FEEDING BEHAVIOUR OF THE GUPPY, POECILIA RETICULATA (PISCES: POECILIIDAE)

by

GERTRUDE V. DUSSAULT

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M.Sc. **ABSTRACT** Biology

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Digestive tracts of wild guppies, *Poecilia reticulata* (Pisces, Poeciliidae) contained mainly benthic algae and invertebrates. In the laboratory, guppies matured on diets consisting solely of *Chlorococcum* (Chlorophyceae), *Daphnia*, or dried fish food, but rates were slowest on algae. Fish grazing benthic algae performed rapid pecks with jaws maximally protracted to cover a relatively large area. Pecks were performed in series at intervals of 0.55 s. Jaw movements required 0.17 s, while substrate contact lasted 0.03 s. Ingestion/peck varied with fish size, sex and algal density. Males fed on lower densities and ingested more per peck than females of similar weight. Ingestion rates were high and showed no consistent daily pattern. Females had longer feeding bouts than males.

ABSTRACT

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M.Sc. RESUME Biology

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par

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RESUME

Dans la nature, l'appareil digestif du guppy, *Poecilia reticulata* (Pisces, Poeciliidae), contient principalement invertébrés et algues benthiques. En laboratoire, le taux de croissance des guppys nourris avec *Chlorococcum* (Chlorophyceae) fut plus lent que celui des poissons nourris avec la nourriture sèche ou des *Daphnia*. Les poissons se nourissant d'algues, accomplissent des mouvements d'ingestion rapides, avec leurs mâchoires maximalement ouvertes pour couvrir le plus de surface possible. Ces mouvements se répètent en série, à intervalles de 0.55 s. Le mouvement d'ouverture des mâchoires dure 0.17 s, le temps de contact avec le substrat 0.03 s. Le rapport ingestion/bouchée varie avec la taille du poisson, son sexe et la densité des algues. Les mâles se nourrissent sur des plus faibles densités et ingérent plus par bouchée que les femelles du même poids. Les taux d'ingestion sont élevés et ne suivent pas de cycles journaliers. Les femelles ont des périodes d'ingestion plus longues que les mâles.

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INTRODUCTION

The guppy, Poecilia reticulata, is a small ovoviviparous poeciliid fish which lives in fresh and brackish waters of tropical regions. Its original range appears to have been the northeastern regions of South America and the adjacent islands of the eastern Caribbean. Now, having been widely dispersed by man, it is essentially pan-tropical (Haskins et al., 1961). This species has been widely studied, both in the laboratory (e.g. Winge, 1922, 1927, 1930, 1948; Baerends et al., 1955; Hester, 1964; Davis, 1968; Doi, 1969; Uematsu, 1971; Ballin, 1973; Seghers, 1973; Murdoch et al., 1975; Farr, 1976; Crow and Liley, 1979; Kramer and Mehegan, in preparation), and in the field (e.g. Haskins et al., 1961; Farr and Herrnkind, 1974; Liley and Seghers, 1975; Endler, 1978). However, the literature indicates that virtually nothing is known of its feeding behaviour or, with the exception of studies by Green et al. (1976,1978), and Yamagisti (1967) on introduced Asian populations, of its natural diet.

Guppy feeding behaviour is also of particular interest because it offers an opportunity to examine the consequences of strongly developed sexual dimorphism on the organization of foraging. In this species, females are much larger than males. In a natural population studied by Seghers (1973) females averaged 30 mm total length (TL) and males 22 mm TL. Maximum size for females was 46.5 mm TL and for males only 26.5 mm TL. Males are also strikingly more brightly coloured than females, and differ to an equal extent in their behaviour. Males show a high rate of courtship behaviour, displaying

7 to 13 times per 5 minutes, while females in mixed sex groups are almost never observed to show sexual responsiveness (Liley, 1966; Ballin, 1973; Farr and Herrnkind, 1974; Farr, 1976).

These intersexual differences in size and behaviour might result in differences in food type and in a differential opportionment of the time budget for feeding between males and females. Many studies have related size or structural dimorphism to intersexual differences in diet. Selander (1966) and Ligon (1968) have showed that dimorphism in bill size in woodpeckers can result in different foraging strategies and a reduction in intraspecific competition for food, and Selander (1966) reviewed the topic in birds. Schoener (1967) has shown that sexual dimorphism in size in the lizard Anolis conspersus results in the males capturing significantly larger prey items than those caught by females. Baird (1965) found that in a goby, Microgobius gulosus, which is sexually dimorphic in size and mouth proportions, males are able to ingest significantly larger food items than females. Hoffman (in prep.) has shown that female hogfishes, Bodianus rufus, spend much more time feeding than males. In his study, reduced foraging time of males appeared to result from increased time demands for social and mating activity.

Initial investigations of gut contents confirmed preliminary observations by Liley (personal communication) that guppies graze the benthic detrital aggregate of streams. The aggregated mixture of non-living organic matter, heterotrophic and autotrophic micro-organisms (Seki, 1972) is an important route of energy cycling in tropical aquatic ecosystems (Odum, 1962). Studies on fish which feed on it have concentrated on the problems of dietary composition (e.g. Thompson, 1954), food quality (e.g. Darnell, 1967; Odum, 1970; Bowen, 1979), and food distribution (Bowen, 1978). With the exception of a study by Odum (1970) on the mullet, *Mugil cephalus*, little has been done in studying the actual feeding behaviour. Yet, both quantitative and qualitative aspects of feeding ought to be quite different in such species from the more thoroughly studied insectivorous and carnivorous fishes.

The present study was conducted to determine the diet of guppies in their natural habitat, and to investigate in more detail their benthic grazing behaviour by looking at the speed and patterning of jaw movements used by the fish when feeding. After determining that guppies could grow on a diet comprised solely of algae, and comparing their growth rate on it to rates obtained for guppies fed other foods, the influence of size, sex and algal density on uptake rate per feeding peck was studied. Finally, sexual dimorphism in feeding time budgets, the temporal organization of feeding behaviour, and daily ingestion rates were examined.

MATERIALS AND METHODS

Gut Contents

A large, representative sample of guppies was collected by hand net in two streams of northern Trinidad, the Naranjo, a head-stream, and the Lower Tacarigua, a heavily polluted lowland stream. They were captured at 1500 hrs on June 5th and 1200 hrs on June 6th, 1978, respectively, immediately placed on ice to minimize regurgitation, and preserved in 10% formalin. After six weeks, the fish were soaked in fresh water overnight and then preserved in 70% ethanol.

Twenty-five mature males and females from each habitat were used for gut analysis. The standard length (S.L., tip of the upper jaw to the posterior end of the caudal peduncle) of each fish was measured with a ruler to the nearest 0.5 mm. The weight of each fish used was determined to the nearest mg, after removing excess surface fluid with a paper towel. Using scissors, the body wall was removed from the right side of the peritoneal cavity. Then, with the aid of a dissecting microscope, the digestive tract, from the oesophagus to the first 180^{o} bend, was cut and removed to a small dish containing three drops of water. The contents were extracted by cutting the section into three or four pieces, and squeezing out the contents, using a forceps and probe. Since the gut wall is quite transparent, it was evident when all or most of the contents had been removed. The gut wall was discarded, and the contents mixed and broken up with a probe. The entire contents of the dish were placed on a microscope slide for analysis. Fish with only traces of food in the gut were not included in the analyses.

The following food categories were used: 1) invertebrates, 2) higher plant fragments, 3) filamentous algae, 4) diatoms, 5) unicellular algae other than diatoms, 6) algal remains (mixture of broken cell remains and green amorphous material), 7) mineral particles, and 8) other. Four methods of analysis were used: (a) Occurrence - Each category was scored as to whether or not it occurred in the gut contents of each individual fish. (b) Dominance - The volumetrically most predominant food type was estimated for each fish after looking at the whole slide of gut contents. (c) 70% Content - Food types estimated to comprise 70% of the contents were recorded. (d) Frequency - The frequency of different items, at ten evenly distributed points on each slide, was determined at 100x magnification, by scoring one point to the appropriate food category, each time an item contacted one of 57 predetermined intersection points of an ocular grid. Point totals and the percent occurrence of each category were then calculated. This method, which is an adaptation of that used by Jones (1968), yielded from 19 to 359 counts per individual fish, with a mean of 94.

Fish Culture

Two different stocks of guppies were used in the following experiments. The first was a stock originating in St. Augustine, Trinidad, from a pool on the campus of the University of West Indies. This pool, measuring about 25 m in diameter, is concrete lined, less than 1.5 m deep and supports several species of cichlid fishes as well as a large population of guppies (Tej Singh, personal communication).

The second was a domestic stock of unknown origin maintained for many years in the greenhouse of the McGill University Biology Department.

These fish were maintained in 90 x 30 x 35 cm aquaria at 26 ± 2^{o}C in aerated, filtered dechlorinated water which was changed monthly. A minimal 12 h photoperiod was maintained by fluorescent lighting augmented by natural light from the windows. Fish were fed Tetra-min, presoaked to make it sink, trout chow, and occasionally *Daphnia pulex*.

Chlorococcum (Carolina Biological Supply No.15-2090), a unicellular green alga, was chosen as an algal food for experiments because of its small size, thin wall, adherent qualities, and relative ease of culture. It was grown in 40 ℓ continuous cultures maintained at 15 ± 2^{o}C, with a 12:12 photoperiod, in a 9:1 mixture of Bristols and Soil-water media (Starr, 1964), one-fourth of which was replaced every four weeks. Each culture contained three plexiglas racks, each of which was designed to support sixteen, 10 x 6.3 x 0.15 cm plates, in a horizontal position. These plates could be individually removed for presentation to the fish. The density of algae adhering to the plates was varied by changing the number of days they were left in the culture.

In some experiments algae were used from a dense open culture containing principally *Scenedesmus sp*, *Ankistrodesmus sp*, *Chlorella sp*, and *Selenastrum sp*, as well as a few protozoans and rotifers. This was collected with a net, spread on 10 x 6.3 x 0.15 cm plexiglas plates, and air-dired to promote adhesion to the plates before being presented to the fish.

Adult Daphnia pulex raised on algae from the open culture were used as food, in growth and feeding studies. In the growth studies live Daphnia were simply added to the aquaria. This diet was supplemented with freeze-dried Daphnia (Rolf C. Hagen, Ltd.) when stocks of live Daphnia became depleted. These were presented to the fish in chunks which gradually disintegrated in the aquarium water.

Live Daphnia were used as an attached food source in one experiment. Approximately 200 Daphnia were randomly, but separately, placed on 10 x 6.3 x 0.15 cm plexiglas plates which had been previously spread with 3-4 drops of liquid gelatin. The gelatin acted as an adhesive but left most of the body of each Daphnia exposed above it.

Adequacy of Algae as a Food

In order to verify that guppies would eat and digest Chlorococcum, a microscopic examination of the appearance of algae in the digestive tract of both preserved and freshly killed guppies was made. Then growth rates of guppies raised on Chlorococcum were compared to growth rate on Daphnia and on Tetra-min. Twenty fry of McGill stock were weighed and placed in each of three 40 x 19.5 x 21 cm aquaria kept throughout a 10-week experimental period, under identical conditions of temperature (26-28^{o}C) and photoperiod (12:12). Once a week, one quarter of the water in each tank was replaced, the filter was cleaned and the fish were individually weighed. Food was provided in excess to the fish each day, as follows: Tank 1. Chlorococcum supplemented after week 6 with algae from the open culture. Tank 2. Tetra-min. Tank 3. Live Daphnia pulex supplemented from weeks 7-10 with freeze-dried Daphnia.

In an additional experiment at a later date, but under the same conditions, fish were fed a diet of Oedogonium sp for two weeks.

Feeding Mechanism

Guppies feeding on algae were filmed in order to analyze in detail the feeding mechanism used.

Mature female guppies of McGill stock weighing 500-600 mg were habituated to the tank and to the method of food presentation for two days prior to filming. The set-up consisted of a clear plexiglas plate (17.7 x 24.8 cm) placed vertically 1.7 cm from the front of a 40 x 20 x 24 cm aquarium. Attached to the front of this plate was a 1.7 cm wide shelf, 18.3 cm above the bottom, onto which Chlorococcum-coated plexiglas strips (7 x 1 x 0.3 cm) were placed as food. This set-up facilitated filming by localizing the feeding and forcing the fish to feed in a position approximately perpendicular to the camera lens. Illumination was provided by two 500-watt flood lights placed approximately 50 cm from the aquarium. These lights increased water temperature from 27 to 29^{o}C during filming, but did not appear to disturb the fish. A Bolex H-16 movie camera, with a 10 mm Switar lens and Kodak Tri-X Reversal film, was used to record feeding behaviour at 64 frames/s. Frames were converted to milliseconds using the conversion 14.06 ms/frame. This was used rather than the expected 15.62 ms/frame after the camera speed was checked against an oscilloscope and found to be running about 10% faster than indicated (Kramer, 1978).

Twenty individual feeding pecks selected on the basis of clarity, were analyzed, frame by frame, using a photographic enlarger to project the image onto a sheet of white paper at a constant magnification (about 4x). The following measurements were made to the nearest 0.5 mm for each sequence:

1) Reference Distance - The minimum distance from the center of the eye to the posterior edge of the operculum.
2) Position - The horizontal and vertical positions of the center of the eye and of the outside midpoints of the premaxilla and dentary , using the left edge of the frame and the feeding surface as reference points.
3) Extent of Protraction of the Premaxilla - The minimum and maximum distances from the center of the premaxilla to the center of the eye and the frame number in which these occurred.
4) Body Position - The angle of the body in relation to the feeding substrate, determined by a line drawn from the center of the eye to the vertical midpoint of the body at the level of the dorsal fin. The angle between this line and the horizontal feeding surface was measured to the nearest 0.5^{o}.
5) Peck Duration - The number of frames comprising each peck from the first visible sign of protraction of the premaxilla to its complete retraction.
6) Contact Duration - The number of frames from start to end of contact by one or both jaws with the feeding surface.
7) Context - Whether a peck was temporally isolated or occurred within a rapid series.

Sequences were grouped into two categories, those having short contact of both jaws with the feeding substrate (1 frame) and those having a longer one (2 or 3 frames), in order to facilitate grouping data for the calculation of average movements of the premaxilla and dentary. The variation resulting from fishes of different sizes feeding at slightly different angles, was minimized by dividing each position measurement by the reference distance of that peck.

In combining data from different pecks, the first frame in which both jaws were in contact with the feeding substrate was used as a reference point. The mean movements of the premaxilla and dentary were calculated in relation to this frame.

In order to supplement the filming, the dentition of preserved male and female guppies was examined, and compared to that of other poeciliids. Photographs were taken of the scrape marks made by the teeth, when fish were feeding on a low density of algae.

Ingestion Rate

Laboratory-raised St. Augustine guppies were used to examine the effects of sex, body size and algal density on the ingestion rate. Twenty-four males (range 13.0-19.5 mm SL) and nineteen females (range 17.0-28.5 mm SL) were allowed to feed from algae-coated plates ranging in density from 156 to 611 $\mu g/cm^2$. In most cases, males were allowed to take 50 pecks and females 100 pecks, but one series of tests varied peck number from 10-90 pecks.

Each fish was weighed, measured, and conditioned for three days to feed from the plates in a 40 x 20 x 24 cm aquarium. Then, after 22 hr food deprivation, each fish was transferred to a similar tank containing a companion fish of the same sex and permitted to take the predetermined number of pecks on a Chlorococcum-coated plate. After feeding, the fish was removed from the tank and isolated without food for 30 min, before being sacrificed in an ice bath. Gut contents were extracted, using the procedure outlined above, placed on a 2.2 x 2.2 cm cover glass, previously weighed to the nearest 10 μg, dessicated for 48 hr at 22^{o}C, and then reweighed to determine the weight of the gut contents. Preliminary experiments indicated that the weight of gut contents stabilized within 48 hr. Algal density on the plates was determined by using a razor blade to scrape all algae from a 24.57 cm^2 area (3.9 x 6.3 cm) onto a weighed cover glass, and determining the weight in the same manner as with the gut contents. The results were used to examine separately the effect of the number of pecks, fish size and algal density on the ingestion rate per peck, using all data in which two factors could be held constant while the third varied. Then, a multiple linear regression relating ingestion rate per peck to fish size and algal density for each sex, was calculated.

Feeding and Courtship Rates

This experiment was done to determine the apportionment of time to feeding and courtship behaviour over the day in relation to size and sex of fish. Five males (92-146 mg) and four females (216-670 mg) of McGill stock, were placed in an aerated, filtered, 90 x 30 x 35 cm aquarium maintained at 26 ± 1^{o}C with a photoperiod of 0730-1930, and permitted to become familiar with the aquarium conditions for seven days. Tetra-min, presoaked so that it sank to the bottom, was fed in excess each morning during the period of familiarization, and during the four-day experiment.

Feeding and courtship behavior of individual fish, recognized by color pattern and size, were recorded on an eight-channel event recorder, for 5 min per fish in six observation sessions per day, for four days. Recording sessions started at 0800, 0900, 1100, 1300, 1600 and 1900 hr. Feeding pecks were defined as contact of the jaws with the substrate. Courtship included Orientation, Display and Contact Movements (Liley, 1966). For females, the courtship received was recorded. Each 5 min record was divided into 15 s intervals. Each interval was scored for the presence or absence of courtship, and for the total number of feeding pecks. The percent of intervals with courtship and the average feeding rate per 30 min were calculated from these data. In addition, the frequency distribution of pecks per 15 s interval was determined.

Temporal Organization of Feeding

This experiment was designed to investigate the rate and temporal organization of feeding in relation to sex and size. It was done by videotaping the feeding behavior of a group of guppies over a two-day period, and then recording from the videotape the timing of the feeding pecks.

Forty-five guppies were selected to make up three size classes of fifteen fish each, as follows: large females of 300-420 mg ($\bar{x} \pm SD = 371.8 \pm 39.7$ mg), small females of 100-140 mg ($\bar{x} \pm SD = 119.0 \pm 16.8$ mg), and males of 100-140 mg ($\bar{x} \pm SD = 117.6 \pm 10.1$ mg). These fish were placed in a 90 x 30 x 35 cm aquarium maintained at 26 ± 0.5°C and allowed 10 days to become accustomed to the tank, the lights (two 500 W photographic lamps), the photoperiod (12:12, with no natural light), and the method of food presentation. Food was presented to the fish on plexiglas plates, supported by a 23.5 x 14.5 x 10 cm plexiglas rack. Two rows of two plates each, with a vertical distance of 6 cm between them, were presented at a time. The rack was briefly removed from the aquarium to replace plates as they became depleted. The fish rapidly grew accustomed to this procedure, and subsequently appeared undisturbed by it. For the first week of habituation, both Chlorococcum adhering to the plate and loose Tetra-min were given as food. For the last three days of habituation, and the two days of videotaping, only attached Chlorococcum and Daphnia were used. Four plates, two with algae and two with Daphnia, were the only food sources available in the aquarium. They were replaced as they became depleted, so food was always present in excess during the day. No food was given during the twelve hours of darkness. Each day, three samples of algae were taken to determine density.

Feeding from the plates was videotaped for five minutes each hour during the light phases of two consecutive days, using a Sony television camera, Model 4200, equipped with a 22.5-90 mm zoom lens. All food was within the camera's field. By repeated playback of each 5-minute videotaped period at real time over a monitor, the feeding pecks of individual fish were manually recorded as they occurred on a Datamyte-900 (Electro General Corp., Minnetonka, MN, USA), which recorded to the nearest 0.01 min. The Datamyte is a battery powered, portable, data collection system that performs data collection, storage, and computer interface. Numerically coded data is entered into the unit, by the observer, through a keyboard. The current time is logged automatically.

Before recording individual records, operator accuracy was tested by repeated recording of the feeding pecks videotaped over a set period of time (about 1 min). Accuracy achieved in these three recordings was over 94%. The videotaped pecks of individual fish were then recorded. The automatic timer was reset to 0 at the start of the recording for each individual fish. The size class of each fish, the type of food being eaten, and feeding records starting or ending off the videotape, were noted. Using the direct computer input capacity of the Datamyte, a printout of the full record was obtained. This allowed for the division of each fish's feeding pecks into bouts. A bout consisted of one or more pecks, separated by less than 0.04 min. The bout criterion of 0.04 min was chosen because it appeared to be just below the minimum time required for a male to cease feeding, court, and then return to feeding.

Bout durations were then determined. Single pecks were given a duration of 0.01 min. The duration of a longer bout was calculated as $t_f - t_o + 0.01$ min, where t_o and t_f were the times of the first and last pecks in the bout, respectively. Data on fish were then combined, by size class and type of food, for each of the twelve daily recorded periods of feeding for each day. Mean peck duration within a bout was calculated by dividing bout duration by the number of pecks in the bout. To compare the mean duration of pecks of each class, 61 bouts of more than one peck were chosen for each food for each class, by using a random number table to select five bouts from each hour of each day.

The mean number of pecks per fish per hour on each of the two foods, was calculated for each size class, by dividing the total pecks per 5 min by 15 (the number of fish) and multiplying the result by 12 (to put each on an hourly basis). The mean number of pecks per fish per day was the sum of these hourly rates for each of the two days. Similarly, the mean time spent in feeding per fish per hour and per day were calculated by summing the bout lengths of each class and multiplying by 12/15. Ingestion rates of each class were estimated using the relationship between ingestion per peck, body weight, and algal density, previously determined.

To compare the bout organization of the three classes of fish on each food, the percent frequency distribution of the number of pecks per bout was computed and plotted as log survivor curves (Fagen and Young, 1978). The relationships between mean bout lengths of each class, time of day, and mean feeding rates were then examined. Incomplete bouts were excluded from all bout length analyses.

RESULTS

Gut Contents

Invertebrates, diatoms, and algal remains, were the three most important categories of food (Fig. 1, Table 1). The diatoms were mainly Cymbella sp, while the invertebrates identified included protozoans, rotifers, and most importantly, aquatic insect larvae. No crustaceans, oligochaetes, or fish were found. Less than 1% of gut contents could not be categorized.

Dietary differences between populations were found for total diet composition, using the relative abundances of each food category, for both males ($x^2 = 42.08$, $df = 6$, $p < 0.001$) and females ($x^2 = 45.89$, $df = 6$, $p < 0.001$). Comparisons of the relative abundances of each food category, showed that most of the differences arose in the invertebrate, diatom, and mineral particle categories, with the Tacarigua guppies containing more diatoms and mineral particles, and fewer invertebrates, than did the Naranjo (Table 2). Statistically significant differences in the consumption of filamentous algae are probably not biologically important, since this category constituted less than 1.7% of the diet in both populations.

While x^2 comparison of the overall diet between the sexes of Tacarigua fish showed no significant difference, the Mann-Whitney U Test indicated a significant difference in the occurrence of diatoms and algal remains. Females contained more diatoms and fewer algal remains than the males (Table 2). These differences also appeared in the dominance analysis (Table 1), where 15 females had diatoms and 9 algal remains as the dominant food, as compared to 3 and 18, respectively, for the males (Fisher Exact Probability, $p < 0.01$).

Algal remains and invertebrates made up most of the diet of the Naranjo population. No significant intersexual differences were found, although the difference approached significance for invertebrates ($p = 0.13$), probably because females showed decreased invertebrate consumption with increased size (Fig. 2).

A comparison between the dominant food category and the food category with the highest relative abundance, indicated agreement in 87 of the 89 fish analyzed (97.7%). A similar comparison of foods estimated to comprise 70% of the diet, and the foods reaching a relative abundance score of 70% or more, showed agreement in 73 of 89 fish (82%). These methods, therefore, give an accurate picture of the composition of the food, although in fish where a major food component is constant, the methods provide no information on the abundance of lessor components.

Adequacy of Algae as a Food

Growth over the ten-week experimental period is shown in Fig. 3. Guppies survived and grew on an exclusive diet of algae, although at a slower rate than fish fed *Daphnia* or Tetra-min. This was especially marked in females. Males fed Tetra-min had a slower initial growth rate than those on *Daphnia*, but they caught up over weeks 8 to 10, having an almost identical mean weight at the end. Growth rates of all males and of females fed algae declined by week 10, although the females fed *Daphnia* and Tetra-min were still showing large weekly weight gains.

In a later experiment when 10 fish were fed Oedogonium, the fish were not observed to feed on the algae at all during the first four days. After two weeks the experiment was terminated because three fish had died, and the seven remaining had each lost 1-6 mg.

Guppies fed Daphnia began to mature earliest. The first female was recognizable at week 3, and the sex of ten additional fish could be determined a week later (Table 3). Six fish fed Tetra-min started to mature by week 4, while none from the algae tank could be sexed before week 5. One female fed Daphnia produced young during the eighth week. When the fish were sacrificed at week 10, all males were mature and all females except the smallest (16 mm, SL) in the algae group had either embryos or large, yolky eggs present in the ovary.

The ratio of females to males in each tank differed greatly. At week 6, when all fish had matured, except one which later died, the ratios were 12:4 for those fed Daphnia, 7:9 for those fed Tetra-min, and 5:8 for those fed algae.

Over the ten-week experimental period, mortality was high with eight fish dying in the Daphnia tank, four in the Tetra-min, and nine in the algae. Possible causes of this include the entrapment of fry in the filter, the inability of some small juveniles to handle Daphnia, and the stress of weekly weighings.

Microscopic examination showed some undigested algal cells throughout the length of the digestive tracts in the preserved fish used for gut analysis and in freshly-killed fish, which had been fed algae over several days, although the majority of the cells had been broken down. In the freshly-killed fish those cells which had been recently ingested appeared bright green in color and those which had been consumed earlier were dark olive green. The intestine lengths of the guppies at the end of the growth experiment averaged 1.65 times the SL in females and 1.13 times in males. The effect of diet on intestine length could not be determined because of the small sample and the differences in body length between the treatment groups.

Feeding Mechanism

Film analysis showed that the guppy approached the food with the mouth closed, than quickly protracted the premaxilla and abducted the dentary to their maximal extent just before contacting the substrate. The dentary was then adducted closing the mouth with the premaxilla still strongly protracted. Adduction of the dentary and retraction of the premaxilla continued together as the fish rose from the substrate. This is illustrated by a print taken from a filmed sequence of a complete peck (Fig. 4). Protraction of the premaxilla began at frame 1, and was complete at frame 8 when contact began. The premaxilla remained protracted during contact and was retracted from frames 11 to 15. Abduction of the dentary started in frame 2 and continued until frame 8, while adduction occurred from frame 8 to 15.

The movements of the fish as a whole as indicated by eye position, and the positions of the premaxilla and dentary relative to the substrate, can be more clearly seen in Fig. 5 for a single sequence and in Fig. 6A and 6B for the means of 20 sequences. Figures 6C and 6D show movements relative to the head. These figures demonstrate the features described above, and also emphasize that the substrate is scraped exclusively by movement of the dentary. The dentary swings outward in an arc of over 100^o and moves along the substrate as a result of both its own movements and the forward progression of the fish. Protraction starts when the fish is at most 1 unit above the substrate. For a fish of approximately 500 mg, SL - 29 mm, this is 3.4 mm. When the jaws hit the substrate the tips of the premaxilla and dentary are 0.6 units apart, 2.0 mm for a 500 mg fish. A fish of this size has a mouth width of about 1.5 mm and, since the opening is approximately rectangular, this suggests an area covered of about 3.0 mm^2. Speed of descent of the fish calculated over the last four frames, was equal to 0.22 units or, for a 500 mg female, 1.33 cm/s and 0.35 total body lengths per second. The premaxilla itself contacts the substrate while travelling at 3.51 cm/s or 0.93 total lengths/s, its greater speed being due to the combined effects of forward movement of the whole fish and of protraction.

It is noteworthy that the guppy approaches the substrate with a forward as well as downward movement but leaves it vertically (Fig. 5). The protracted premaxilla seems to act as a barrier to the loosened algae although it does not move in relation to the substrate. Protraction is important to allow the dentary room for a larger angular movement, and allows the mouth to open in a ventral direction.

The peck in Fig. 4 lasted 0.21 s, slightly longer than average, but was representative in other characteristics. The mean length of single pecks was 0.17 s (range 0.15-0.20 s). Pecks occurring in series were similar ($\overline{x}$ = 0.16 s, range 0.10-0.21 s). It took the fish about twice as long to descend to the feeding surface as to ascend from it. On the average, guppies took 0.095 s to descend, and 0.041 s to ascend ($n = 20$). Actual contact averaged only 0.032 s, range 0.014-0.042 s. The jaws hit the feeding surface in the same frame in 17 of 20 pecks. In two cases, the dentary touched first and in one, the premaxilla. The angle of the body was quite variable but changed little during contact. It averaged 56.3° (range $37.5\text{-}69.0^{\circ}$) at the start of a peck and 59.8° (range $41.0\text{-}72.0^{\circ}$) at the start of contact. It was 59.0° (range $41.0\text{-}72.5^{\circ}$) at the end of contact and 54.2° (range $33.0\text{-}67.0^{\circ}$) at the end of the peck.

Examination of cleared and alizarin stained specimens of McGill stock females showed that each premaxilla supports a tooth plate with 10-12 large, closely-spaced, inwardly-curved, spatulate teeth, and each dentary supports a similar set of 11-13 teeth. Both jaws have many small teeth posterior to the main row. The guppy possesses a set of phargngeal tooth plates remarkedly similar to those described in *Tilapia esculenta* by Greenwood (1953). The upper set consists of two ovoid plates each possessing numerous long teeth with posteriorly curving tips. The lower set is triangular and formed of two plates lying side by side. The principal teeth lie on the posterior edge of the triangle, forming a brush-like layer with the tips directed upward. The gill rakers are quite short and widely spaced. On thin layers of algae, the tooth plates left scrape marks on the algal surface (Fig. 7), indicating that the teeth were the main means of loosening the algae. However, on thicker layers, which adhered less strongly to the plates, all algae was removed from the area covered by the mouth. This suggests that at higher densities, the pressure of the lip along the plate was sufficient to loosen any algae which were not scraped up by the teeth.

Ingestion Rate

Nine males (range 15.0-17.0 mm SL) and nine females (range 17.0-22.0 mm SL) taking from 10-90 pecks on algae of 342 $\mu g/cm^2$ and 411 $\mu g/cm^2$, respectively, were used first to determine the effect of the number of pecks on the ingestion rate per peck (Table 5). There was no indication of any effect.

The effect of fish size on ingestion rate was examined using six males (range 13.0-19.5 mm SL) and seven females (range 19.0-28.5 mm SL) (Fig. 8). At a constant algal density (326-354 $\mu g/cm^2$) ingestion rate increased in both males and females, as a function of size. Examination of the correlation coefficients for SL, SL^2 and weight gave a marginally better fit for SL^2, and this was therefore used as an index of size. The linear regressions are $z = 0.0074\ y + 0.654$ ($r = 0.71$) for males, and $z = 0.0072\ y - 0.526$ ($r = 0.86$) for females, where z = μg of algae ingested per peck, and $y = SL^2$ of the fish. Males showed a higher rate of intake than females of the same size.

The ingestion rate of 19 males (range 16.0-20.0 mm SL) and 11 females (range 17.5-22.5 mm SL) feeding at algal densities ranging from 156 to 611 $\mu g/cm^2$ were used to examine the effect of algal density (Fig. 9). Algal density affected ingestion rate. The linear regressions are $z = 0.125\ x - 0.717$ ($r = 0.89$) for males, and $z = 0.167\ x - 3.654$ ($r = 0.79$) for females, where z = μg of algae ingested per peck, and x = algal density in $g \times 10^{-5}$ per cm^2. Males would eat algae of lower densities than females would, but increased their ingestion rate with algal density slightly more slowly than did the females.

Multiple linear regressions for the 24 males and 19 females were calculated in three ways, using weight, SL, and SL^2. These yielded relationships in the form $z = a + bx + cy$, where z = μg of algae ingested per peck, x = algal density in g x 10^{-5} per cm^2, y = weight of fish in mg, SL in mm, or SL^2 in mm^2, and a, b, and c are constants. Results for males and females are indicated in Table 5.

The area of the plate cleared by the fish with each peck can be estimated using these formulae. For example, a 100 mg male with a SL of 17.3 mm feeding on a density of 300 μg/cm^2 would ingest 3.14 μg/peck, or the equivalent of 0.0105 cm^2 per peck. An ingestion of 3.14 μg/peck would also indicate that the fish was consuming 0.0314 μg per mg body weight with each peck. Similarly, a female of 500 mg, SL = 29.0 mm, feeding on 350 μg/cm^2 would ingest 5.56 μg/peck, clearing the equivalent of 0.0159 cm^2 with each peck. This equals a gain of 0.011 μg of algae per mg body weight per peck.

Feeding and Courtship Rates

Females fed at much higher rates than males (Fig. 9) with about seven times their rate in total pecks per 30 min. They fed in an average of 71% of the 15 s intervals, while males fed in only 18%. Feeding rate was significantly correlated with female size ($r = 0.90$, $n = 4$) but not with male size ($r = 0.02$, $n = 5$). Figure 10 indicates the frequency distribution of peck rates per interval. The females showed a wide range of peck rates in the 1,920 intervals observed, while the majority of the 2,400 feeding intervals for males contained only 1 or 2 pecks.

Figure 11 compares the percentage of 15 s intervals with courtship behavior, and the total recorded feeding pecks each day for males and females, to the individual weights of the fish. Courtship occurred in about 70% of the recorded intervals. The rate at which females were courted was strongly correlated with their weights ($r = 0.86$, $n = 4$). Male courtship rates also correlated strongly with their own weights ($r = 0.95$, $n = 5$). Females were frequently courted while feeding, but males did not feed and court simultaneously.

Temporal Organization of Feeding

No consistent daily patterns in the amount of time spent feeding per hour were apparent when hourly rates were plotted by time of day (Fig. 12). Therefore, hourly data for each size class were combined for each day. Large females spent an average of 10.1 min/hr feeding on day 1 and 6.3 min/hr on day 2. Small females averaged 6.8 min/hr on day 1 and 7.8 min/hr on day 2. Males spent 6.5 min/hr and 5.5 min/hr on days 1 and 2, respectively. There were no significant differences between the groups for the total amount of time spent feeding on either day.

Figure 13 indicates the hourly rates of each size class feeding on algae and on *Daphnia* over the two days. All three classes spent much more time feeding on algae than on *Daphnia* the first day (4-8X), and all these differences were significant ($p < 0.05$). On the second day, all classes continued to spend more time on algae than *Daphnia* (1.2-2.7X), but the differences were significant only for small females. The decrease in time spent on algae the second day probably resulted from the lower density of algae presented to the fish, 320 $\mu g/cm^2$ as compared to 466 $\mu g/cm^2$ on the first day. However, it was evident that algae were an attractive food. The relative amount of time spent on a food and the number of pecks made on it were not necessarily equivalent to relative ingestion rate. Fish often had to execute several pecks to loosen the Daphnia and then frequently had to give chase to capture it. In the case of algae, many pecks were made by fish on areas already cropped down by other fish.

Table 7 indicates the mean peck rates for each food, size class, and day. Knowing the algal density presented each day and the mean weight of each class, the amount of algae ingested per peck, per hour, and per day was estimated from the multiple regression equations previously determined. Large females performed the most pecks on both algae and Daphnia on day 1. On day 2, they still showed more pecks than males on both foods, but small females exceeded them in pecks on algae. Even when their peck rate on algae was higher, large females gained less algae as a percent of body weight than did the other groups. When fish of the same size are compared, it appears that small females took more pecks on algae and fewer on Daphnia on both days than did the males. However, because of the males' greater ingestion rate per peck, they obtained more algae than the small females. The actual ingestion rates, ranging from 16-25% of body weight on the denser algae, demonstrate a remarkably high ingestion capacity for algae, especially when it is considered that this is dry weight and that the fish also were ingesting Daphnia.

Table 8 indicates peck durations of each size class when feeding on algae or on Daphnia. These show that large females took the least time per peck on algae, and males the most. Peck durations on Daphnia yielded the opposite results, males taking the least time and large females the most. The only statistically significant differences were between large females and the other classes feeding on algae.

Log survivor functions were used to compare bout lengths of the three classes of fish feeding on algae and on Daphnia (Fig. 14). Bouts of feeding on Daphnia were much shorter than bouts on algae and similar for all groups. In general, females of both size classes had longer bouts on algae than did males. Males and small females showed similar patterns on both days. However, large females had a steeper slope of the survivor function on day 2 when their feeding rates on algae also dropped markedly. If the probability of any bout ending remains constant with time, regardless of the number of previous pecks in the bout, the slope of the log survivor function should be constant. This was the case when the fish fed on Daphnia. When log survivor functions are significantly different from straight lines, changing probabilities with time are indicated. A convex section of the function indicates that the probability of a bout ending increases with bout length, while a concave section indicates a decrease in the probability of ending. The log survivor functions for algae tend to be concave in the vicinity of short bout lengths, suggesting that once a bout gets beyond the first four pecks its chances of continuing are greater. A similar but fairly weak trend is also evident in some of the functions at higher bout lengths.

Mean bout lengths were compared with average hourly feeding rates in order to determine whether changes in feeding rate were achieved through changes in the number or the lengths of bouts (Fig. 15). The correlations were moderately strong for large females ($r = 0.46$) and males ($r = 0.62$), but weak for small females ($r = 0.11$). Thus, increased feeding rates are achieved partly by longer bouts.

Intense courtship by males can disrupt the feeding behaviour of females, especially small females, and this may partially explain the weak correlation between feeding rates and bout lengths. Small females also avoid the large females; thus, even at high feeding rates they may have many short bouts.

an important component. Insect larvae were significant only in Naranjo, the hill-stream population. The streams sampled differ in a number of physico-chemical features such as temperature, water hardness, turbidity, current regimes, shade and nutrient levels, as well as in the number of other fish species which could act as potential competitors (Seghers, 1973; Liley and Seghers, 1975). Any of these features could affect the availability of both algae and invertebrates to guppies. The importance of algae to the diet of guppies is supported by the ingestion rate studies, in which guppies, given excess amounts of both Daphnia and Chlorococcum, spent 54-88% of their feeding time on the algae.

The general conclusion that Poecilia reticulata feeds opportunistically with a major component of algal material, seems supported by the literature on other poeciliids. For example, Poecilia latipinna appears to feed mainly on vascular plant detritus but will take invertebrates such as mosquito larvae when available (Harrington and Harrington, 1961; Odum and Heald, 1972). Poecilia sphenops ate only algae in the study of Zaret and Rand (1971), but has been observed to ingest detritus and mineral particles in other streams in Panama (Kramer, unpublished observations), and in the Netherland Antilles it has been reported to feed on a wide range of plant and animal material including zooplankton and small fish (Kristensen, 1970). Such mixed diets seem characteristic of other poeciliid genera, although clear differences between sympatric species may be seen. Examples include Gambusia affinia, Heterandria formosa (Odum and Heald, 1972), Poeciliopsis monacha and monacha lucida (Vrijenhoek, 1978), and Neoheterandria tridentiger in which Zaret and Rand (1971) found exclusively terrestial and aquatic arthropods while

Kramer (unpublished observations) also recorded an important algal component in the diet.

The intestine length of the guppy, ranging from 1-2 times the SL, corresponds to that of cichlid, characoid and cyprinoid fishes eating mixed diets of plant material and invertebrates. Many species in each of these groups which specialize on detritus, phytoplankton or periphyton, have much longer intestines (Fryer and Iles, 1972; Kapoor *et al.*, 1975).

The observation of an item in the digestive tract of a fish does not necessarily imply that that item is nutritionally available to the fish. Mineral particles are an obvious example. The finding of live algal cells in the feces or digestive tracts of fish has raised doubts about the digestibility of some or all species of algae (e.g. Fish, 1952, 1955; Gunn *et al.*, 1977; Rabe *et al.*, 1973; Kitchell and Windell, 1970). A number of recent studies have confirmed that algae do contribute significantly to the nutrition of fishes, even in cases in which not all cells may be lysed. The species studied include *Tilapia nilotica* and *Haplochromis nigripinnis* (Cichlidae, Moriarty and Moriarty, 1973), in which there is a strong daily cycle of assimilation efficiency. The first algae ingested each day pass through the gut almost undigested. Filamentous algae are assimilated by the bullhead, *Ictalurus nebulosus* (Gunn *et al.*, 1977). Menzel (1959) showed that angelfish, *Holacanthus bermudensis*, can gain some nutrition from algae, and Kitchell and Windell (1970), found a very slight effect of the algae *Chara* on the growth of bluegills, *Lepomis macrochirus*. The last two species mentioned, however, require animal protein for significant growth.

The present study confirms that guppies can live and grow on an exclusive diet of green algae, Chlorococcum, but not on the filamentous green, Oedogonium. The change of appearance of Chlorococcum in the guts of guppies is similar to that observed during digestion of algae by Tilapia (Moriarty, 1973) and Ictalurus (Gunn et al., 1977). Fish fed algae grew at a slower rate than those on the Tetra-min and Daphnia diets. The growth rates of the Daphnia group were comparable to the most rapidly growing stocks fed live invertebrates by Bertlanffy (1938), and the algal diet resulted in a growth rate similar to his slow group fed "Piscidin". The algal diet resulted in a growth rate higher than the most rapid growth observed in freshwater by Gibson and Hirst (1955), but it was slower than that recorded by Davis (1968) for guppies fed ad libidum on a mixed diet. Further evidence that the algal diet was not excessively restrictive comes from the observation that fish on this diet began to mature at about six weeks of age, assuming the fish were about one week old at the start of the experiment. This corresponds to the observation by Goodrich et al. (1934) that guppies would develop secondary sexual characteristics at about seven weeks from birth under "optimal" conditions, but that this development could be delayed as long as six months under adverse conditions. The fastest growing males in Gibson and Hirst's (1955) study matured at 26-57 days and Thibault and Schultz (1978) gave 7-9 weeks as the age of first brood production in female guppies. Gestation required about three weeks.

The observation of slower growth on algal diets suggests that a lack of animal material in the diet of wild populations could restrict their growth rate and maximal size. Seghers (1973; Liley and Seghers, 1975) noted that guppies in Trinidad hill streams tend to be larger than those in lowland habitats. For example, he found that male guppies averaged 21.75 mm (total length) in Tacarigua and 25.25 mm in the Naranjo population, and female sizes were correlated with those of males. Although he suggested that differences in predation pressures were responsible for the differences in mean size between the two populations, it is possible that the more diverse fish fauna of lowland streams in Trinidad restricts guppy size through competition for invertebrate prey.

The guppy feeding mechanism shows adaptation to benthic feeding. When the premaxilla is protracted the mouth opening changes from a dorsal terminal to a ventral terminal position. Alexander (1966) in a study of another poeciliid, Xiphophorus, using only flash photography, showed that protraction serves a similar function in this species. This mouth position allows a guppy to feed from a more horizontal position which should facilitate feeding in a current as well as more rapid escape from predators, as Alexander (1967b) suggested.

Like a number of other species with protractible jaws, the feeding guppy closes its mouth with the premaxilla extended. Alexander (1967b) suggested several functions for this, including increased speed of closing the mouth, increased capacity of the mouth allowing prey to be sucked in from greater distances, and holding large prey in a horizontal position. This study suggests that in a benthic scraping mode, it is essential to keep the premaxilla protracted during the entire peck, so that small particles will not be lost during the feeding movement. The premaxilla appears to act as a "backstop" to the scraping movement of the dentary. Despite these adaptations, it is clear that the feeding apparatus is quite generalized, and certainly does not preclude the guppy from feeding on midwater and surface prey. Keast and Webb (1966) suggested the ventral protrusion of the mouth of Pimephales notatis (Cyprinidae) actually prevented surface feeding.

The feeding peck of a guppy appears quite rapid, averaging only about 0.17 s from the start to end of protraction. However, in some predatory species, the duration of mouth opening can be much shorter, e.g. Hoplias (Erythrinidae) 0.03 s and Amia (Amiidae) 0.07 s (Lauder, 1979) and Lebiasina (Lebiasinidae) 0.05 s (Lauder, in preparation). Measurement made in the ingestion rate experiment showed that the mean interpeck interval was 0.55 s for large females. Thus the actual jaw movements appear to occupy about one-third of the total interval.

Ingestion rate per peck increased with the size of the fish. This was presumably due to an increase in mouth size. Such an increase should be proportional to the square of the body length. In fact, the ingestion rate per peck divided by the SL^2 changed little over the range of fish sizes observed.

Algal density also influenced the rate of algal uptake. This was more clearly shown for males than for females, in part because females would not feed at the lower densities. Males appeared to have a higher ingestion rate for a given size than females, even though the slopes of the regressions of ingestion rate on size were very similar. It is not known whether this may be accounted for by morphological or behavioral differences between the sexes, but it may explain why males will feed at lower densities than females will.

Algal uptake rates suggested that a 500 mg female would clear about 1.6 mm^2 per peck. Measurement of the mouth in conjunction with the film analysis suggested that about 3.0 mm^2 is covered by the mouth of a fish of this size on each peck. Thus, about half the algae from the area covered by the mouth are ingested.

Hourly ingestion rates did not show a consistent daily pattern. Although there was variation there was no apparent rhythm of feeding activity under the aquarium conditions used. Daily ingestion rates, estimated in the final experiment seemed high, especially considering that the fish also had *Daphnia* available. The dry weight of algae ingested per day ranged from 5 to 25% of body weight. However, these figures may overestimate ingestion by assuming that the fish gained as much algae with each peck as they did in the experiment from which the multiple regression equation was calculated. This was probably not the case, since fish frequently pecked on areas previously cropped down by other fish. Odum (1970) estimated that a 200 mm SL mullet would filter 1500 g dry weight of sediment per day to ingest 15 g dry weight of food. Assuming that a mullet of 200 mm weighs about 175 g, on the basis of measurements made on other species of similar body form, this would represent about 9% of body weight ingested per day. In the only other estimate of ingestion rate for an herbivorous fish, Moriarty and Moriarty (1973) estimated that *Tilapia* in the wild ingested a dry weight of phytoplankton equivalent to about 2% of body weight per day. However, both availability and aquisition of food would differ between a wild population eating phytoplankton and fish fed unlimited amounts of a concentrated and easily procured food in the lab.

In a species like the guppy, which is polygamous without parental care, females allocate more resources to each offspring than males do. When food is in such short supply that females cannot achieve satiation, female reproductive success is likely to be well correlated with time allocated to feeding. The reproductive success of individual males is potentially greater than that of individual females, but this requires that males allocate some potential feeding time to searching, courting and mating with females, and to decreasing the success of other males in these activities. Thus, one would expect male guppies to allocate less time to feeding than females do (Hoffman, in preparation; Trivers, 1972). Sexual size or structure demorphism could help accomplish this.

Both feeding rate and food type could be affected by the intersexual size differences seen in the guppy. A large fish must take more pecks than a smaller fish on a particular food to ingest the same percentage of its body weight, since the size of the mouth probably increases with SL^2 while weight increases with SL^3. However, metabolic requirements probably increase with $(weight)^{0.7}$ (Gordon, 1977). Evidence for the discrepancy between feeding rate and proportional ingestion is seen in the last experiment, where the large females showed the highest feeding rates but actually ingested the least amount of algae as a percent of body weight. The difference in feeding rates of males and females of the same size was not significant. In the experiment with Tetra-min the rate of feeding was positively correlated with female size, but not with the narrower range of male sizes. Too, females showed much higher feeding rates than the smaller males.

The size of a fish should also affect the type of food taken, since a larger fish can ingest larger prey. Keast (1977) has suggested that this is especially important in fishes, as a means of reducing both inter- and intraspecific competition. In the experiments reported here, all sizes of fish fed readily on algae, Tetra-min and *Daphnia*, and no preference was shown by larger females for *Daphnia* in the final experiment. In the gut analysis of wild populations, the largest females of the Naranjo population, actually contained the fewest invertebrates, which were the largest food item. Therefore, the data obtained do not support the suggestion that larger guppies may specialize on larger prey.

Sexual dimorphism in the relative proportions of the trophic apparatus could also result in a reduction in feeding time by the males, not only by permitting them a wider range and size of potential prey, but also by increasing their rate of food intake. Such intersexual structural differences have been studied in relation to feeding in birds (e.g. Selander, 1966; Storer, 1966) and fiddler crabs (Valiela *et al*., 1974), and Baird (1965) indicated that it can also occur in fishes. He found that goby males have proportionally larger mouths than females and take larger prey in the laboratory. Some results of the present experiments indicate that there may be differences in the trophic apparatus of male and female guppies. Males ingested more algae per peck, and, although they took slightly longer per peck, subsequently ingested a larger percent of their body weight per day with fewer pecks than did females of the same size. Too, they appeared to take somewhat less time per peck on *Daphnia*.

That males allocate a lot of their potential feeding time to courtship is evident from both this and other studies. Courtship by males was observed in about 70% of the recorded intervals when the fish were feeding on Tetra-min. In both laboratory and natural populations males have been found to display to females from 7 to 13 times per 5 min on the average (Farr and Herrnkind, 1974; Farr, 1975). Farr (1976) has shown too that there is social facilitation of the courtship display rate, and that it is increased by a high degree of polymorphism among the males. In this study, the time expenditure in courtship was positively correlated with both male and female size, the largest males courting more than the smaller and the largest females being courted the most. There is an advantage for males to court the largest females since they will produce the most fry (Thibault and Schultz, 1978). This pattern has been observed by previous workers (Haskins and Haskins, 1949; Baerends *et al.*, 1955).

Time constraints on the male might also have an influence on the organization of feeding bouts. His reproductive success depends on being present when a female becomes receptive in order to compete successfully with other males. If female receptivity is unpredictable, the best trade-off between courtship and feeding may be to intersperse courtship with short periods of feeding behaviour. This strategy is suggested by the shorter bouts of males feeding on algae and Tetra-min in these experiments. When feeding on algae, males had fewer longer bouts than either size class of female, while on Tetra-min the majority of their bouts contained only 1-2 pecks.

I hope that continued study of laboratory and field populations of guppies will be facilitated with the results presented in this paper, and that the questions raised will stimulate further study of the feeding behaviour of herbivorous fishes.

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BIBLIOGRAPHY

Alexander, R. McN. 1966. Mechanisms of the jaws of some atheriniform fish. Zool., Lond. 151:233-255.

_____. 1967. The functions and mechanisms of the protrusible upper jaws of some acanthopterygian fish. J. Zool. Lond. (1967) 151:43-64.

Baerends, G.P., R. Brouwer, and H.T.J. Waterbolk. Ethological studies on Lebistes reticulatus (Peters). Behav. 8:249-334.

Baird, R.C. 1965. Ecological implications of the behaviour of the sexually dimorphic goby Microgobius gulosus (Girard). Publ. Inst. Marine Sci. Texas 10:1-8.

Ballin, P.J. 1973. Geographic variation in courtship behaviour of the guppy (Poecilia reticulata). Unpublished M.Sc. thesis. Univ. of British Columbia.

Bertalanffy, L. von. 1938. A quantitative theory of organic growth (inquires on growth laws II). Human Biol. 10:181-213.

Bowen, S.H. 1978. Benthic diatom distribution and grazing by Sarotherodon mossambicus in Lake Sibaya, South Africa. Freshwater Biol. 8:449-453.

_____. 1979. A nutritional constraint in detritivory by fishes: the stunted population of Sarotherodon mossambicus in Lake Sibaya, South Africa. Ecol. Monogr. 1979:17-31.

Comfort, A. 1961. The longevity and mortality of a fish (Lebistes reticulatus Peters) in captivity. Gerontol. 5:209-222.

Crow, R.T., and N.R. Liley. 1979. A sexual pheromone in the guppy, Poecilia reticulata (Peters). Can. J. Zool. 57:184-188.

Darnell, R.M. 1967. The organic detritus problem in Estuaries. G.H. Lauff (Ed.). AAAS Publ. 83:397-407.

Davis, C.C. 1968. Quantitative feeding and weight change in Poecilia reticulata. Trans. Amer. Fish. Soc. 97(1):22-27.

Doi, T. 1969. Experimental study on the feeding of the guppy, Poecilia reticulata. Jap. J. Ecol. 19:62-66.

Endler, J.A. 1978. A predator's view of animal color patterns. Evol. Biol. 11:319-364.

Fagen, R.M., and D.Y. Young. 1978. Temporal patterns of behaviours: durations, intervals, latencies and sequences. pp 79-114 in Quantitative Ethology. P.W. Colgan (Ed.). John Wiley & Sons, N.Y.

Farr, J.A. 1975. The role of predation in the evolution of social behaviour of natural populations of the guppy, Poecilia reticulata (Pisces: Poeciliidae). Evol. 29:151-158.

_____. 1976. Social facilitation of male sexual behaviour, intrasexual competition, and sexual selection in the guppy, Poecilia reticulata (Pisces: Poeciliidae). Evol. 30:707-717.

Farr, J.A., and W.F. Herrnkind. 1974. A quantitative analysis of social interaction of the guppy, _Poecilia reticulata_, as a function of population density. Anim. Behav. 22:582-591.

Fish, G.R. 1952. Digestion in _Tilapia esculenta_. Nature, Lond. 167:900-901.

_____. 1955. The food of _Tilapia_ in East Africa. Uganda J. 19:85-89.

Fryer, G., and T.D. Iles. 1975. The cichlid fishes of the great lakes of Africa. Proc. Natl. Acad. Sci. U.S.A. 72:4669.

Gibson, M.B., and B. Hirst. 1955. The effect of salinity and temperature on the preadult growth of guppies. Copeia 1955(3):241-243.

Goodrich, H.B., J.E. Dee, C.M. Flynn, and R.W. Mercer. 1934. Germ cells and sex differentation in _Lebistes reticulatus_. Biol. Bull. 67(1):83-96.

Gordon, M.S. 1977. (ed.), Animal Physiology: Principles and Adaptations. MacMillan Publishers, London.

Green, J., S.A. Corbet, E. Watts, and O.B. Lan. 1976. Ecological studies on Indonesian lakes. Overturn and restratification of Ranu Lamongan. J. Zool. London 180:315-354.

_____. 1978. Ecological studies on Indonesian lakes. The montane lakes of Bali. J. Zool., Lond. 186:15-38.

Greenwood, P.H. 1953. Feeding mechanism of the cichlid fish, _Tilapia esculenta_ Graham. Nature 172:207-208.

Gunn, J.M., S.U. Qadri, and D.C. Mortimer. 1977. Filamentous algae as a food source for the brown bullhead (Ictalurus nebulosus). J. Fish. Res. Board Can. 34(3):396-401.

Harrington, R.W., and E.S. Harrington. 1961. Food selection among fishes invading a high subtropical salt marsh: from onset of flooding through the process of a mosquito brood. Ecol. 42(4): 646-666.

Haskins, C.P., E.F. Haskins, J.J.A. McLaughlin, R.E. Hewitt. 1961. Polymorphism and population structure in Lebistes reticulatus, an ecological study. pp 320-395 in: Vertebrate Speciation. W.F. Blair (Ed.), Univ. Texas Press, Austin.

Haskins, C.P., and E.F. Haskins. 1949. The role of sexual selection as an isolating mechanism in three species of poeciliid fishes. Evol. 3:160-169.

Hester, F.J. 1964. Effects of food supply on fecundity in the female guppy, Lebistes reticulatus. J. Fish. Res. Board Can. 21:757-764.

Hoffman, S.G. Sex change as a determinant of foraging activity in a hermaphroditic reef fish. In preparation.

Jones, R.S. 1968. A suggested method for quantifying gut contents in herbivorous fishes. Micronesica (2):369-371.

Kapoor, B.G., H. Smit, and I.A. Verighina. 1975. The alimentary canal and digestion in teleosts. Adv. mar. Biol. 13:109-239.

Keast, A., and D. Webb. 1966. Mouth and body form relative to feeding ecology in the fish fauna of a small lake, Lake Opinicon, Ontario. J. Fish. Res. Board Can. 23:1847-1874.

Kitchell, J.F. and J.T. Windel. 1970. Nutritional value of algae in bluegill sunfish, Lepomis macrochirus. Copeia 1970:186-190.

Kramer, D.L. 1978. Ventilation of the respiratory gas bladder in Hoplerythrinus unitaeniatus (Pisces, Characoidei, Erythrinidae). Can. J. Zool. 56:931-938.

Kramer, D.L. and J.P. Mehegan. Aquatic surface respiration, an adaptive response to hypoxia in the guppy, Poecilia reticulata (Pisces, Poeciliidae). In preparation.

Kristensen, I. 1970. Competition in three cyprinodont fish species in the Netherlands Antilles. in Hummelinck, P.W. (Ed.). Studies on the fauna of Curacao and other Caribbean islands. No.119. 32:82-101.

Lauder, G.V. 1979. Feeding mechanics in primitive teleosts and in the halecomorph fish Amia calva. J. Zool., Lond. 187:543-578.

_____. Intraspecific functional repertoires in the feeding mechanism of the characoid fishes Lebiasina, Hoplias, and Chalceus. In preparation.

Ligon, J.D. 1968. Sexual differences in foraging behaviour in two species. Auk 85:203-215.

Liley, N.R. 1966. Ethological isolating mechanisms in four sympatric species of poeciliid fishes. Behav., Suppl. 13:1-197.

Liley, N.R., and B.H. Seghers. 1975. Factors affecting the morphology and behaviour of guppies in Trinidad. in Function and Evolution in Behaviour, G. Baerends, C. Beer, and A. Manning (Eds.), Oxford.

Menzel, D.W. 1959. Utilization of algae for growth by the angelfish, Holacanthus bermudensis. J. Cons. Perm. Int. Explor. Mer. 24: 308-313.

Moriarty, D.J.W., J. Darlington, I.G. Dunn, C.M. Moriarty, and M.P. Tevlin. 1973. Feeding and grazing in Lake George, Uganda. Proc. R. Soc. Lond. B. 184:299-319.

Moriarty, C.M., and D.J.W. Moriarty. 1973. Quantitative estimation of the daily ingestion of phytoplankton by Tilapia nilotica and Haplochromis nigripinnis in Lake George, Uganda. J. Zool., Lond. 171:15-23.

Murdoch, W.M., S. Avery, and M.E.B. Smyth. 1975. Switching in predatory fish. Ecol. 56:1094-1105.

Odum, E.P. 1962. Relationships between structure and function in the ecosystem. Jap. J. Ecol. 12:108-118.

Odum, W.E. 1970. Utilization of the direct grazing and plant detritus food chains by the striped mullet Mugil cephalus. pp 222-240 in Marine Food Chains, J. Steel (Ed.). Univ. of California Press, Berkeley, California.

Odum, W.E., and E.J. Heald. 1972. Trophic analysis of an estuarine mangrove community. Bull. Marine Sci. 22:671-738.

Rabe, J.R., A.A. Echelle, and H.E. Schlichting, Jr. 1973. Viability of algae in the digestive tracts of two cyprinodontids. Prog. Fish Cult. 35:147-149.

Rose, S.M. 1959. Population control in guppies. Am. Midl. Nat. 62: 474-481.

Schoener, T. 1967. The ecological significance of sexual dimorphism in size in the lizard Anolis conspersus. Science 155:474-477.

Seki, H. 1972. The role of microorganisms in the marine foodchain with reference to organic aggregate. Memorie dell'Istituto italiano di Idrobiologia 29:245-259.

Seghers, B.H. 1973. Analysis of geographic variation in the anti-predator adaptations of the guppy Poecilia reticulata (Peters). Ph.D. thesis. Univ. of British Columbia.

Selander, R.K. 1966. Sexual dimorphism and differential niche utilization in birds. Condor 68:113-151.

Serebrov, L.I. 1973. Effect of a current on the intensity of feeding in certain fish. Hydrobiol. J. 9(2):68-72.

Silliman, R.P., and J.S. Gutsell. 1958. Experimental exploitation of a fish population. Fish Bull (U.S.), 58(133):215-252.

Starr, R.C. 1964. The culture collection of algae at Indiana University. Amer. J. of Bot. 51(9):1013-1044.

Storer, R.W. 1966. Sexual dimorphism and food habits in three North American accipiters. Auk 83:423-436.

Thibault, R.E., and R.J. Schultz. 1978. Reproductive adaptations among viviparous fishes (Cyprinodontiformes: Poeciliidae). Evol. 32(2):320-333.

Thompson, J.M. 1954. The organs of feeding and the food of some Australian mullet. Aust. J. mar. freshwat. Res. 5:469-485.

Trivers, R.L. 1972. Parental investment and sexual selection. pp 136-179 *in* Sexual selection and the descent of man, 1871-1971. B.G. Campbell (Ed.). Aldine, Chicago.

Uematsu, T. 1971. Social facilitation in feeding behaviour of the guppy II. Jap. J. Ecol. 21:54-67.

Valiela, I., D.F. Babiec, W. Atherton, S. Seitzinger, and C. Krebs. 1974. Some consequences of sexual dimorphism feeding in male and female fiddler crabs *Uca pugnax* (Smith). Biol. Bull. 147: 652-660.

Vrijenhoek, R.C. 1978. Coexistence of clones in a heterogeneous environment. Science 199:549-552.

Warren, E.W. 1973. Modification of the response to high density conditions in the guppy, *Poecilia reticulata* (Peters). J. Fish. Biol. 5:737-752.

Winge, O. 1922. One sided masculine and sex-linked inheritance in *Lebistes reticulatus*. Compt. rend. d. Lab. Carlsberg 14(18); (1922). J. Genet. 12:145-162.

_____. 1927. The location of eighteen genes in *Lebistes reticulatus*. J. Genet. 18:1-42.

_____. 1930. On the occurrence of XX males in *Lebistes*, with some remarks on Aida's so called "Non-Disjunctional" males in *Aplocheilus*. J. Genet. 23:69-76.

Winge, O., and E. Ditlevsen. 1948. Colour inheritance and sex determination in *Lebistes*. Compt. rend. d. Lab. Carlsberg. Ser. Physiol. 24:227.

Yamagishi, H., T. Okino, N. Nakamoto, Y. Nakamura, and Y. Wade. 1967. Ecological studies on the guppy, *Lebistes reticulatus* (Peters). III. On the guppy population acclimated in a water of Togura-Kamiyamada spa. Jap. J. Ecol. 17:206-213.

Zarat, T.M., and A.S. Rand. 1971. Competition in tropical stream fishes: support for the competitive exclusion principal. Ecol. 52:336-342.

Figure 1. The relative abundance of dietary categories in the microscopic examination of the gut contents of females (shaded) and males (unshaded) from two populations of Trinidad guppies, Naranjo (A) and Tacarigua (B). Bars indicate means and vertical lines the range of the percent of the frequency with which the various items contacted predetermined points on an ocular grid.

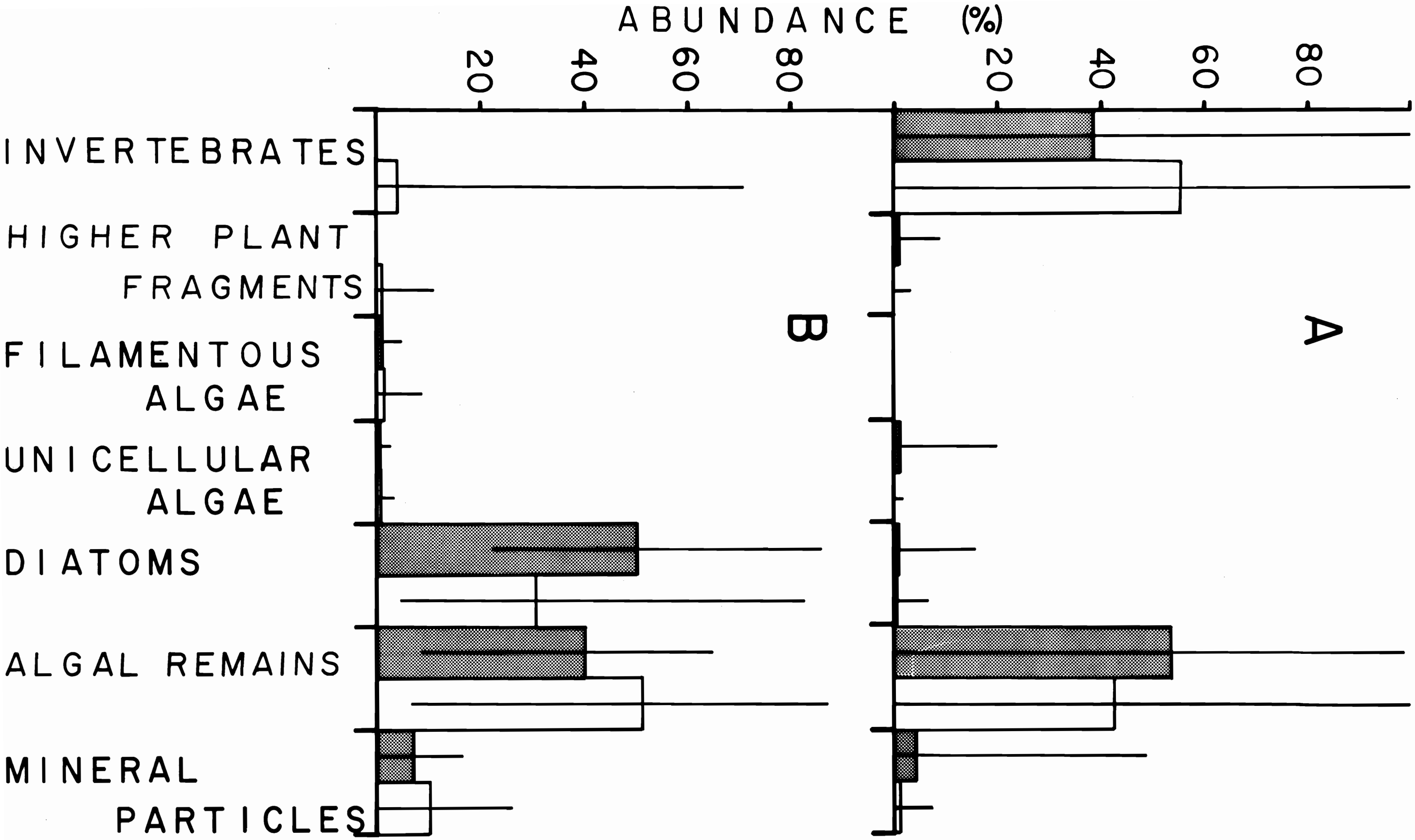

ABUNDANCE (%)
20
40
60
80
20
40
60
80
INVERTEBRATES
HIGHER PLANT
FRAGMENTS
FILAMENTOUS
ALGAE
UNICELLULAR
ALGAE
DIATOMS
ALGAL REMAINS
MINERAL
PARTICLES
B
A

Figure 2. The relationship between the frequency of invertebrates in the gut contents and the weights of Naranjo male (circles) and female (triangles) guppies.

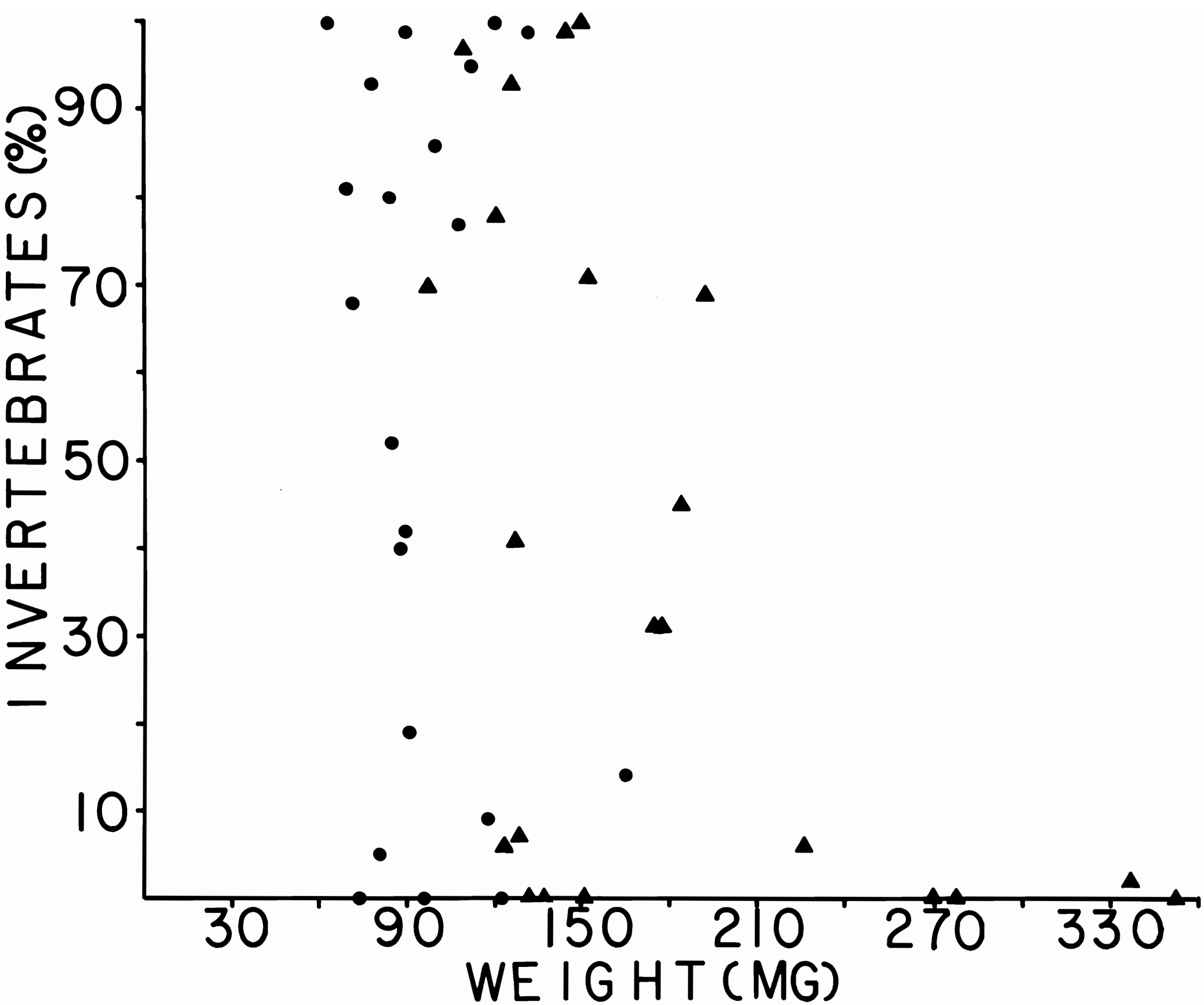

INVERTEBRATES (%)
90
70
50
30
10
30
90
150
210
270
330
WEIGHT (MG)

Figure 3. Growth of guppies on three diets: *Daphnia* (squares), Tetramin (circles), and algae (triangles). Change in weight in relation to time is shown for all fish from 0 to 5 weeks (A), and separately for males (B) and females (C) from 5 to 10 weeks. 95% confidence limits are indicated by vertical lines only where they do not overlap with the confidence limits of one or both other groups.

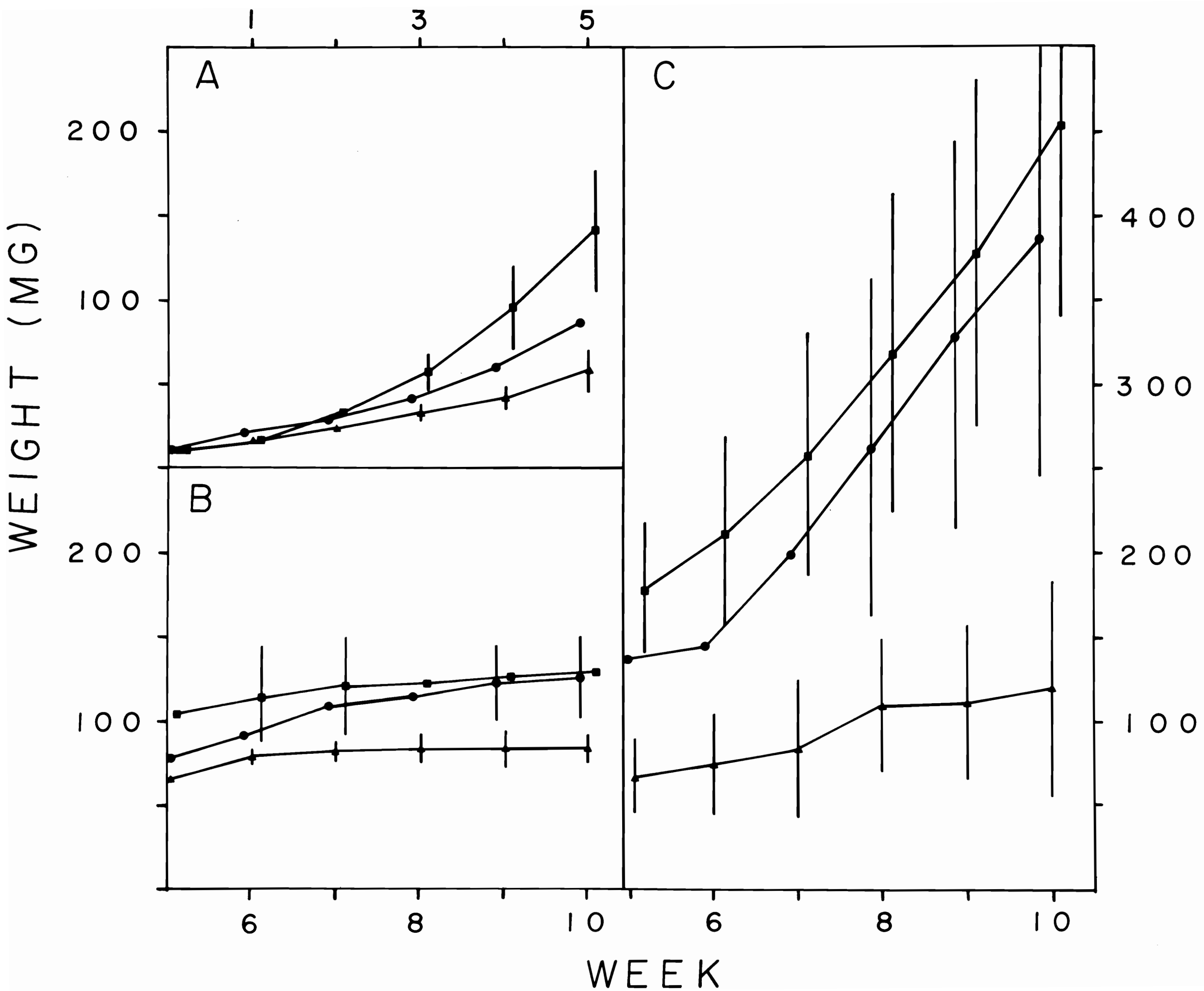

A
B
C
WEIGHT (MG)
WEEK
200
100
200
100
400
300
200
100
1
3
5
6
8
10
6
8
10

Figure 4. Prints taken from fifteen consecutive frames of a film shot at 64 frames/s, which show the movements of the jaws of a female guppy during a single feeding peck.

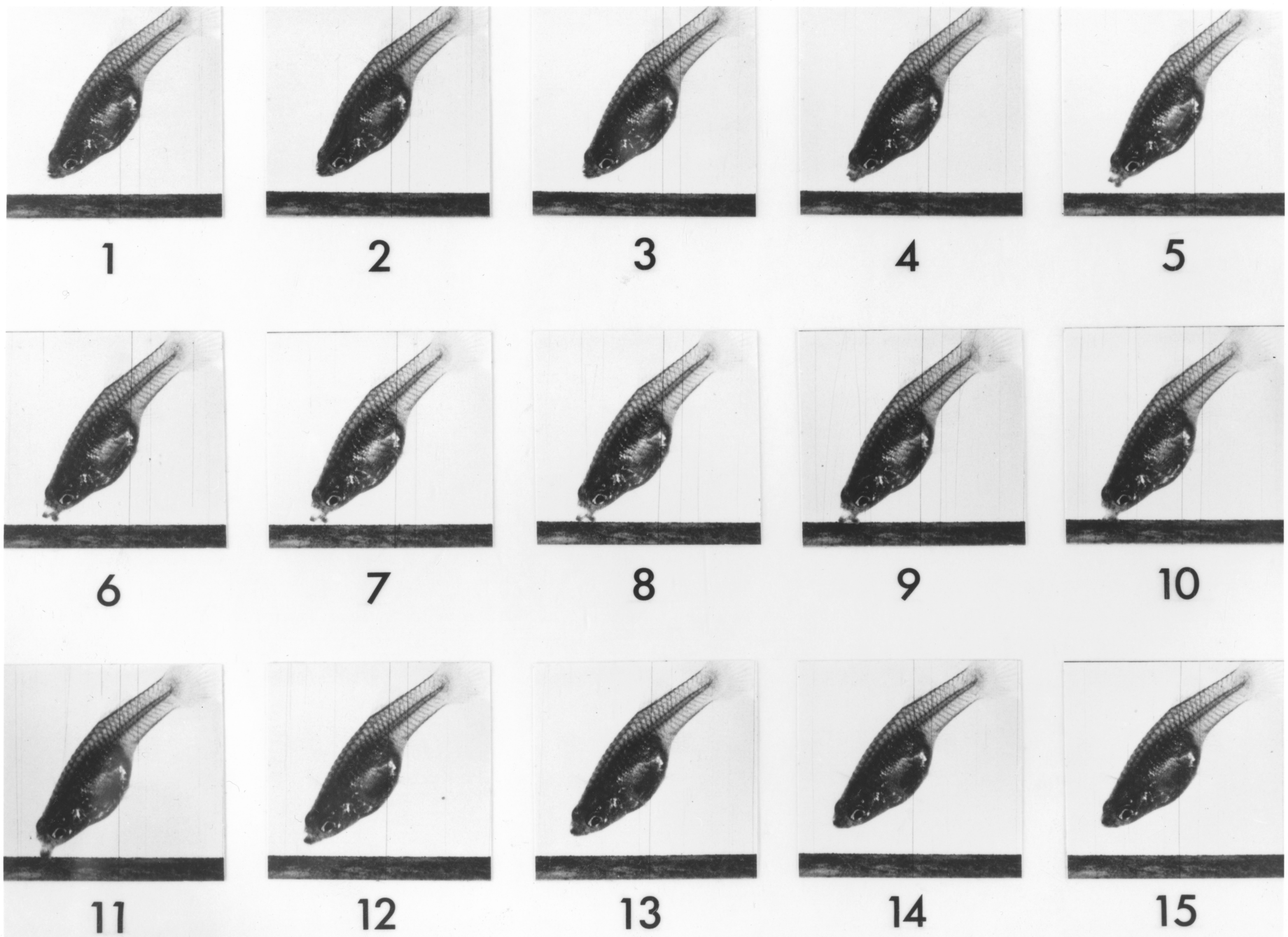

1
2
3
4
5
6
7
8
9
10
11
12
13
14
15

Figure 5. Diagram of the head of a guppy with lines to indicate the movement in relation to the feeding substrate of the eye (E), the premaxilla (P), and the dentary (D) in a feeding peck lasting 0.21 s. The positions on consecutive frames are indicated by dots. Although the fish was not perfectly lateral to the camera, accurate vertical and horizontal movements were calculated by expressing them as ratios of the reference distance, the minimum distance from the center of the eye to the posterior edge of the operculum.

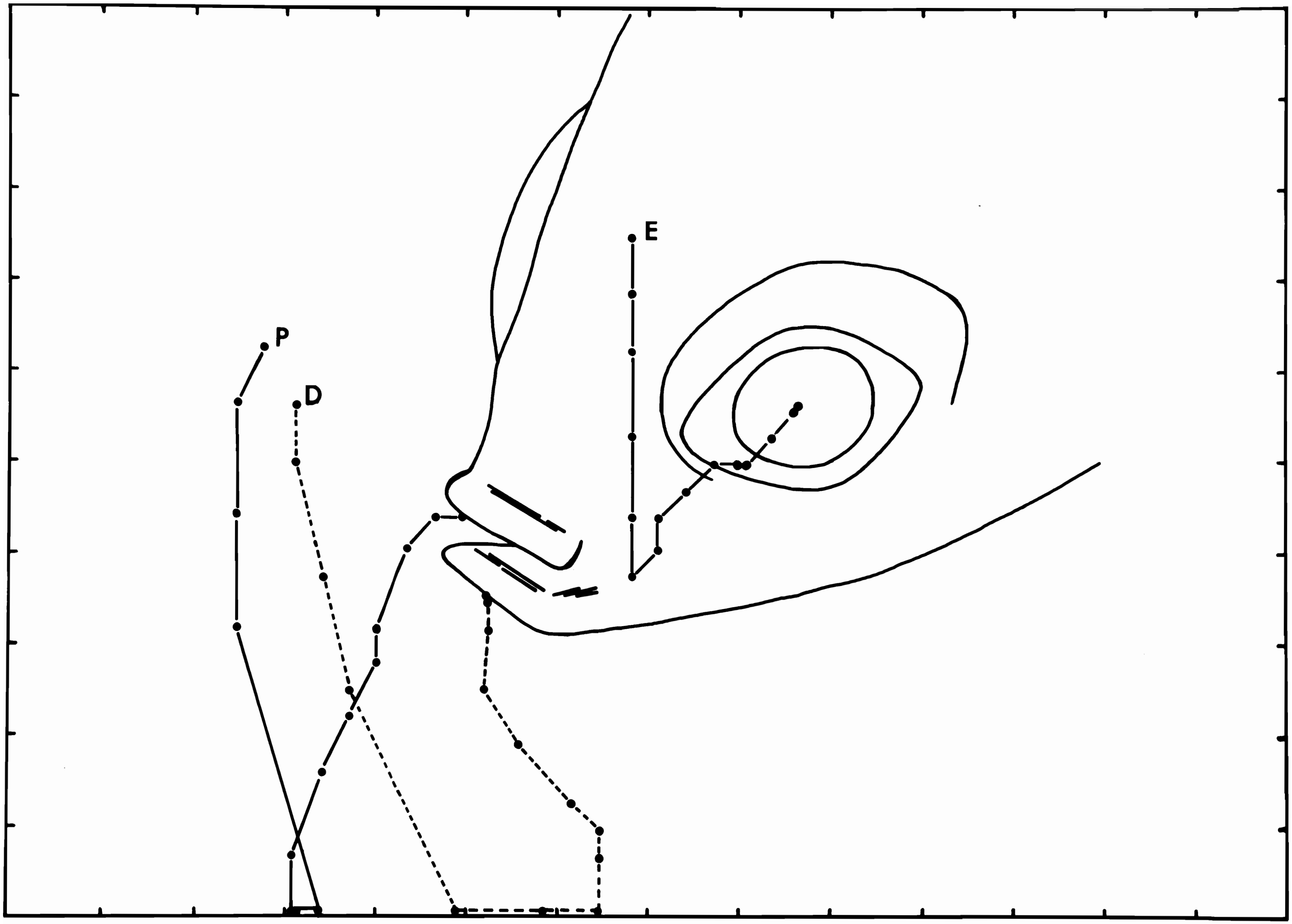
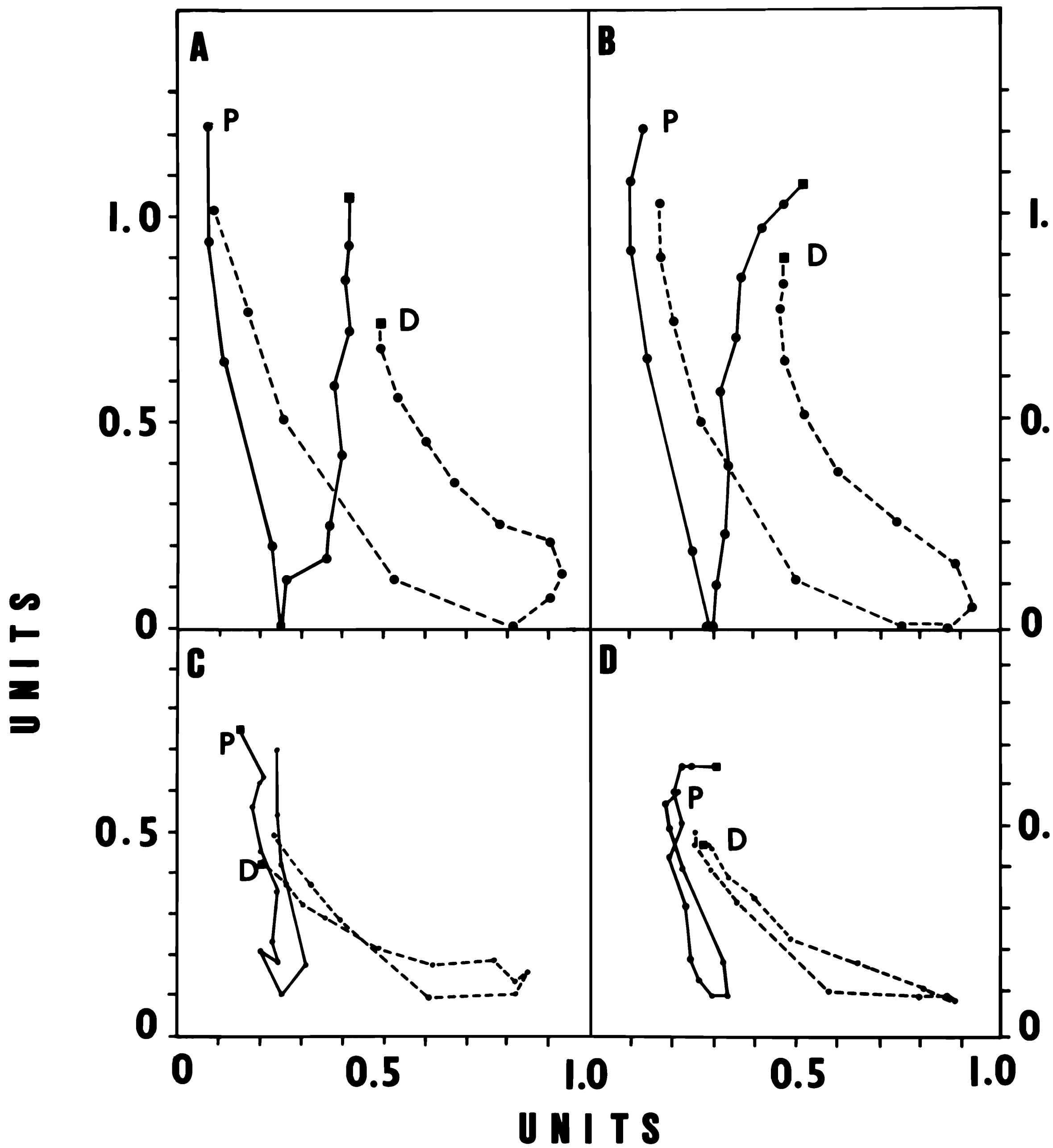

E
P
D

Figure 6. The mean movements of the premaxilla (P) and the dentary (D), relative to the substrate (A and B), and relative to the head (C and D), in 8 sequences with short contact (A and C), and 12 with long (B and D). All are graphed to the same scale. Squares show the initial positions of the premaxilla and dentary in each set. Dots show the mean position on consecutive frames. Units indicated represent fractions of the mean reference distance.



A
B
C
D
P
D
P
D
P
D
P
D
1.0
0.5
0
0.5
0
0
0.5
1.0
0.5
1.0
UNITS
UNITS

Figure 7. Scrape marks left by the teeth of a female guppy feeding on a thin layer of algae on a plexiglas plate.

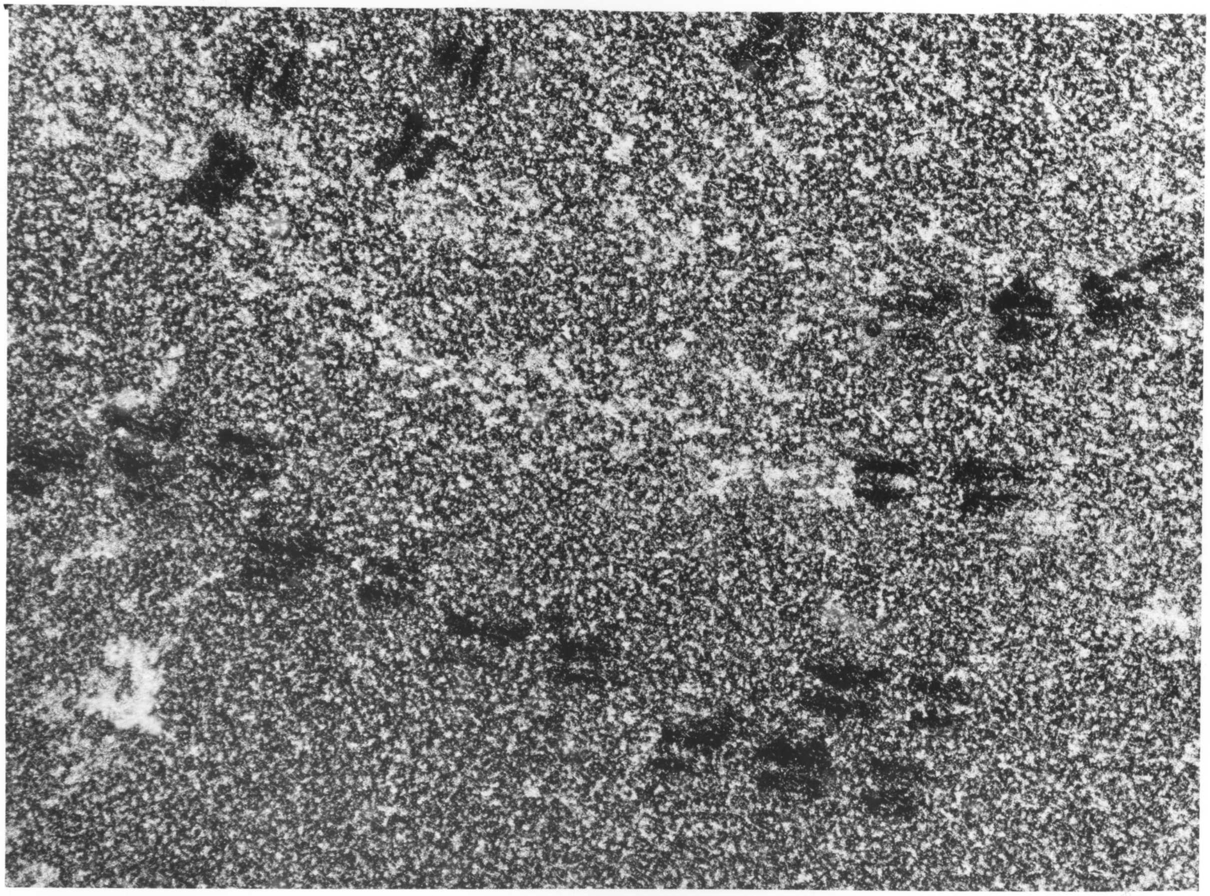
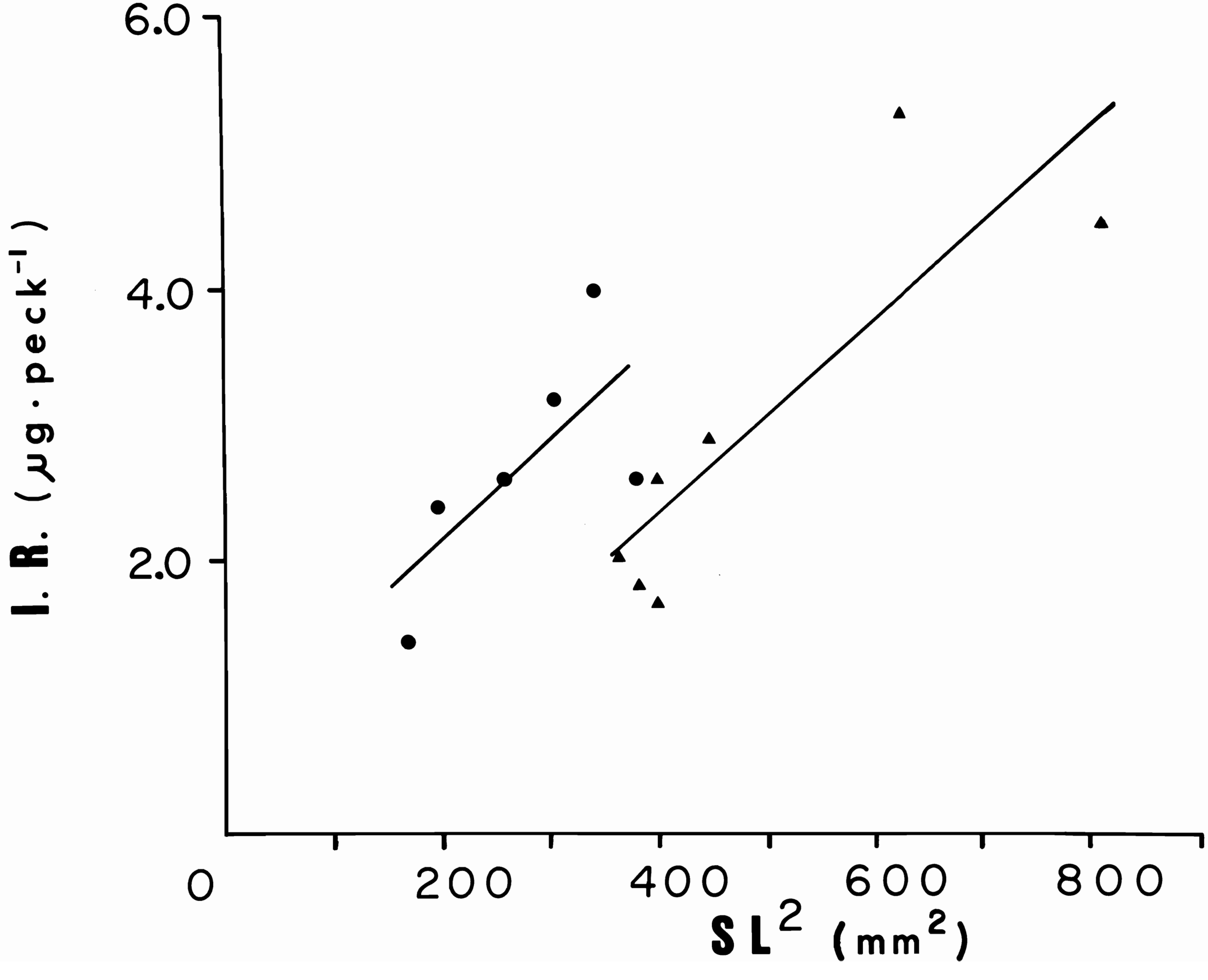
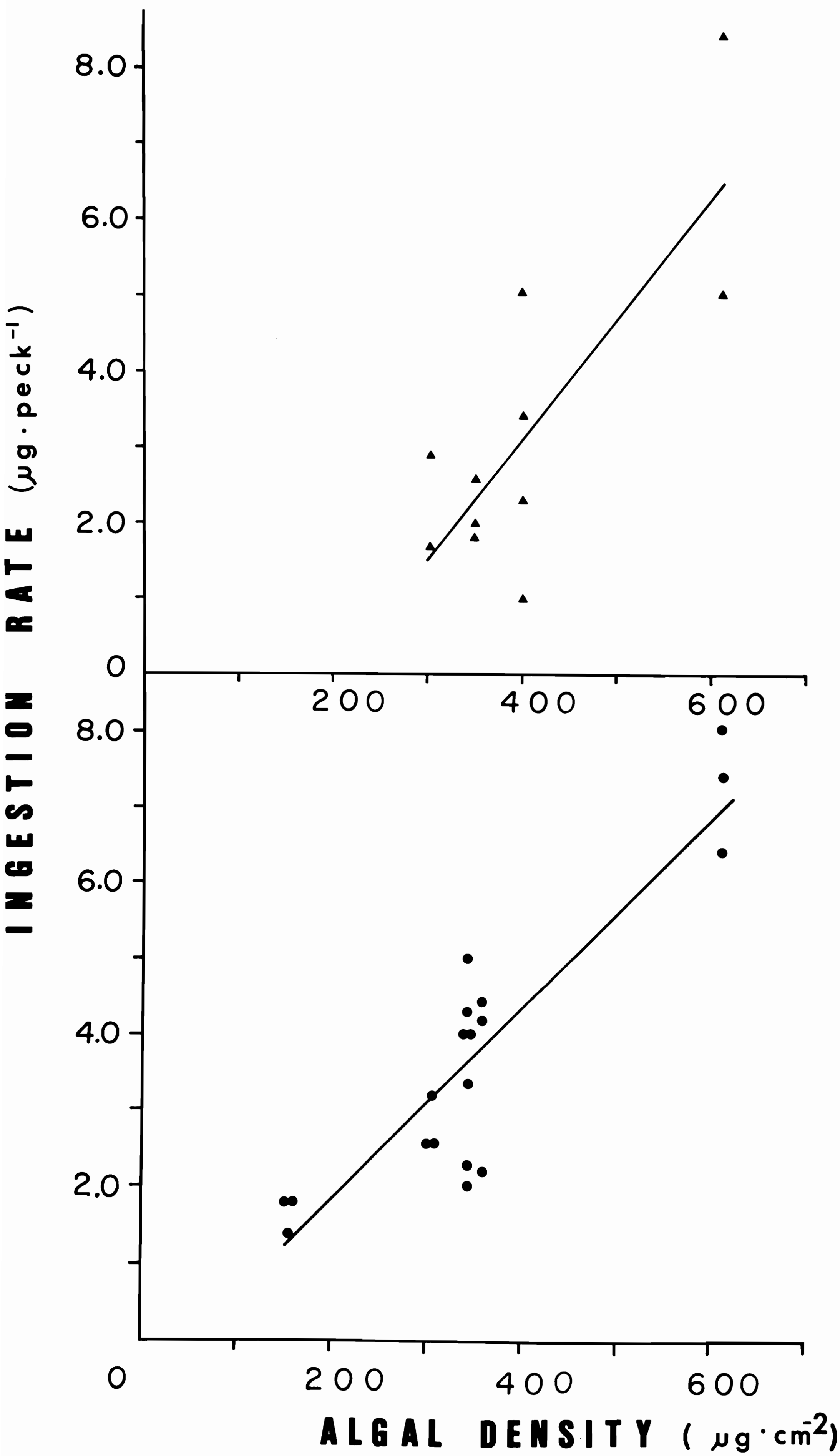


Figure 8. The ingestion rate (I.R.) of guppies in relation to body size (standard length squared, SL^2). The rates of six males (circles) and seven females (triangles) feeding at a fixed density of *Chlorococcum* (326 $\mu g/cm^2$). Calculated regression lines are shown.



I. R. (μg · peck⁻¹)
6.0
4.0
2.0
0
200
400
600
800
SL2 (mm2)

Figure 9. The ingestion rates of 11 female guppies (triangles) and 19 males (circles) in relation to algal density. Calculated regression lines for each sex are shown. Males ranged from 15.5 mm to 19.5 mm and females from 19.5 mm to 22.5 mm SL.



INGESTION RATE (μg · peck⁻¹)
8.0
6.0
4.0
2.0
0
200
400
600
8.0
6.0
4.0
2.0
0
200
400
600
ALGAL DENSITY (μg · cm⁻²)

Figure 10. The frequency distribution of the number of pecks per 15 s interval for 4 female guppies (A) and 5 males (B) feeding on Tetra-min on the substrate. The distributions are based on 1920 intervals for females and 2400 for males.

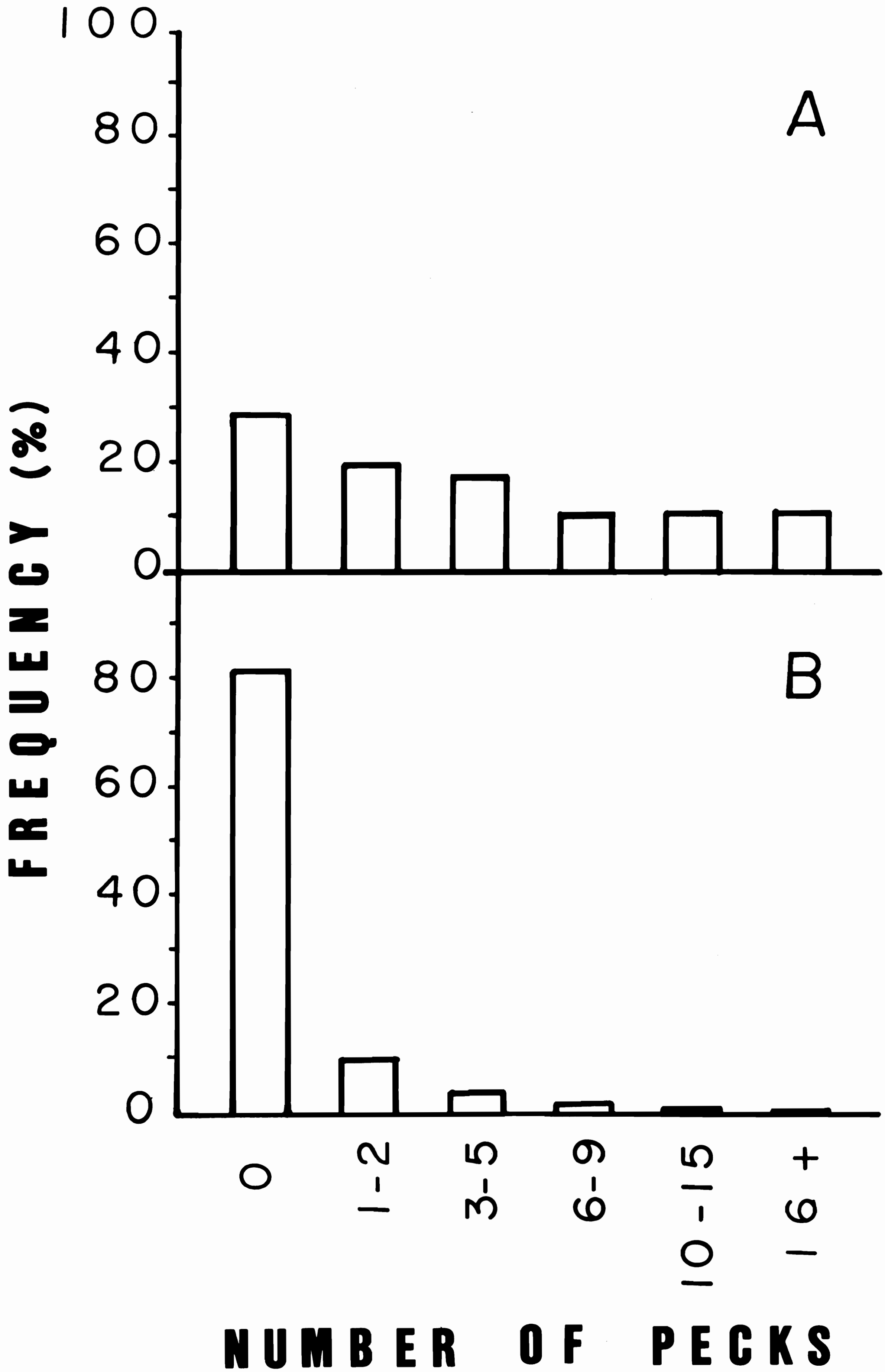

100
80
60
40
20
0
80
60
40
20
0
A
B
FREQUENCY (%)
0
1-2
3-5
6-9
10-15
16+
NUMBER OF PECKS

Figure 11. The relationships between body weight, feeding rate (A), the mean total feeding pecks recorded in six 5 min observations per day over 4 days, and courtship rate (B), the mean daily percent of 15 s intervals averaged over 4 days (n = 120/fish per day). Ranges of the values for the 4 days are shown by vertical lines.

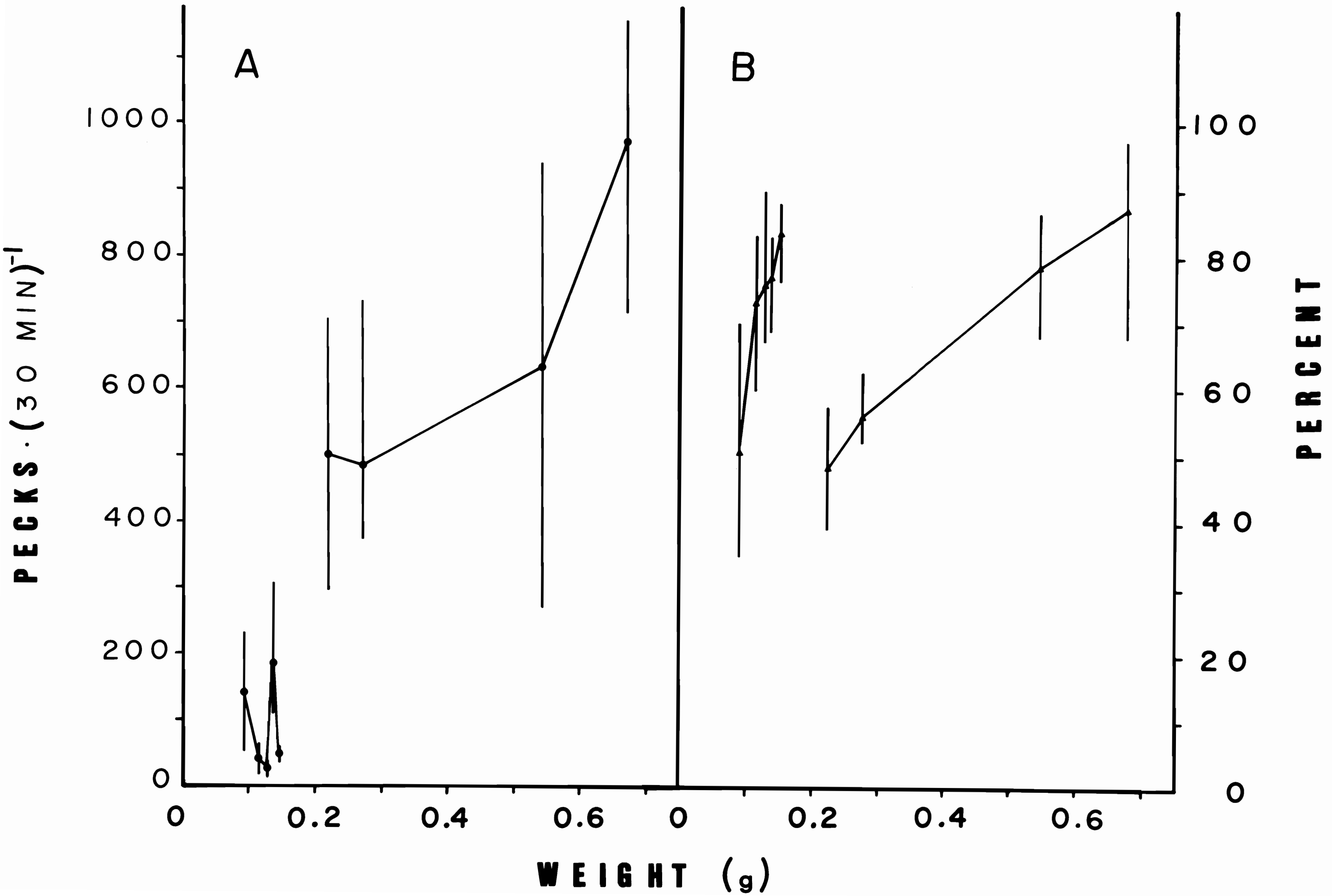

A
B
PECKS·(30 MIN)$^{-1}$
PERCENT
WEIGHT (g)
0
200
400
600
800
1000
20
40
60
80
100
0.2
0.4
0.6

Figure 12. The amount of time spent feeding in relation to time of day for three classes of 15 guppies each. The records for large females (A), small females (B) and males (C) are indicated for day 1 (above) and day 2 (below).

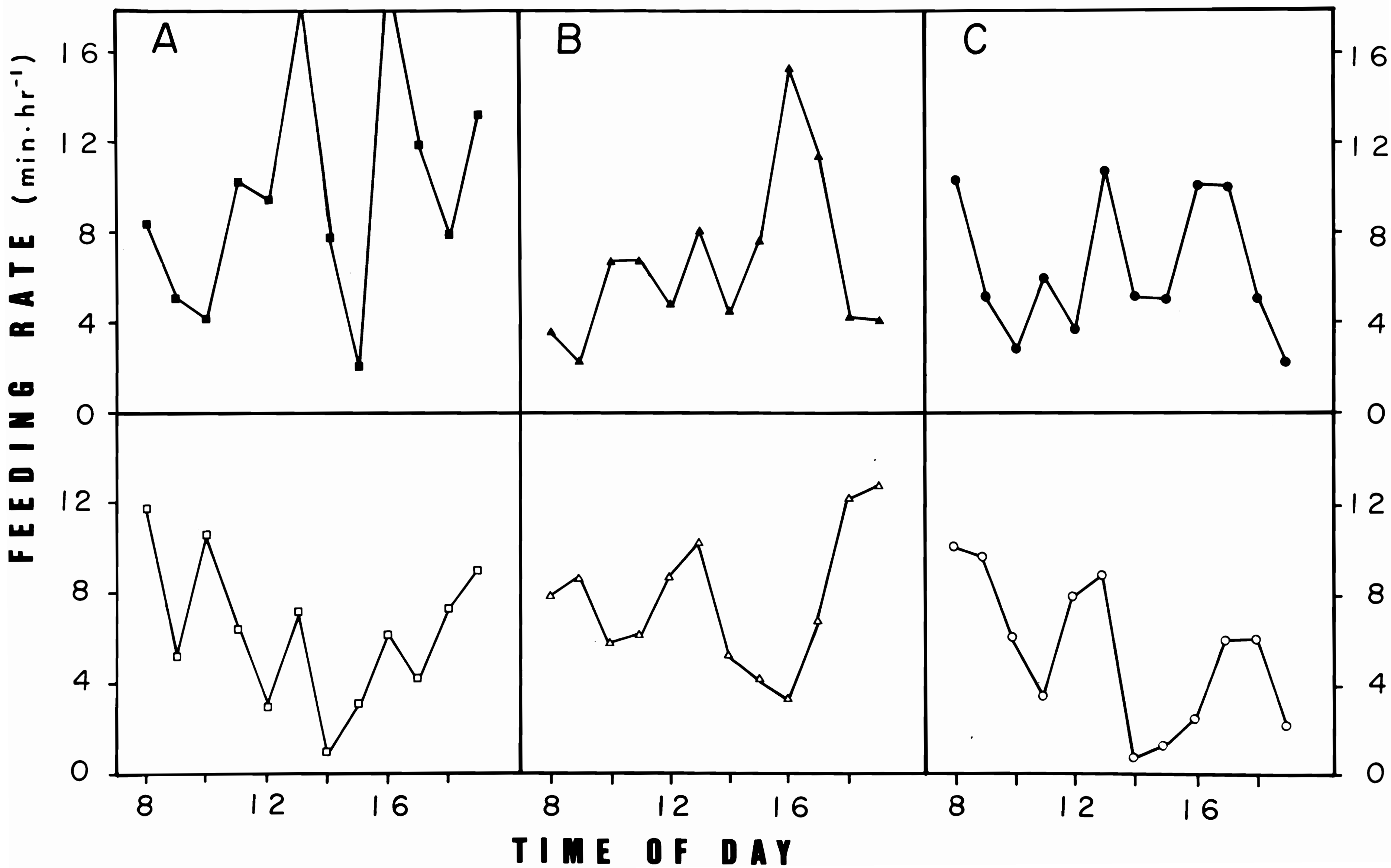

FEEDING RATE (min·hr⁻¹)
TIME OF DAY
A
B
C
0
4
8
12
16

Figure 13. The mean (squares), 95% C.L. (enclosed rectangles) and ranges (vertical lines) of the time spent feeding (min/hr) of three classes of guppies, each consisting of 15 fish. Large females (LF), small females (SF) and males (M), feeding on algae (A) and Daphnia (B) are shown for each of two days.

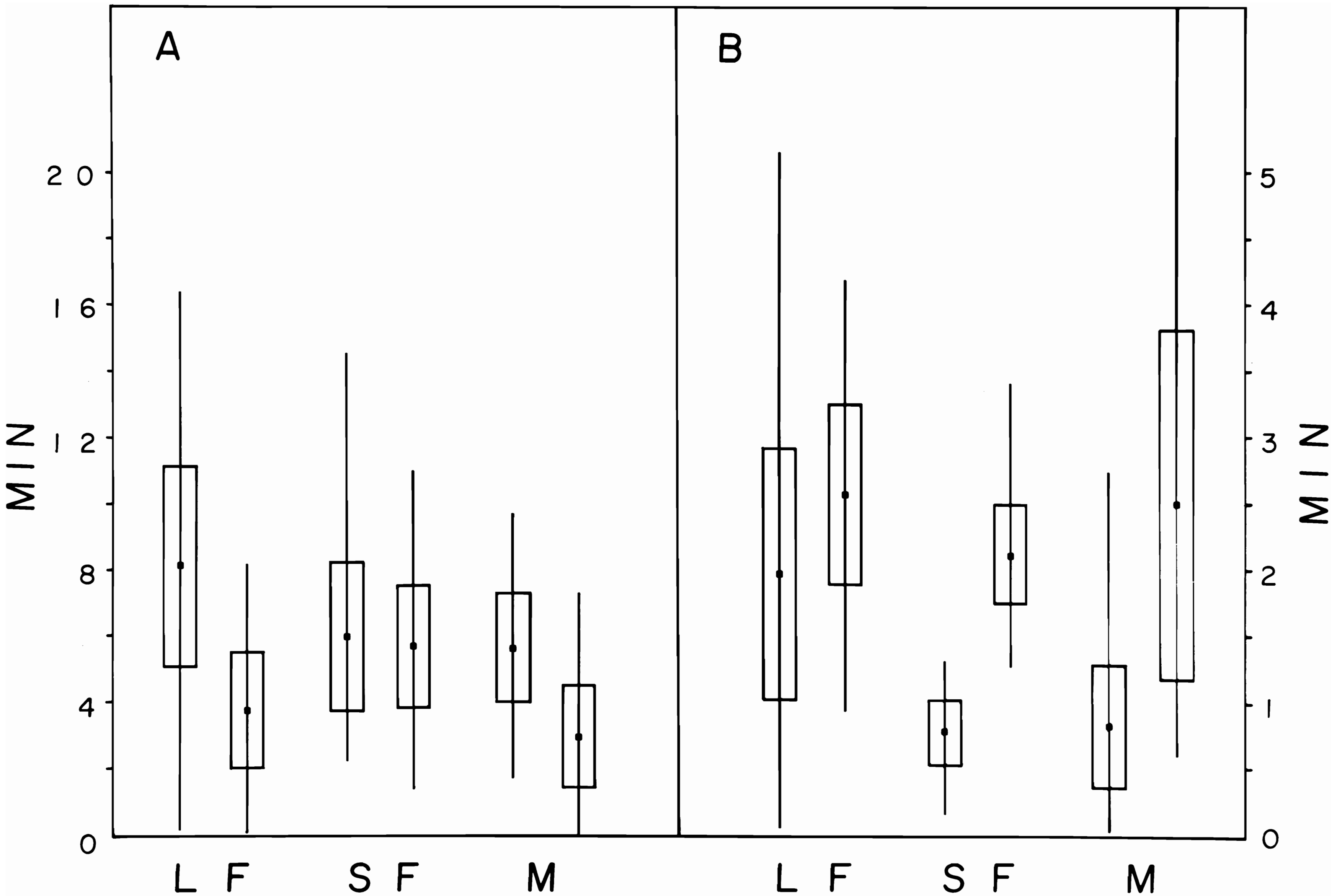

A
B
MIN
0
4
8
12
16
20
L F
S F
M
L F
S F
M
0
1
2
3
4
5
MIN

Figure 14. Log survivor curves for feeding bout length in guppies measured as the number of pecks per bout for each of two days for large females (A), small females (B) and males (C) feeding on *Chlorococcum* (C) and *Daphnia* (D). Where the lines overlap for *Daphnia* only a single line is shown.

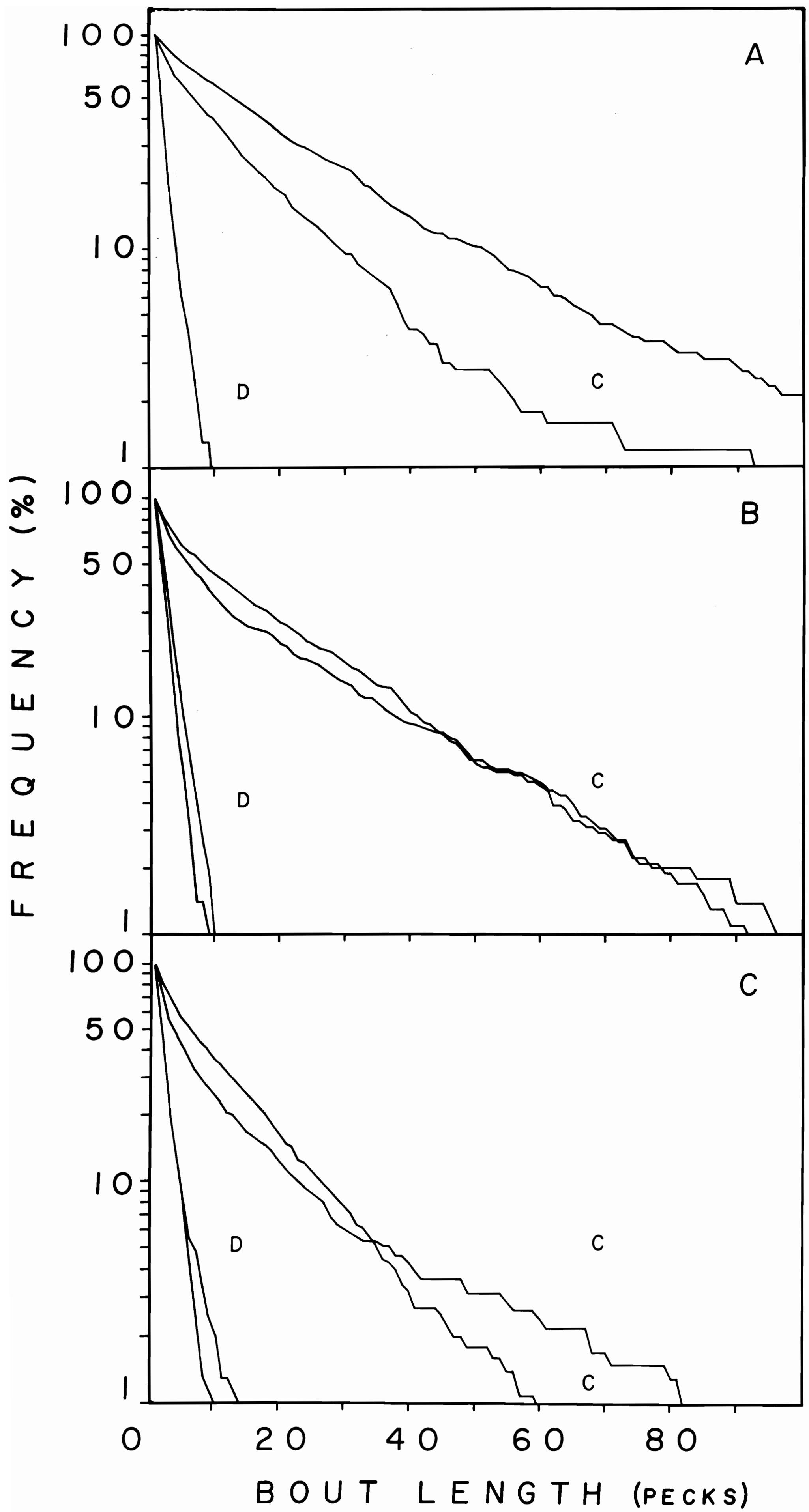

A
B
C
D
c
FREQUENCY (%)
100
50
10
1
0
20
40
60
80
BOUT LENGTH (PECKS)

Figure 15. The relationship between the mean hourly bout length and the mean hourly feeding rate in guppies feeding on algae. Data are shown separately for large females (A), small females (B), and males (C), and for day 1 (closed) and day 2 (open).

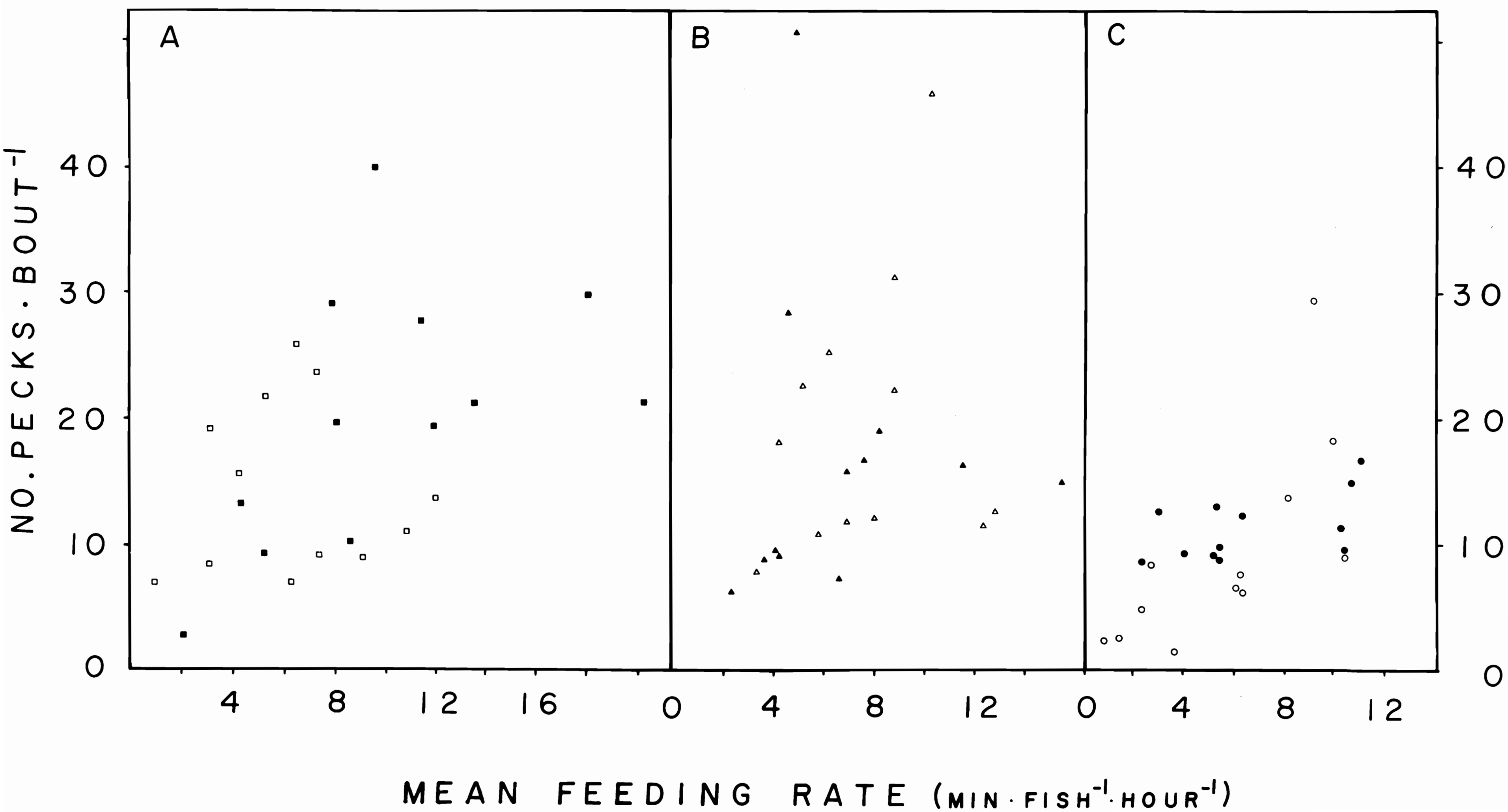

A
B
C
NO. PECKS · BOUT⁻¹
MEAN FEEDING RATE (MIN · FISH⁻¹ · HOUR⁻¹)

Table 1. The occurrence and dominance of food categories in male and female guppies from two populations. For each food category, the number of fish containing the item (O), and the number in which that item was established to be volumetrically dominant (D), is shown.

	Tacarigua				Naranjo			
	Females N=24		Males N=22		Females N=22		Males N=21	
	O	D	O	D	O	D	O	D
Invertebrates	3	0	5	1	19	8	20	12
Higher plant fragments	1	0	4	0	10	0	5	0
Filamentous algae	22	0	21	0	6	0	1	0
Unicellular algae	24	0	22	0	15	0	15	0
Diatoms	24	15	22	3	7	0	9	0
Algal remains	24	9	22	18	22	13	20	9
Mineral particles	24	0	22	0	21	1	21	0

Table 2. Dietary differences between sexes and between populations, in the percentage contribution of each of seven categories to the diet of Trinidad guppies. The table indicates for each comparison, the two-way Mann-Whitney U level of significance of the difference between the two groups. a) $p \leq 0.001$ (***), b) $p \leq 0.01$ (**), c) $p \leq 0.05$ (*), d) not significant (NS).

	Between Populations		Between Sexes	
Category	Females	Males	Naranjo	Tacarigua
Invertebrates	***	***	NS	NS
Higher plant fragments	NS	NS	NS	NS
Filamentous algae	**	*	NS	NS
Unicellular algae	NS	NS	NS	NS
Diatoms	***	***	NS	***
Algal remains	NS	NS	NS	*
Mineral particles	**	***	NS	NS

Table 3. Onset of sexual maturation of groups of twenty guppies each fed one of three exclusive diets: Daphnia (D), Tetra-min (T), or algae (A). Mortality accounts for totals that do not add up to 20 fish for each diet.

	Females			Males			Juveniles		
Week	D	T	A	D	T	A	D	T	A
2	-	-	-	-	-	-	20	19	19
3	1	-	-	-	-	-	18	19	17
4	8	3	-	3	3	-	6	12	17
5	11	5	4	4	6	7	2	7	4
6	12	7	5	4	9	8	-	1	-

Table 4. Ingestion rate per peck in relation to number of pecks taken by (A) male (N=9) and (B) female (N=9) guppies feeding on algae-coated plates with densities of 342 and 411 μg/cm^2, respectively.

	SL (mm^2)	Fish Weight (mg)	No. of Pecks	Total Algae Ingested (μg)	Algae Ingested Per Peck (μg)
(A)	17.0	97	10	50	5.0
	17.0	97	20	40	2.0
	17.5	95	30	100	3.3
	16.5	80	40	90	2.3
	15.5	79	50	200	4.0
	15.0	69	60	180	3.0
	16.0	81	70	300	4.3
	16.5	90	80	320	4.0
	15.5	73	90	350	3.9
(B)	19.5	163	20	20	1.0
	18.0	115	30	70	2.3
	18.0	128	40	60	1.5
	17.0	82	50	230	4.6
	18.0	111	60	60	1.0
	20.0	136	70	240	3.4
	19.5	135	80	410	5.1
	17.5	108	90	260	2.7
	22.0	187	90	210	2.3

Table 5. The calculated value of constants a, b, and c, in the formula $z = a + bx + cy$, where z is ingestion per peck, x is algal density in g x $10^{-5}/cm^2$, and y is either weight of fish in mg, SL of fish in mm, or SL^2 in mm^2. Values for males (n=24) and females (n=19) are shown separately.

	Males			Females		
y =	Weight	SL	SL^2	Weight	SL	SL^2
a =	-2.387	-4.170	-2.367	-4.629	-10.052	-6.377
b =	0.119	0.124	0.124	0.152	0.156	0.158
c =	0.021	0.206	0.006	0.010	0.345	0.008

Table 6. The weight and the total number of feeding pecks recorded per day for individual male (n = 5) and female (n = 4) guppies. Individual fish were observed for six 5 min periods giving a total of 30 min per day for four days while feeding on Tetra-min particles dispersed on the substrate.

	Females				Males				
Weight (mg)	216	268	540	670	128	136	146	92	116
Recorded pecks/day									
Day 1	907	408	929	1155	37	139	38	56	20
Day 2	300	436	274	960	18	307	60	213	65
Day 3	506	375	942	718	29	186	39	232	21
Day 4	300	734	385	1051	15	112	59	69	56
Mean weight	423.5 mg				123.6 mg				
Mean recorded pecks over 4 days	2595 pecks				354 pecks				

Table 7. The mean hourly rate of feeding pecks on Daphnia and algae by guppies given an unlimited supply of both foods, and the estimated daily ingestion rate of algae. Algal density was 466 $\mu g/cm^2$ on day 1 and 320 $\mu g/cm^2$ on day 2. Three classes of fish, each composed of 15 individuals, feeding in a single aquarium were videotaped for 5 min/hr for 12 hr/day to obtain the feeding rates. Ingestion rates per peck were estimated from a multiple regression equation determined in a separate experiment.

	Large Females ($\bar{x}$ = 372 mg)		Small Females ($\bar{x}$ = 119 mg)		Males ($\bar{x}$ = 118 mg)	
Day	1	2	1	2	1	2
No. pecks/hr on Daphnia	138	185	58	144	61	177
No. pecks/hr on algae	818	365	510	574	429	257
Ingestion/peck (μg dry wt)	6.17	3.95	3.64	1.43	5.63	3.89
Ingestion/hr (mg dry wt)	5.05	1.44	1.86	0.82	2.42	1.00
Ingestion/day (mg dry wt)	60.60	17.28	22.32	9.84	29.04	12.00
Ingestion/day (% body wt)	16	5	19	8	25	10

Table 8. Mean peck durations (min x 10^{-2}) and 95% CL for three size classes of guppies feeding on algae and *Daphnia*. Each was calculated from 61 feeding bouts, randomly chosen from 2 days of videotaped feeding behaviour.

	Large Females	Small Females	Males
Algae	0.92 ± 0.06	1.11 ± 0.07	1.19 ± 0.09
Daphnia	1.62 ± 0.08	1.57 ± 0.09	1.51 ± 0.08