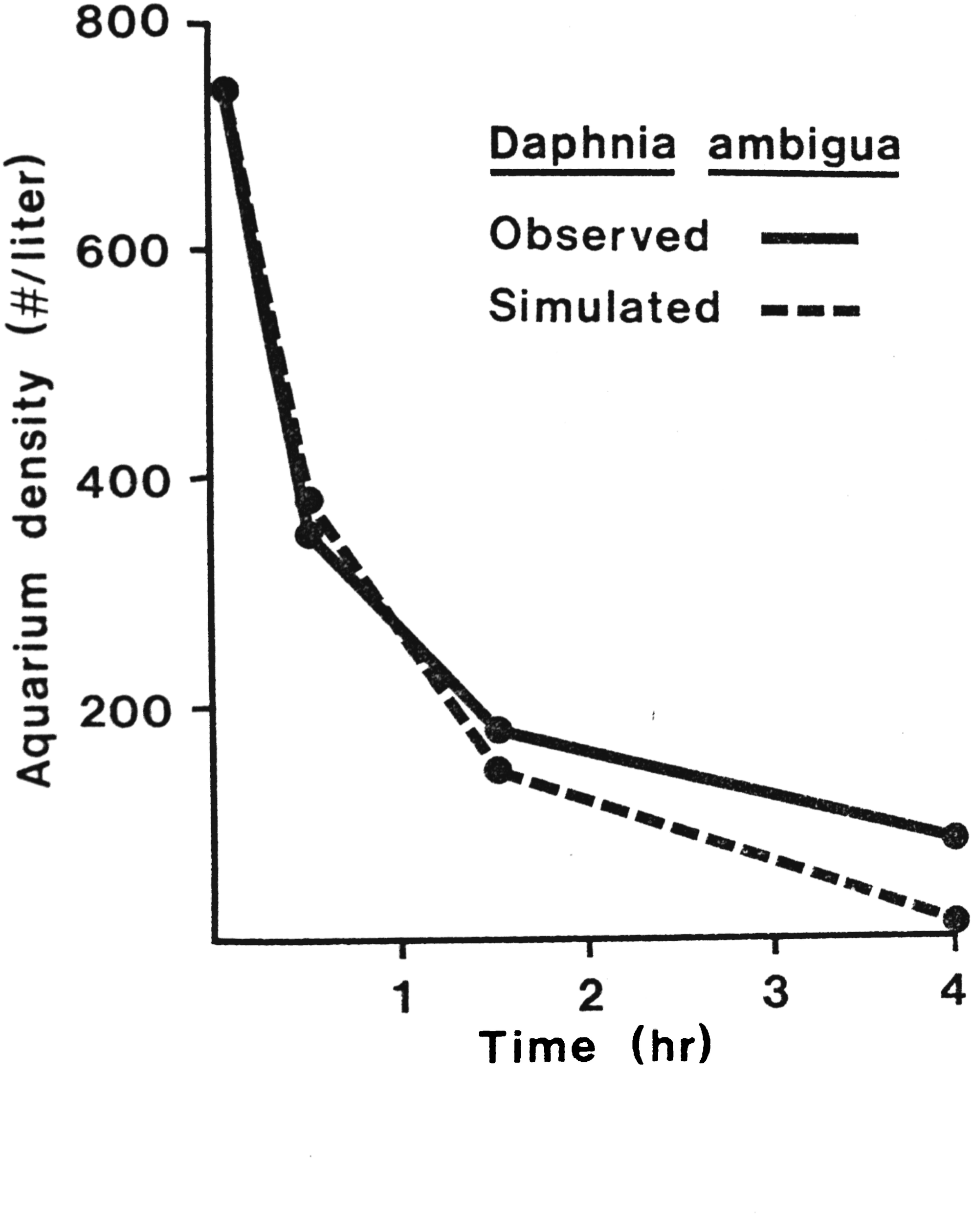

800
600
400
200
Aquarium density (#/liter)
1
2
3
4
Time (hr)
Daphnia ambigua
Observed
Simulated

Figure 18. Observed and simulated changes in _Cyclops_ sp. density in an aquarium with a filter-feeding shad.

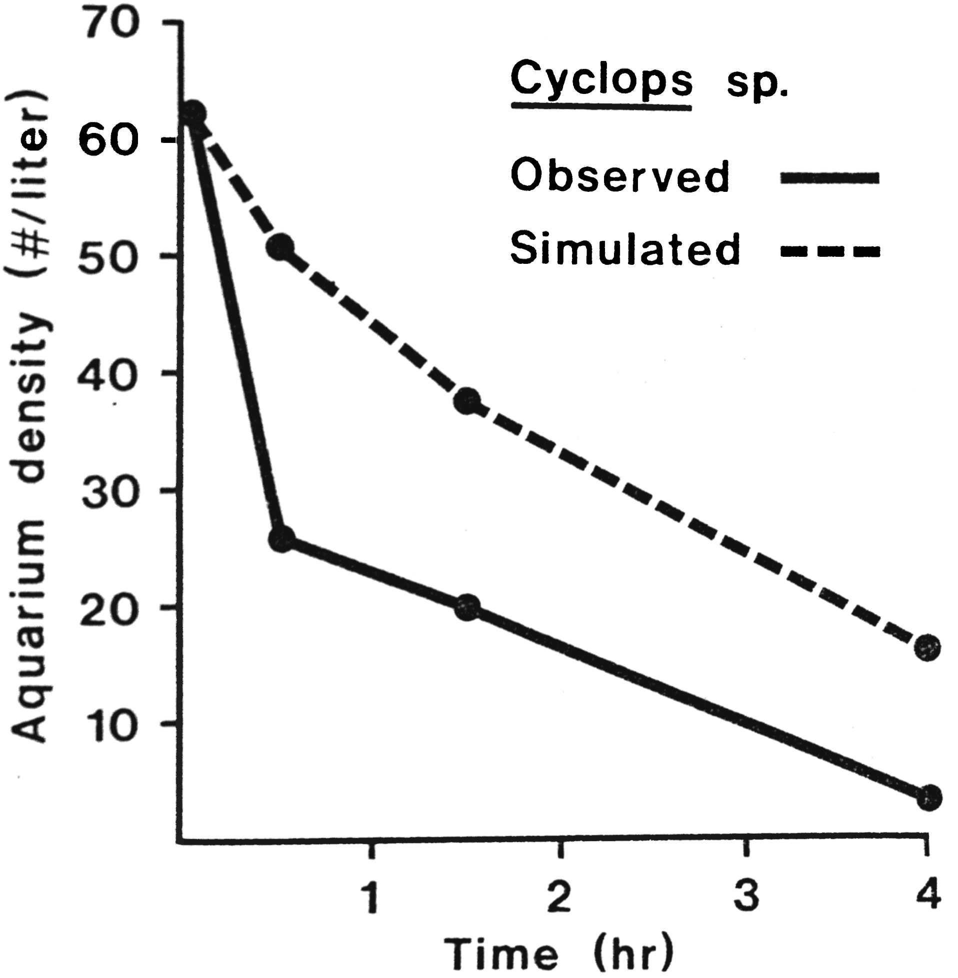
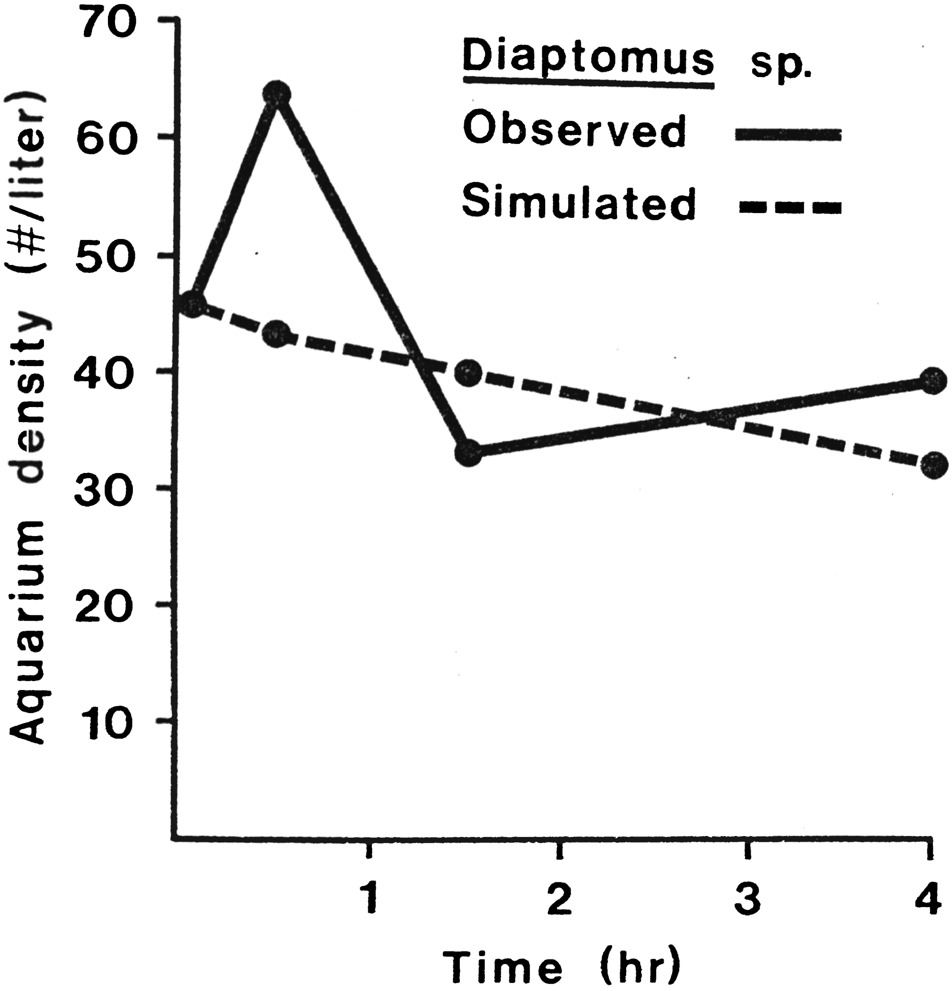

Cyclops sp.
Observed
Simulated
Aquarium density (#/liter)
70
60
50
40
30
20
10
1
2
3
4
Time (hr)

Figure 19. Observed and simulated changes in Diaptomus sp. density in an aquarium containing a filter-feeding shad.


Diaptomus sp.
Observed
Simulated
Aquarium density (#/liter)
70
60
50
40
30
20
10
1
2
3
4
Time (hr)

low escape abilities (Figs. 15-17). The discrepancy between the simulated and the observed changes in Cyclops sp. density (Fig. 18) probably reflects sampling error in capturing a mobile prey. These problems were exaggerated because only one sample was made at the start of the experiment to avoid disturbing the shad. If this sample was an overestimate of the initial Cyclops sp. density, it would result in a continued overestimate throughout the computer simulation as seen in Fig. 18 because the simulation used the initial prey density as its beginning point. Notice that the two curves are similar in slope (Fig. 18). Although sampling variability is also evident in the observed Diaptomus sp. densities (Fig.19), the slope of the observed and simulated changes correspond well. The general agreement between the simulated and observed density changes for the variety of prey types tested confirms the feeding rate model and substantiates the results used in it.

It is important to recognize the limitations of these results and the feeding rate model. Filtering rates were determined in water ranging from 19 to 21°C. Because cooler temperature would probably reduce the filtering rate, these results apply to the warmer seasons. Also, shad have been observed by scuba divers to feed by gently pecking at the bottom (personal communication by Jenkins to Baker and Schmitz, 1971). Whether this is used in conjunction with the filter-feeding mechanism or is another feeding mechanism needs further field and laboratory study.

DISCUSSION OF SHAD AND LAKE ECOSYSTEMS

Competition with gamefish

The omnivorous feeding of adult gizzard shad on the first and second trophic levels permits this species to be numerically the most significant fish in many lakes of the eastern half of the United States. Studies of shad abundance found shad biomass to be 50% or more of total fish biomass (Martin and Campbell, 1953; Schoonover and Thompson, 1954; Jenkins, 1955; Jenkins, 1967). Their large populations led some researchers to speculate that shad populations suppressed gamefish populations by sheer weight alone (Madden, 1951). Such speculation was followed by shad eradication programs using selective poisoning with rotenone (Bowers, 1955). Zeller and Wyatt (1967) reported that states of Arkansas, Florida, Georgia, Kentucky, Louisiana, Mississippi, Oklahoma, and Texas had utilized shad eradication as a reservoir management technique. Little information exists about the fish population changes following shad removal. Increases in catch per hour of gamefish following shad removal (Zeller and Wyatt, 1967) may be due to the low prey availability increasing the number of hungry or catchable fish. This would explain why the increase in catch of gamefish per hour was limited to the three to five years before shad populations returned to pretreatment abundance. The decrease in catch per hour three years after shad removal may also reflect a decrease in the gamefish population caused by years of low shad availability. Swingle (1949) found that stocking of largemouth bass in combination with shad produced more pounds of bass than bass-goldfish, bass-golden shiner or bass-bluegill combinations.

Shad do compete with young gamefish such as largemouth bass, crappie, and yellow perch for zooplankton resources. Decrease in zooplankton density has been correlated with increase in young shad abundance (Cramer and Marzolf, 1970). The intensity and effects of this competition on gamefish are unknown. The feeding mechanics and diets of shad and young gamefish are similar for a very short time. Shad are apparently visual-feeding carnivores up to 25 mm in total length when they switch to nonvisual filter-feeding. As filter-feeders, gizzard shad feed on zooplankton for which they have high capture probabilities such as rotifers, copepod nauplii and small cladoceran zooplankton. In contrast, fingerling gamefish feeding focuses on zooplankton for which they have high encounter and attack probabilities such as large adult cladoceran and copepod zooplankton. Although there is still overlap between shad and gamefish utilization of zooplankton resources, it is reduced by the difference in feeding mechanics. However, shad feeding on immature copepods and cladocerans may still affect gamefish by indirectly reducing adult zooplankton densities.

The detrimental effects of shad on gamefish populations due to competition for zooplankton resources is offset by the shad's ability to graze on large phytoplankton and its role as forage for gamefish. Shad channel the energy in large phytoplankton to the higher trophic levels. This energy is unavailable to other trophic levels through zooplankton grazing because most zooplankton cannot ingest particles greater than 40 microns in diameter (Burns, 1968). Shad channel this energy directly to gamefish because they are often the most important forage of gamefish (Dendy, 1946; Bonn, 1952; Jester and Jensen, 1972). Such high utilization of shad as forage is probably due to their abundance and their vulnerability to gamefish predation (Mauck and Coble, 1971).

This channeling of energy to other trophic levels may cause an increase in the standing crops of other fish populations in the lake. Jenkins (1967) analyzed the results of fish population studies of 127 reservoirs. He found a mean of 53 pounds per acre of nonclupeid fishes in lakes not containing clupeids (clupeids were mostly shad) and 121 pounds per acre of nonclupeid fishes in lakes containing clupeids. This increase in nonclupeid biomass with clupeid presence as well as the difference in feeding mechanics of shad and gamefish, the ability of the shad to feed on large phytoplankton and the heavy utilization of young shad as forage by gamefish suggest that shad may not be detrimental to gamefish populations as has been hypothesized (Madden, 1951; Bowers, 1955; Bodola, 1966; Zeller and Wyatt, 1967).

Biological control of bluegreen algae

After finding that the gizzard shad selectively fed on the colonial bluegreen algae *Microcystis aeruginosa* and the filamentous bluegreen *Anabaena spiroides*, Kutkuhn (1957) speculated that shad might be used as a control of objectionable bluegreen algae. Several other studies have found bluegreen algae in shad stomach contents (Tiffany, 1921a; Velasquez, 1939; Bodola, 1966; Dalquest and Peters, 1966).

Bluegreen algae are objectionable because when they are abundant they may decrease water quality by making the water distasteful and foul smelling as well as decreasing the asthetic value (Edmondson, 1969). These algae can be controlled by reduction of the factors responsible for their overabundance. The most important factors are (1) high phosphorus concentrations, (2) low grazing mortality caused by their large size making them unusable by herbivorous zooplankton, (3) thermophilic abilities and (4) nitrogen fixing capabilities. The first two factors seem most controllable. However, attempts to reduce phosphorus input into lakes cannot be completely successful. Phosphorus comes not only from point sources such as domestic sewage effluents but also from nonpoint sources such as agricultural runoff. Nonpoint sources cannot be easily controlled by today's technology.

The most economically and ecologically sound control would be to use a native grazer on bluegreens such as the gizzard shad. Shad feeding would offset the low mortality bluegreens experience because zooplankton are unable to use bluegreens as a food item. The potential of shad as a biological control will be determined by three factors: (1) shad densities, (2) shad feeding rates, and (3) the ability of shad to digest and assimilate the nuisance algae.

Estimates of shad densities and standing crops are usually determined using rotenone (Schoonover and Thompson, 1954; Jenkins, 1967) and the results vary. Jenkins (1967) analyzed the data from 116 reservoirs in the U.S. that contained clupeids. He found 90 lbs/acre of clupeids which consisted mostly of shad. This is 40,823.10 grams/acre or 255 shad 163 mm in standard length. From my estimates, these shad individually filter 1 liter of water per minute while feeding. The 255 shad would filter 367,200 liters/day or the top 10 acre feet of a reservoir in 33.6 days if they fed constantly. Use of Jenkins' results may underestimate the potential of shad as a control. The clupeid weight per acre is a mean weight for many reservoirs and therefore does not represent maximum shad abundance. Using similar computations on Schoonover and Thompson's (1954) results we get an order of magnitude increase in shad population filtering rate. They found 1103.07 lbs/acre of gizzard shad in Fall River Reservoir, Kansas. Shad at this standing crop would filter the top 10 acre feet in 2.7 days.

These population filtering rates are very rough and are given only as possible maximal rates. The filtering rates used in these calculations are maximum rates for shad feeding at summerlike temperatures. The calculations also assume continuous 24 hr feeding. Smith (1971) believed that shad feed continuously and Blaxter (1966) has calculated that juvenile visual-feeding sardines (*Clupea harengus* must feed most of the available time to account for its growth rate. More field work is needed to thoroughly assess shad population feeding rates.

Shad filtering efficiencies should result in selective ingestion of large algae such as colonial bluegreens. However, the ultimate effects of shad on a phytoplankton community will be determined by shad digestion efficiencies. Two studies have shown that not all algal cells are digested by gizzard shad. Velasquez (1939) and Smith (1963) found 46 genera of algae to survive shad gut passage. The most species surviving were Chlorophycae (30) and the second most were Myxophyceae (12) (Velasquez, 1939). Because neither study determined the percent of undigested to digested cells, digestion efficiency cannot be assessed. The digestion efficiency probably depends on gut passage time which is dependent on feeding rate (Smith, 1971). If shad are able to digest bluegreens, they must be resistant to the toxic effects of bluegreens on fish metabolism (Malyrevskaya, 1972).

Gizzard shad feeding may indirectly reduce bluegreen abundance by reducing grazing pressure on small green algae. The high feeding rates of shad on the easily captured copepod nauplii and cladocerans might have a significant effect on copepod and cladoceran populations. The reduction of populations of herbivorous zooplankton would then reduce grazing mortality on the small green algae, potentially shifting the competitive edge to these small algae and resulting in a decrease in bluegreen abundance. A bluegreen decrease with planktivorous fish presence has been found by Hrbacek (1964).

In summary, gizzard shad appear to have potential as a biological control of bluegreen algae. Shad filtering efficiencies should cause them to feed selectively on large phytoplankton such as bluegreen algae. Shad would channel the normally unavailable energy in large algae to higher trophic levels by producing young which serve as the major forage of gamefish, offsetting their competition with young gamefish for zooplankton resources. Shad predation on herbivorous zooplankton lessens the mortality rate of small algae, reducing the natural competitive advantage of large algae. The potential direct and indirect suppression of bluegreen algae populations by shad warrants further study of the use of the gizzard shad as a biological control.

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