# FOOD, FEEDING SELECTIVITY, AND ECOLOGICAL EFFICIENCIES OF *FUNDULUS NOTATUS* (RAFINESQUE) (OSTEICHTHYES; CYPRINODONTIDAE)

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# FOOD, FEEDING SELECTIVITY, AND ECOLOGICAL EFFICIENCIES OF *FUNDULUS NOTATUS* (RAFINESQUE) (OSTEICHTHYES; CYPRINODONTIDAE)

DISSERTATION

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By

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# INTRODUCTION

Knowledge of the nutrition of an organism is basic to understanding its function in an ecosystem, and a sound conception of the nutritional, or trophic, interrelationships among an ecosystem's biota, in correlation with information about abiotic factors, affords a grasp of the dynamics of the system (Allee, 1934; Tansley, 1935; Lindemann, 1942; Hutchinson, 1957; Odum, 1959). Trophic relationships of the blackstripe topminnow, _Fundulus notatus_ (Rafinesque), are unreported, except for stomach analyses of 475 specimens of both _F. notatus_ and _F. olivaceous_ by Thomerson (1969, _personal communication_). He found the ration of the two composed (in order of decreasing proportions) of terrestrial arthropods, aquatic insects, algae, and other aquatic organisms (mostly microcrustaceans).

Early efforts to define interrelationships between fishes and their food were reviewed by Ivlev (1961), who cited three workers' independent development of the index which was later termed the "forage ratio" (Hess and Swartz, 1941). Ivlev outlined problems associated with the forage ratio (chiefly that its limits are zero and infinity), and proposed the "electivity index," $E = (r_i - p_i)/(r_i + p_i)$, such that $E$ = the electivity index, $r_i$ = the percentage occurrence of a prey organism in the total ration, and $p_i$ = the percentage occurrence of the same prey organism in the environmental food complex. The limits of E are positive- and negative-one. Positive-one results from selectivity for a food organism of zero frequency in samples; negative-one reflects zero frequency in the fish ration of an organism appearing in samples; a value of zero indicates complete randomness, or non-selectivity, toward an organism.

This study was made to further define the trophic dynamics of *Fundulus notatus* by determining its ration composition under natural conditions, measuring feeding selectivity under various laboratory conditions of prey-species composition and availability, and determining the efficiencies with which *F. notatus* utilizes ingested chironomid larvae.

# MATERIALS AND METHODS

## Field Samples

Blackstripe topminnows were seined from pools in three intermittent streams and, in one instance, from a littoral area of Garza-Little Elm Reservoir in Denton County, Texas; 254 specimens, with concurrent bioseston and benthic samples, were taken on 23 collection dates between May, 1967, and October, 1969. February, June, November, and December each were represented by 10 fishes; at least 20 specimens were collected in other months, except that no collections were made in March or April. Day and night collections were made August 22-24, 1967, to determine circadian feeding patterns.

Benthic and bioseston samples were made prior to seining. Sampling locations were biased (Cummins, 1962) to assure inclusion of microhabitats in which topminnows were observed to forage. The number of samples from favored areas was kept proportional to those from mid-pool and other "barren-appearing" areas by estimating the proportion of each microhabitat to the total collecting area and taking a representative proportion of samples from each area. Bioseston samples were taken with a 2000-cc Kemmerer water sampler, held horizontally and operated by hand. Samples were drained into 1-liter bottles, stored overnight in a refrigerator at 10 C, filtered through sand by standard methods (American Public Health Association, 1960), concentrated to 5 ml, and preserved in 6:3:1 formalin-alcohol-water solution. Bottom samples, taken with a 15.5-cm$^2$ Ekman dredge, were washed through a number 40 U. S. Standard Sieve, and the organisms were stored in 6:3:1 preservative. The volume of 70% isopropanol displaced in a 1-cc volumetric cylinder (made from a glass syringe) by each benthos and bioseston taxon sample was measured before and after storage to the nearest 0.1 µl with a 25-µl syringe. Stored organisms lost a mean 47% of their original displacement volume.

Captured topminnows were bagged in plastic at streamside and buried in crushed ice until examination about 24 hr later. Standard length (S. L.) measurement and assignment to a length class was made for each fish as follows: I, <38 mm; II, 38-47 mm; III, 48-58 mm; IV, >58 mm.

## Ration Analysis

There is no discrete stomach in Fundulus (Prosser and Brown, 1950); the common bile duct opens into the gut approximately 2 mm posterior to the pharyngeal region, and the gut bends 180° twice, forming a complete, flattened loop. The hindgut was arbitrarily designated to be that section extending posteriorly from the loop at the point of the first bend.

Samples of contents from the fore- and hindguts of 92 specimens, selected at irregular intervals throughout the study, were cultured to show the role of algae in the diet. Guts were cut at the anus with flamed scissors, and a sample of hindgut contents was transferred aseptically with a flamed needle to a 32-ml vial containing 16 ml of 1:1 sterile soil-water extract (Stewart and Schlichting, 1966) and modified Bristol's medium (Bold, 1949). A foregut sample was secured similarly.

Cultures were kept at 25 C in a 12-hr photoperiod in a controlled environment chamber (Sherer-Gillett, Model CEL-44; Marshall, Mich.) and examined after two and four-weeks incubation. Each was shaken with a Vortex Jr. Mixer (Scientific Instruments, Inc., Queen's Village, N. Y.), and four 1-ml samples were taken from each culture with sterile pipettes and examined microscopically. Smith's (1950) and Prescott's (1954) keys were used in algal identifications. The hindgut was excised and discarded after sampling, since contents were unidentifiable. Control consisted of randomly selected vials of uninoculated medium, sham-inoculated medium, and sham-sampled medium, surveyed as were experimentals. No algal contamination was detected.

Alcohol displacement volumes of intact foreguts were measured before and after storage in 70% isopropanol; stored guts had an average loss of 49% of the original displacement volume. Contents of dissected guts were sorted into taxa corresponding to those of environmental samples; the volumetric displacement of each was measured, and its percentage of the total food volume displacement was calculated. A hierarchical analysis of variance was employed (Snedecor and Cochran, 1967) to statistically compare (F-test) volumes of ingested taxa between sexes, classes within sexes, and ration groups within classes (Table 1). Data from gut-content analyses and corresponding bioseston and benthic samples were used to determine the electivity index, E, for each food subgroup (Ivlev, 1961).

## Prey Selectivity

Laboratory feeding tests were conducted to test E values determined from field data and to provide a basis for evaluating major complex variables comprising the E value, *viz.*, predator preference, prey availability, and sampling efficiency. Pairs of topminnows from classes III-IV, seined from Hickory Creek in June of 1969 and held without

TABLE 1. Organisms ingested by size classes of Fundulus notatus[a]

| Ingested Organisms | Size Classes | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| | I-III | | I | | II | | III | |
| | f | r | f | r | f | r | f | r |
| Terrestrial Arthropods | 84.8 | 40.9 | 21.3 | 35.0 | 31.1 | 42.7 | 33.3 | 43.9 |
| Aquatic Insects | 42.6 | 15.6 | 46.7 | 12.7 | 32.4 | 13.9 | 47.9 | 20.2 |
| Chironomid | 36.5 | 4.7 | 8.2 | 7.1 | 8.1 | 1.9 | 10.4 | 5.9 |
| Ceratopogonid | 20.5 | 3.2 | 5.7 | 1.4 | 4.1 | 6.3 | 8.3 | 1.4 |
| Other Diptera | 6.1 | tr[b] | 1.6 | tr | - - | - - | 2.1 | tr |
| Ephemeroptera | 29.5 | 2.8 | 5.7 | 0.7 | 5.4 | 1.0 | 6.3 | 6.8 |
| Odonata | 7.4 | 0.9 | 0.8 | 0.2 | 2.7 | 0.4 | 2.1 | 2.1 |
| Other Aquatic Insects | 25.0 | 3.9 | 9.0 | 3.3 | 4.5 | 4.3 | 10.4 | 4.0 |
| Crustaceans | 31.6 | 10.4 | 35.2 | 27.5 | 36.5 | 6.0 | 14.6 | 0.7 |
| Cladocera | 28.7 | 8.2 | 6.6 | 24.0 | 8.1 | 3.4 | - - | - - |
| Copepoda | 17.6 | 1.1 | 4.1 | 1.8 | 0.9 | 1.5 | - - | - - |
| Ostracoda | 8.2 | 0.4 | 3.3 | 0.5 | 1.4 | 0.7 | - - | - - |
| Other Crustaceans | 12.7 | 0.7 | 2.0 | 1.2 | 4.1 | 0.4 | 6.2 | 0.7 |
| Snails | 41.8 | 18.6 | 9.0 | 13.1 | 9.5 | 29.6 | 10.4 | 11:0 |
| Algae | 41.4 | 14.5 | 4.9 | 11.7 | 4.4 | 7.9 | 14.6 | 24.2 |

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[a] f = frequency of occurrence; r = percent of ration volume. Ration-group figures are underlined; subgroup figures below ration-groups not underlined.

[b] tr < 0.01.

food 36-48 hr, were introduced into each of four 5-liter aquaria. Two of the aquaria were without prey-cover; two contained sand and silt substrate, anchored *Chara* sp., floating *Ceratophyllum* sp., and a scattering of duckweed (*Lemna* sp.). Twelve hours before fishes were introduced, the aquaria were stocked with fifty 2 x 3-mm snails (*Physa* sp.), 50 chironomid larvae (*Glyptotendipes* sp.), and 50 adult Corixidae (*Trichocorixa kanza* Hungerford). Fifty apterous termites (*Neotermes* sp.) were added just prior to introducing topminnows. Isopropanol displacement volumes for representative samples of each prey species were measured, and the percentage component of the total ration was computed for each as follows: chironomids, 53%; corixids, 25%; termites, 18%; snails, 4%. The fishes began to feed within 2 min after introduction into the aquaria. They were removed after 3 hr, bagged in ice, and examined for ingested organisms.

A subsequent test employed 50 chironomids, 25 corixids, 25 termites, and 100 amphipods (*Hyallela azteca* [Saussure]) in respective percentage volumes of 63%, 18%, 10%, and 9%; in a third test, 50 chironomids, 25 corixids, and 50 *H. azteca* were combined in respective volumetric percentages of 73%, 21%, and 6%. Test data were used to calculate electivity for a prey species, E; predator preference, Ep; and prey accessibility, A (Ivlev, 1961).[1]

## Ecological Efficiencies

Trophic efficiencies and daily maintenance requirements for growing fishes were measured by feeding topminnows diets of calculable calorific value and quantifying their feces and calorific growth. Fishes seined from Hickory Creek on August 4, 5, and 6, 1969, were held 10 days at 23 C in a 25-gal aquarium and fed whole and minced larvae of *Glyptotendipes* sp. Since the fishes were collected after the breeding season (Carranza and Winn, 1954), they were not investing energy in reproduction, and reassimilation of gametes appeared essentially complete. Two groups of 12 fishes of size classes I and II, respectively, and three individuals of S. L. 53, 54 (III), and 65 mm (IV), respectively, were selected for experimental feeding. Experimental fishes were starved for three days, then each was isolated

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[1] Assumptions are that E = Ep + A, and that in the absence of cover, E = Ep, and A = 0. Since A = E - Ep, $A = [(r_i - p_i)/(r_i + p_i)] - [({}_pr_i - p_i)/({}_pr_i + p_i)]$, such that $r_i$ = percentage component of a prey organism in the ration; $p_i$ = percentage component of the same prey organism in the environmental food complex; ${}_pr_i$ = percentage component of the same prey organism in the ration when A = 0.

in a container of distilled, aerated water; 5-liter aquaria were used for the three larger fishes, and 3-liter jars for the smaller. Jars were juxtaposed so that the topminnows could see other fishes and be stimulated to feed. Fishes were not fed for 12 hr after the weight and length measurements.

A separate group of fishes, hereafter called standards, was sacrificed for determination of representative dry/wet weight ratios and calorific values. Standards consisted of two groups of seven fishes, respectively comparable in size to each of the two smaller experimental size groups, and five standards comparable to the three larger experimentals. Gram-calorie values of standards were determined with a Parr adiabatic oxygen-bomb calorimeter (Parr Instrument Co., Moline, Ill.); calorific values herein are based on ash-free dry weights. The estimated original dry weight (Wo) and cal x $gWo^{-1}$ of experimental fishes were extrapolated from their measured wet weights and the mean dry/wet weight and cal x $g^{-1}$ values of standards. These data were the basis for calculating the change ($\Delta$) in cal x $gWo^{-1}$ x $day^{-1}$ of experimental fishes.

Experimental fishes were fed weighed quantities of whole Glyptotendipes sp. larvae, a food organism selected because it was available in a broad size range from nearby sewage oxidation lagoons (Aubrey, Texas). Four class I fishes were assigned to each of three groups. Each group-one individual was daily fed larvae approximating 20% of its initial wet weight; each group-two and group-three fish was individually fed a daily amount about equal to 15% and 10%, respectively, of its original wet weight. Grouping and feeding rates were duplicated with class II fishes. The 63, 53, and 54-mm fishes were fed approximately 20%, 15%, and 10% of their respective body weights in larvae daily. Uneaten larvae were removed after two hours. Dry/wet weight ratios were determined for each of two groups of 50 Glyptotendipes sp. larvae of mixed sizes (instars), as were cal x $g^{-1}$. The mean values and the measured wet weight ingested per day were used to calculate cal ingested x $gWo^{-1}$ x $day^{-1}$ for each fish.

Experimental fishes were fed for up to 39 days. Those, exclusive of the 54-mm fish, which were fed a daily ration about equal in wet weight to 10% of their original wet weight died after five days of feeding; the eight were not included in final calculations. The 54-mm fish (fed at the 10% rate) and six of the nine fish fed at the 15% rate survived for 11 days. Three of the 15%-group and the nine fed at the 20%

rate survived for 39 days, and five of the latter evidenced a positive value for $\Delta$cal x gWo$^{-1}$ x day$^{-1}$. Based on the calculated Wo and cal x gWo$^{-1}$ of each experimental fish, the number of days it was fed, and its final dry weight and cal x g$^{-1}$, $\Delta$cal x gWo$^{-1}$ x day$^{-1}$ was calculated for each.

Water from each jar was removed and filtered every second day; the feces of each fish were oven-dried, weighed to a constant dry weight, and stored in a dessicator until a quantity sufficient for calorific measurement was amassed.

The ecological efficiencies, A/I (assimilation efficiency), R/I, NP/I (ecological growth efficiency), and NP/A, were calculated separately for size class groups I-II and III-IV. (I = ingestion; Df = defecation; A = assimilation = I - Df; R = respiration = A - NP [includes energy of excretions, external secretions]; NP = net productivity = $\Delta$cal x gWo$^{-1}$ x day$^{-1}$). Data from fishes which showed growth were fitted to the regression equation, $Y = a + bX$, for respective size class groups (Snedecor and Cochran, 1967), such that X = cal ingested x gWo$^{-1}$ x day$^{-1}$; Y = $\Delta$cal x gWo$^{-1}$ x day$^{-1}$; a = mean daily energy expenditure in cal x gWo$^{-1}$; b (regression coefficient) = net efficiency of food utilization for growth.

# RESULTS

## Prey

Topminnows begin feeding at dawn and continue until midday. They apparently do not feed from near noon until near 2 PM (standard time), then feed until dark (Figure 1). Based on volumes of various prey organisms ingested, statistically significant differences exist between the rations of separate size classes and in utilization within size classes of various ration groups ($P < 0.01$; SD = 1.64; coef of variation = 0.007). Difference in diet between sexes is not statistically significant, but it is between size classes ($P = 0.05$; Table 1 and Figure 2). Isolation in dry-seasonal pools resulted in increased E values for snails and slightly lessened values for aquatic insects (Table 2).

Thirty-eight genera of algae, plus unidentified diatoms, representing five divisions, were cultured from 79% of 92 guts (Table 3). Frequency of occurrence of *Chlorella* sp. was 48%; that of diatoms was 41%. Filamentous algae found during gut analyses were always in the form of a wad containing animal prey, and such algae appeared at the anus undigested and viable.

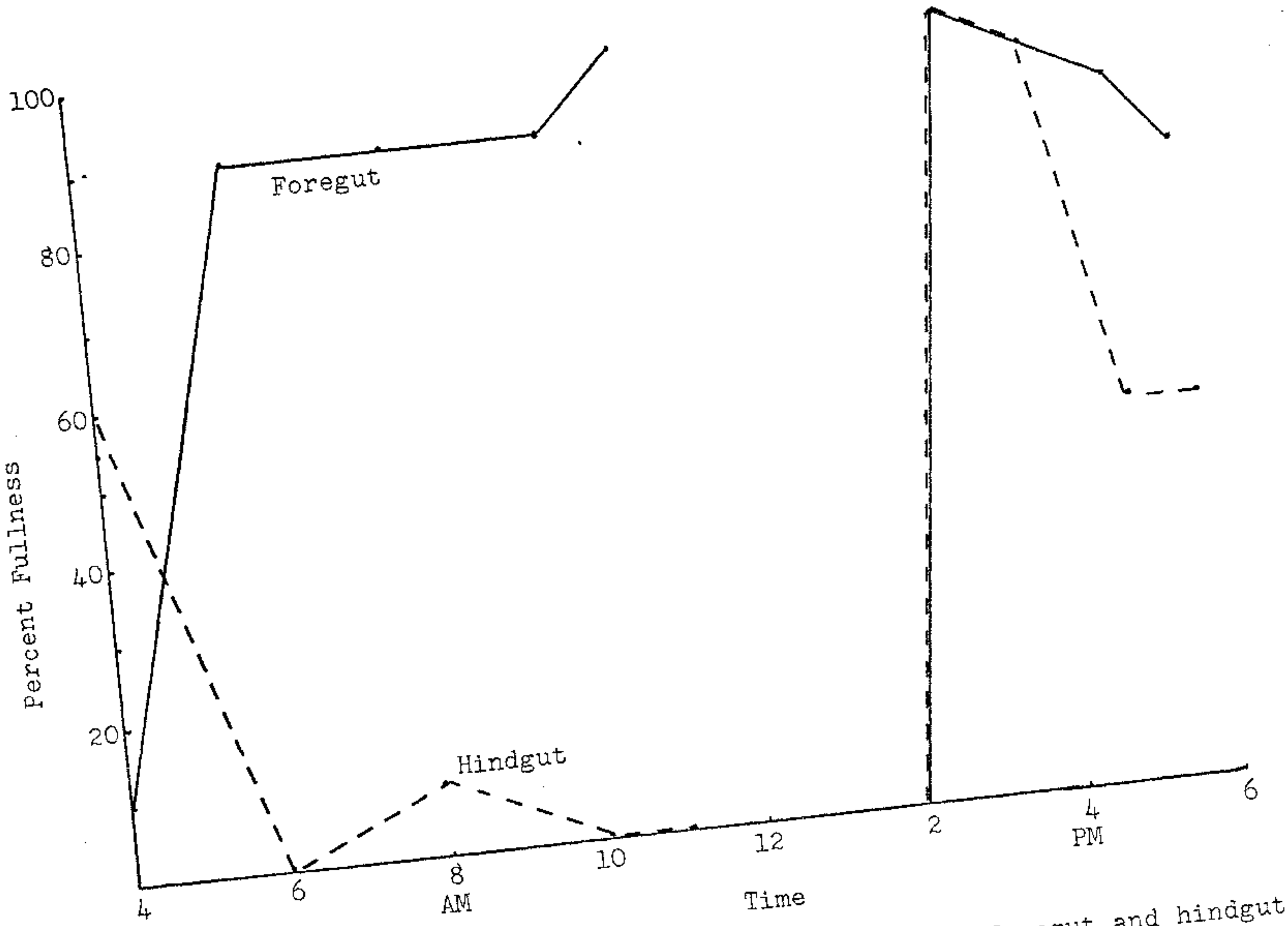

Fig. 1. Hourly pattern of mean relative fullness of foregut and hindgut in 90 specimens of <u>Fundulus notatus</u>, August, 1967. No noon collections were made.

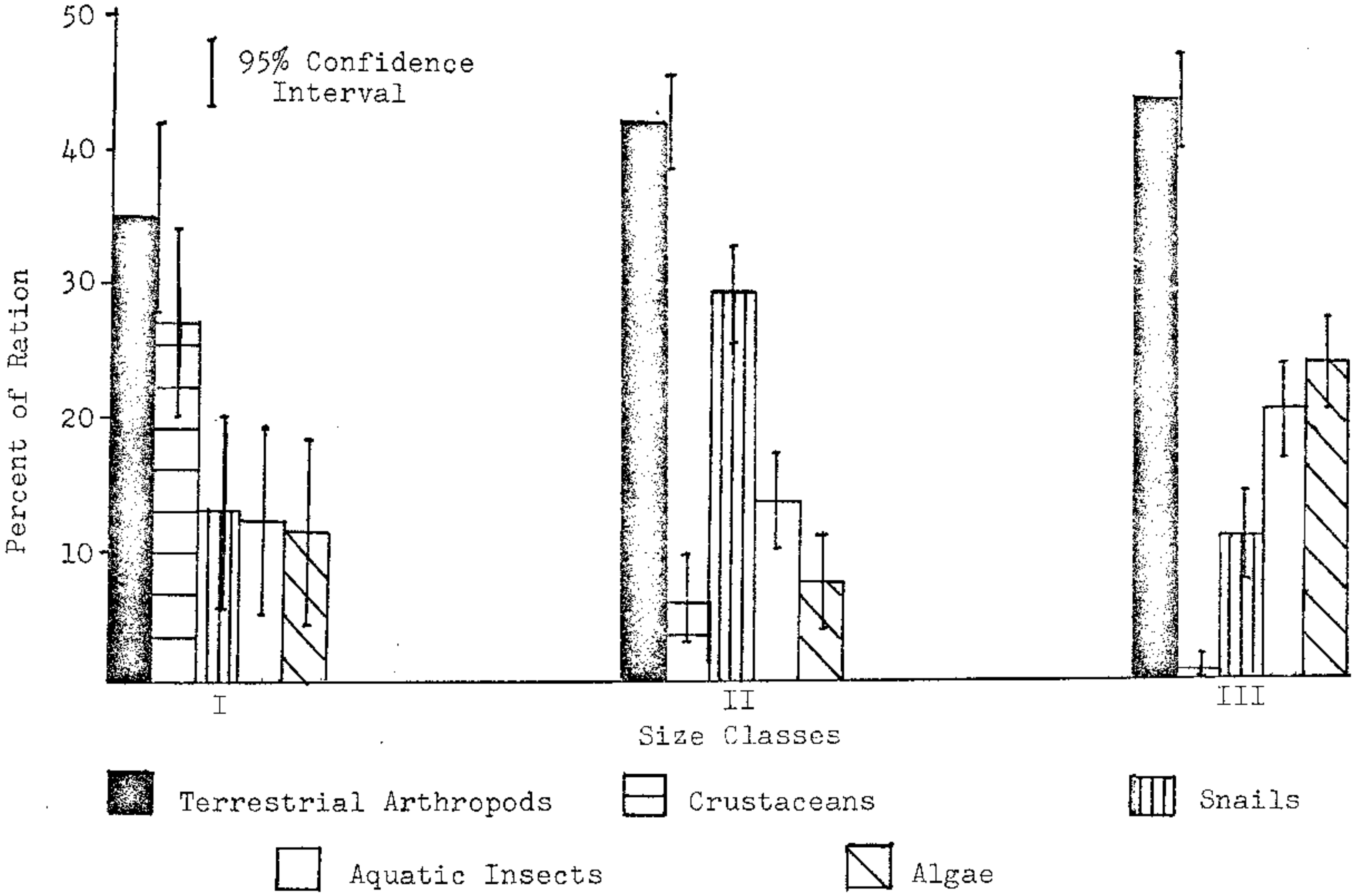

Fig. 2. Composition of rations ingested by size classes of Fundulus notatus.

TABLE 2. Feeding selectivity by Fundulus notatus in seasonal habitats[a]

| Ration-Groups | Running Streams Nov-July<br>120 fishes from 11 collections; 115 had items in gut | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|
| | Hickory Creek<br>7 collections<br>Avg temp 18 C (5-30) | | | Denton Co. Golf Course<br>2 collections<br>Avg temp 24 C (20-28) | | | Denton Creek<br>2 collections<br>Avg temp 32 C (31-32) | | |
| | p | r | E | p | r | E | p | r | E |
| Terrestrial Arthropods | 0 | 18 | +1 | 0.1 | 3.6 | +0.9 | 0.14 | 76 | +1 |
| Aquatic Insects | 29 | 36 | +0.1 | 6 | 27 | +0.6 | 8 | 24 | +0.5 |
| Crustaceans | 47 | 22 | -0.4 | 50 | 5 | -0.8 | 92 | 0 | -1 |
| Snails | 13 | 8 | -0.2 | 38 | 26 | -0.2 | 0 | 0 | 0 |
| Algae | 3 | 7 | +0.4 | 1 | 3 | +0.5 | 0 | 0 | 0 |

| Ration-Groups | Stagnant Pools Aug-Oct<br>114 fishes from 10 collections; 114 fishes had items in gut | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|
| | Hickory Creek<br>6 collections<br>Avg temp 25 C (22-30) | | | Denton Co. Golf Course<br>3 collections<br>Avg temp 21 C (21-25) | | | Denton Creek<br>1 collection<br>Temperature 32 | | |
| | p | r | E | p | r | E | p | r | E |
| Terrestrial Arthropods | 0 | 49 | +1 | 0 | 73 | +1 | 0 | 83 | +1 |
| Aquatic Insects | 4 | 12 | +0.5 | 60 | 7 | -0.8 | 17 | 4 | -0.6 |
| Crustaceans | 15 | 5 | -0.5 | 0.3 | 28 | +1 | 81 | 0 | -1 |
| Snails | 6 | 10 | +0.3 | 0 | 0 | 0 | 0 | 9 | +1 |
| Algae | 69 | 13.5 | -0.7 | 7 | 6 | -0.1 | tr[b] | 4 | +1 |

| Ration-Groups | Garza-Little Elm Reservoir, October<br>10 fishes from 1 collection<br>10 fishes had items in gut<br>Temperature 21 C | | |
|---|---|---|---|
| | p | r | E |
| Terrestrial Arthropods | 0 | 16 | +1 |
| Aquatic Insects | 91 | 7 | -0.9 |
| Crustaceans | 1 | 0.5 | -0.3 |
| Snails | 0 | 6 | +1 |
| Algae | 3 | 67 | +0.9 |

[a] p = percent volume of environmental food complex; r = percent of ration; E = the electivity index.

[b] $tr < 0.1$.

TABLE 3. Genera of algae cultured from fore- and hindgut of Fundulus notatus

| Divisions, Genera and Orders | No. of Foreguts | No. of Hindguts | No. of both Fore-, Hindguts |
|---|---|---|---|
| Chlorophyta | | | |
| Volvocales | | | |
| Chlamydomonas | 6 | 6 | 5 |
| Tetrasporales | | | |
| Asterococcus | - | 1 | - |
| Gloeocystis | 3 | 3 | - |
| Tetraspora | 1 | 1 | - |
| Chlorangium | - | - | 1 |
| Dactylothece | 1 | - | - |
| Nannochloris | - | 1 | - |
| Ulotrichales | | | |
| Hormidium | - | - | 1 |
| Stichococcus | - | 1 | - |
| Microspora | 1 | - | - |
| Oedogoniales | | | |
| Oedogonium | - | - | 1 |
| Chlorococcales | | | |
| Chlorococcum | 5 | 2 | 9 |
| Ankistrodesmus | 5 | 4 | 1 |
| Chlorella | 10 | 15 | 19 |
| Closteridium | - | 2 | - |
| Dictyosphaerium | 2 | 4 | - |
| Protosiphon | - | 1 | - |
| Eremosphaera | 2 | 4 | - |
| Kirchneriella | 3 | - | - |
| Oocystis | 2 | - | - |
| Planktosphaera | 1 | 1 | - |
| Crucigenia | 1 | 1 | - |
| Scenedesmus | 8 | 4 | 3 |
| Tetradesmus | 1 | - | - |
| Zygnematales | | | |
| Spirogyra | 1 | - | 1 |
| Roya | - | 1 | - |
| Mesotaenium | - | - | 1 |
| Euglenophyta | | | |
| Euglena | - | 2 | - |
| Trachelmonas | 1 | 1 | - |
| Cryptoglena | - | - | 1 |

TABLE 3. *Continued*

| Divisions, Genera and Orders | No. of Foreguts | No. of Hindguts | No. of both Fore-, Hindguts |
|---|---|---|---|
| Chrysophyta | | | |
| Heterococcales | | | |
| *Botrydiopsis* | 1 | 1 | 1 |
| Bacillariophyceae | 8 | 17 | 5 |
| Cryptophyta | | | |
| *Cryptomonas* | 1 | - | - |
| Cyanophyta | | | |
| Chroococcales | | | |
| *Chroococcus* | - | 1 | - |
| *Gloeochaete* | 1 | - | - |
| *Synechococcus* | - | - | 1 |
| *Synechocystis* | 1 | - | - |
| Hormogonales | | | |
| *Oscillatoria* | - | 1 | - |
| *Phormidium* | 1 | - | - |

## Prey Selectivity

Response by blackstripe topminnows to various prey organism combinations in the presence of prey-cover, compared to that in bare aquaria, is presented in Tables 4-6. In the absence of terrestrial arthropods (Table 6) E values were negative, and only one fish filled its gut. Frequency of occurrence of chironomid larvae in guts of fishes from aquaria with no prey-cover was 100%, and from aquaria with prey-cover, 25%. Frequencies of corixid occurrence without and with prey-cover were 100% and 50%, respectively.

## Ecological Efficiencies

Dry weights of standard fishes averaged 23% of the wet weight and ranged from 18%-24%. The original wet weight of each experimental fish x 0.23 produced its estimated Wo.

Cal x $g^{-1}$ varied inversely with fish dry weights ($r = -0.63$; $P < 0.01$), although the calorific difference between the greatest and the least weight subgroups was not statistically significant. Use of cal x $g^{-1}$ mean values corresponding to dry weight subgroups reduced standard error and resulted in coefficients of variation of $< 0.01$ (Table 7). Feces contained 2500 cal x $g^{-1}$.

TABLE 4. Feeding selectivity by Fundulus notatus relative to the presence or absence of prey-cover, and a prey composition of 53% chironomids, 25% corixids, 18% termites, 21% snails[a]

| Prey Organisms | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| Chironomid Larvae | | | Corixid Adults | | | Termite Adults | | | Physid Snails | | |
| $r_i$ | $_pr_i$ | | $r_i$ | $_pr_i$ | | $r_i$ | $_pr_i$ | | $r_i$ | $_pr_i$ | |
| 51 | 87 | | 8 | 12 | | 41 | 1 | | 0 | 0 | |
| E | Ep | A | E | Ep | A | E | Ep | A | E | Ep | A |
| -0.1 | +0.3 | -0.4 | -0.5 | -0.4 | -0.1 | +0.4 | -0.9 | +1.3 | -1.0 | -1.0 | 0 |

[a] Eight fishes were paired in each of four aquaria at 23 C; two aquaria had plants and silty sand; two were without prey-cover. $r_i$ = percent in ration, prey-cover present; $_pr_i$ = percent in ration, prey-cover absent; E = electivity index; Ep = predator preference; A = prey accessibility.

TABLE 5. Feeding selectivity by Fundulus notatus relative to the presence or absence of prey-cover, and a prey composition of 63% chironomids, 18% corixids, 10% termites, and 9% amphipods[a]

| Prey Organisms | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| Chironomid Larvae | | | Corixid Adults | | | Termite Adults | | | Amphipods[b] | | |
| $r_i$ | $p^{r_i}$ | | $r_i$ | $p^{r_i}$ | | $r_i$ | $p^{r_i}$ | | $r_i$ | $p^{r_i}$ | |
| 0 | 59 | | 3 | 1 | | 97 | 36 | | 0 | 4 | |
| E | Ep | A | E | Ep | A | E | Ep | A | E | Ep | A |
| -1.0 | 0 | -1.0 | -0.7 | -0.9 | +0.2 | +0.8 | +0.6 | +0.2 | -1.0 | -0.4 | -0.6 |

[a] For experimental design and meaning of symbols see footnote, Table 4.

[b] *Hyallela azteca*.

TABLE 6. Feeding selectivity by *Fundulus notatus* relative to the presence or absence of prey-cover, and a prey composition of 73% chironomids, 21% corixids, and 6% amphipods[a]

| Prey Organisms | | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| Chironomid Larvae | | | Corixid Adults | | | Amphipods[b] | | |
| $r_i$ | | $p^{r_i}$ | $r_i$ | | $p^{r_i}$ | $r_i$ | | $p^{r_i}$ |
| 18 | | 95 | 82 | | 4 | 0 | | 1 |
| E | Ep | A | E | Ep | A | E | Ep | A |
| -0.6 | +0.1 | -0.7 | -0.6 | -0.7 | +0.1 | -1.0 | -0.7 | -0.3 |

[a] For experimental design and meaning of symbols, see footnote, Table 4.

[b] *Hyallela azteca*.

TABLE 7. Gram-calories relative to dry weight ranges of *Fundulus notatus*

| Weight Range (grams) | Mean Gram-Calories | Standard Error | Coefficient of Variation |
|---|---|---|---|
| 0.07-0.90 | 5621 | 2627 | 0.97 |
| ≤0.10 | 6328 | 1547 | 0.03 |
| 0.11-0.14 | 5805 | 449 | 0.08 |
| 0.15-0.40 | 5767 | 102 | 0.02 |
| >0.40 | 5063 | 516 | 0.10 |

The mean value for larvae was 5341 cal x $g^{-1}$ (5241-5870), with ash values of 6-11%. Dry/wet weight value was 0.159 in both samples.

Energy-budget components and ecological efficiencies for test conditions are listed in Table 8. Components of the ecological growth efficiency, NP/I, for growing fishes are a, and the regression coefficient, b, in the equation, $Y = a + bX$. For classes I-II, $Y = -55 + 0.216X$; for classes III-IV, $Y = -20 + 0.150X$. The difference in net efficiency of food utilization for growth, b, between the smaller and the larger size class groups is not statistically significant, but the difference in mean daily energy expenditure, a, is statistically significant ($P = 0.05$). Fish size does not affect assimilation efficiency (A/I), and for all size classes $A \simeq I$, and $NP/A \simeq NP/I$.

Size classes I-II require a mean daily ration of 253 cal x $gWo^{-1}$ for zero growth. Wet Glyptotendipes sp. larvae, with a cal x $g^{-1}$ value of 848, are required at the rate of 0.06 g per day for a 0.2-g fish. Fishes of classes III-IV required for zero growth 133 cal x $gWo^{-1}$ x $day^{-1}$, a 0.6-g fish requiring 0.09 g per day. The imprecise ration weight-control imposed by feeding whole, live larvae, and the intent to feed no less than the prescribed feeding rate, resulted in rations of little more than minimum daily calorific requirements.

TABLE 8. Mean energy-budget values for 19 specimens of *Fundulus notatus* fed at 23 C for up to 39 days

| Component | Size Classes | | |
|---|---|---|---|
| | I-II | III-IV | I-IV |
| | Calories x gram of initial dry weight$^{-1}$ x day$^{-1}$ | | |
| Ingestion | 422 | 220 | 321 |
| Assimilation | 409 | 213 | 311 |
| Respiration | 373 | 200 | 287 |
| Net Productivity | 36 | 13 | 25 |
| Efficiency | Percentage | | |
| Assimilation/ Ingestion | 96.9 | 96.8 | 96.9 |
| Respiration/ Ingestion | 88.4 | 90.9 | 89.4 |
| Net Productivity/ Ingestion | 8.5 | 5.9 | 7.8 |
| Net Productivity/ Assimilation | 8.8 | 6.1 | 8.0 |

# DISCUSSION

## Sampling

Only two topminnows of size class IV were taken for gut analysis, although approximately one dozen were captured during other phases of the study. Whether the larger size class is selectively preyed upon by belted kingfishers (_Megaceryle alcyon_) which frequent the streams, or by other predators; or the larger topminnows move into larger streams or reservoirs, is unknown. The largest captured topminnow was 65 mm S. L.; the smallest were of 17 mm S. L. Employing a fine-mesh, aquatic insect sampling net in isolated pools produced topminnows of 17 mm S. L., but none smaller.

Drift arthropods occurred in bioseston samples to a disproportionately lesser degree than in gut samples. The high visibility and accessibility of floating insects may result in their ingestion soon after they strike the water; their high E values, then, reflect intensive selective predation. The appearance in the fish ration of aquatic organisms not represented in samples is probably an inevitable result of the mosaic-patterned micro-distribution of stream benthos and the fact that ". . . we have no effective methods for quantitative sampling [of such organisms]" (Hynes, 1970; p. 37).

Sampling efficiency is integral to ration indices, but highly accurate (95% confidence level) estimates of food organisms population weights and numbers are not required because the indices represent a fish's response to differential occurrence frequencies of prey organisms. The non-random, stratified sampling program used in this study was intended to produce samples of organisms quantitatively proportional to their frequency of encounter in the habitat. A relatively small number of samples is required to produce a representative faunal list (Needham and Usinger, 1956), and the occurrence of an unsampled aquatic organism in the fish ration represents selectivity for a low-frequency organism, as the resultant high E value suggests.

## Feeding Selectivity

Forage indices, such as the electivity index, are compounded of predator preference and prey availability (Hess and Swartz, 1941), the latter resulting from relative numbers of prey organisms, their visibility, and accessibility. An index value is mutable, representing the fish's response to a singular set of predator-prey-morphometric conditions, and the alteration of a single component, such as the relative proportions of prey species, or prey-cover, changes the index. A high index value often represents high prey-accessibility, rather than high predator preference (Hess and Swartz, 1941), although feeding history affects the index (Hess and Tarzwell, 1942).

The difference in the prey selected by blackstripe topminnows under varied conditions of prey availability indicates that the fish is an opportunist which preys upon organisms furnishing the highest yield for least effort. In the natural habitat, drift arthropods meet the fish's requirements, with dipteran larvae and occasional larval mayflies supplementing the ration. The negative E values for aquatic insects in stagnant pools may result from interspecific competition with other fishes confined in the pools (species listed by Bonn and Inman, 1956).

Algae pass through the fish's gut without detectable digestion. Filamentous algae are apparently deliberately ingested along with prey which takes refuge therein, a habit similar to that reported for certain other cyprinodontids (Martin, 1970). *F. notatus* probably is an agent of dispersal of algae upstream.

## Ecological Efficiencies

*F. notatus* exhibits high A/I and R/I values and a low NP/I $\doteq$ NP/A value, characteristic of high trophic-level predators (Kozlovsky, 1968), but its small size (near maximum dry wt about 0.85 g), resulting in a high metabolic rate, is probably determinative for the efficiency values.

The ecological efficiencies and required feeding rate of this fish explain the observation that a daily ration of 20% of a topminnow's wet body weight in wet chironomid larvae is insufficient. Topminnows were observed to refuse to ingest more than that ration within the 2-hr feeding period, and on occasions in which larvae were left in the aquaria for up to 4 hr, larvae were not ingested after the first intensive feeding activity. Digestive rate varies with temperature, about 5.5 hr being required by *F. heteroclitus* (L.) at 23 C for complete digestion of the contents of a full gut (Nicholls, 1931). Evidently, two peak feeding periods, about 6 hr apart (Figure 1), are required for maximum growth by blackstripe topminnows at approximately 23 C. The calorific growth efficiency values shown by this study therefore reflect a minimum tolerable feeding level and minimum fat production.

## Trophic Position

F. notatus is a link in the food web based on allochthonous material as an energy source. This fish is a direct consumer of such material in the form of drift arthropods, and as a consumer of dipteran and ephemeropteran larvae, it indirectly utilizes energy from allochthonous plant material, ". . . the most important primary source of energy for the stream fauna . . . , made available to higher trophic levels through the activities of detritus-feeding insects" (Hynes, 1970; p. 29). In feeding upon terrestrial arthropods, F. notatus "processes" insect remains into a form more readily available to microorganisms, supposedly facilitating the flow of such matter and energy (Phillipson, 1966). Microorganisms, which are also utilizing allochthonous plant substances, can be filtered from flowing water by simuliid larvae (Hynes, 1970), and may contribute to chironomid nutrition (Ivlev, 1945). These larvae are eaten by F. notatus, which secures more than one-half of its nutriments directly or indirectly from imported matter, functioning on the third or fourth trophic level, and as a scavenger.

# SUMMARY

1. Gut contents of field-collected blackstripe topminnows were compared to concurrently taken bioseston and benthic samples, and E values were calculated. Topminnows were fed in aquaria, with or without prey-cover, to test predator preference and electivity, and prey availability. Calorific ecological efficiencies for age classes were measured.

2. Terrestrial arthropods formed 41% of the diet, with a consistent E value of positive-one; aquatic insects, microcrustaceans, and snails, respectively, occupied 16%, 10%, and 19% of the diet. Positive E values were maintained for aquatic insects, except in stagnant pools where interspecific fish competition probably occurred. Crustaceans assumed negative E values, except in a single habitat, while snails took positive E values only in stagnant pools. Topminnows smaller than 38 mm, S. L., supplemented terrestrial arthropods with microcrustaceans for 28% of their ration; crustaceans decreased, and aquatic insects increased in relative importance as fish size increased. Algae were ingested with 41% frequency, but apparently not digested.

3. Fishes in feeding experiments showed a preference for chironomid larvae but an electivity for floating, terrestrial insects, which offered high availability. Physid snails, with 42% frequency of occurrence in field-collected fishes, were avoided in the presence of abundant alternative prey.

4. Assimilation efficiency was 97% for all size classes of topminnows. Topminnows of 48 to 65 mm S. L. evidenced a lower ecological growth efficiency than that of smaller fishes (5.9% and 8.5%, respectively). The average daily energy expenditure for 48 to 65-mm fishes was lower, 20 cal x g of initial dry wt$^{-1}$ (gWo$^{-1}$), than the 55 cal x gWo$^{-1}$ for fishes smaller than 48 mm, S. L., but the net efficiency of food utilization for growth in the latter (21.6%) was not significantly higher than that in 48 to 65-mm fishes (15.0%).

5. _F._ _notatus_ facilitates the entrance of allochthonous organic material into the ecosystem by digesting and defecating the remains of terrestrial arthropods, and it indirectly taps the flow of matter and energy from allochthonous plant sources by preying upon aquatic insect detritus-feeders, getting more than one-half of its ration directly or indirectly from basically allochthonous sources. It also functions as a third or fourth-level predator.

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