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# Food of Female Marsh Killifish, Fundulus confluentus Goode and Bean, in Florida

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ABSTRACT: The food of 1945 individuals, 124 to 200 each month of the year, was analyzed. Among the 253 categories identified were: algae, vascular-plant detritus and fresh tissue; three orders, six families and five genera of protozoans; rotifers; a bryozoan; gastropod molluscs of three families, two genera and one species; some pelecypods; polychaete annelids of three families, two genera and one species, some oligochaetes; 18 families, 13 genera and two species of crustaceans, viz., cladocerans, ostracods, copepods (calanoid, cyclopoid, harpacticoid and caligoid), cheliferans, isopods, amphipods, carideans, astacurans and brachyurans; three orders of arachnids; diplopodans; 12 orders, 54 families and 51 genera of insects (one ephemeropteran, five odonate, three trichopteran, 12 dipteran, 10 heteropteran and 20 coleopteran); and three species of fish mostly neonate Gambusia affinis. The total volume was 36% fishes, 21% crustaceans, 18% insects, 11% plant, 7% annelids and 7% molluscs. The breakdown for crustaceans was 9% Palaemonetes, 6% amphipods, 2% ostracods, 2% cheliferans, 1% brachyurans, 1% copepods; for insects, 12% dipterans (6% chironomids, 2% ceratopogonids, 1% stratiomyiids, 1% tipulids, 2% other families), 2% hemipterans, 2% coleopterans, 1% odonates, 1% hymenopterans; for plants, 7% fresh vascular, 3% algae, 1% vascular detritus. There was no evidence of seasonality in the taking of any item except fishes, whose consumption had a bimodal annual curve, flawed by possible sampling error as to predator size, since consumption of fishes increased with size of predator. The percentage frequencies of occurrence were 2 to 7 times the percentage volumes of the above items except copepods (34 times), ostracods (18), vascular-plant detritus (11), tipulids (0.8), fishes (0.6) and Palaemonetes (0.4). Smaller marsh killifish eat fewer Palaemonetes and fishes but not tipulids.

## Introduction

The marsh killifish ranges from Chesapeake Bay southward along the Atlantic coast, around peninsular Florida, and westward along the Gulf coast a few miles into Alabama (Brown, 1957). Typically a brackish-water species (Bailey, Winn and Smith, 1954), it also occurs in some inland fresh waters, at least in Florida (Kilby, 1955, and below), where the notable pattern of high chlorinity in fresh waters allows invasions even of marine forms (Odum, 1953). It is one of about six larvivorous cyprinodontoid fishes in Florida important in the control of salt-marsh mosquitoes, viz. as components of the local complex of mosquito-eating fishes (Harrington and Harrington, 1961). Its eggs can survive 2-3 months out of water in the humid climate on the ground, when stranded by receding waters after having been spawned at the forefront of rising waters (Harrington and Haeger, 1958; Harrington, 1959a). Its reproductive activity is influenced by the interplay of day length and temperature (Harrington, 1959b) and varies in intensity seasonally within a spawning season that encompasses most of the year in Florida (Harrington, unpublished data).

In brackish waters along the middle Atlantic coast of Florida, where we have studied this fish, it is common but extremely vagile and of fluctuating local abundance. Throughout the year at the same station one may obtain as many as 200 or more specimens per month of mosquito fish, Gambusia affinis, sailfin mollies, Poecilia latipinna and sheepshead killifish, Cyprinodon variegatus, but not of marsh killifish. The indications are that this may be so in other regions of Florida as well. Kilby (1955) obtained 1080 marsh killifish in 75 collections at Cedar Key and 599 in 48 collections at Bayport. In the Everglades National Park, Tabb and Manning (1961) found it abundant in the fresh-water everglades and probably third in abundance after Gambusia affinis and Poecilia latipinna in the mangrove habitat, but often difficult to collect with nets. Tabb (1966) rated it the fifth commonest fish in the North River Basin, where he collected more than 500, but Odum (1970) was able to obtain only 16 at the same station 3 years later.

Prior to the present study, we had examined the food in the guts of 88 marsh killifish that invaded a high salt marsh directly after its annual autumn inundation. These exhibited an overwhelming preference for the salt-marsh mosquitoes hatched by the flooding, during the ensuing crash abundance of their successive aquatic stages, then shifted abruptly to a diverse alternative diet upon the emergence and exodus of the mosquito brood (Harrington and Harrington, 1961, esp. Fig. 5). After the same marsh had been impounded for 2-1/2 years to control mosquito breeding, we were able by intensive efforts to obtain only 41 marsh killifish. The food taken by these will be described in a report on effects of impoundment on fishes and their forage. Odum (1970) briefly described the food taken by 84 marsh killifish collected by him (four) and by others (80), which will be considered below. The present study attempts to provide a thorough description of the food organisms taken all seasons of the year by females of this economically important and biologically interesting species, encompassing the full range of sizes at which it is capable of functional sexual maturity. The wide variety of foods taken by this omnivorous fish, as compared with its associates (cf. Harrington and Harrington, 1961), indicates its utility as a qualitative biosampler. The list of organisms sampled by it should have intrinsic interest for students of the little-known faunistics of the increasingly jeopardized subtropical intertidal areas occupied by macrovegetation.

#### MATERIAL AND METHODS

Females alone were used for this study as presumably having greater metabolic, and hence nutritional, demands than males, *viz.* during the maturation of their eggs. Those sampled ranged in size from the largest obtainable down to the smallest at which some, but probably not all, are capable of full functional sexual maturity (30-32 mm Standard Length) as judged by their maximum egg diameters

and gonosomatic indices. To have adequate numbers of guts containing food for each month of the year and size class necessitated dissecting 2863 female Fundulus confluentus collected 1955-61 (in both ditched and impounded salt marshes of Indian River Co. and adjacent counties, Brevard to the N and St. Lucie to the S). These had been obtained variously by seining, trapping and with rotenone. A breakdown per type and location of marsh, month of year and size of fish is given in Table 1 for the 1945 fish that contained food organisms. The contents of the entire alimentary tract of each individual were measured volumetrically; the percentage contributed by each food item to the total food was estimated on a grid; then each percentage was converted to its proportionate volume, such that the computed constituent volumes added up to the total measured volume per individual. These procedures and their rationales have been detailed elsewhere (Harrington and Harrington, 1960, 1961). The component volumes and frequencies of occurrence were summed for each item or group of items and converted to percentage volumes and percentage frequencies of occurrence, for all 1945 fish, for each size class, and for each month of the year. The analysis of the food taken per month of year revealed no clear-cut seasonality except in the amounts of fish eaten, but since the ostensible seasonality of piscivorism is biased by the variable percentages of marsh killifish of different sizes available from month to month, this analysis of the data is omitted below except for brief mention.

## Synopsis of the Food Taken by All Fish Sampled

The constituents of the total food taken collectively by the 1945 marsh killifish were listed in systematic order to the smallest identifiable taxonomic category, each with its percentage volume and frequency of occurrence. The complete list of 253 items is too long for publication, but may be examined upon request. The common referent for the synopsis that follows is Figure 1, which is a graphic breakdown of the major categories of food organisms according to their percentage volumes, in round numbers. Each sequence of subordinate categories considered below is in descending order, from the largest to the smallest of their percentage volumes, all of which, if listed, would add up to the appropriate percentage volume in Figure 1. The primary breakdown was 36% fishes, 21% crustaceans, 18% insects, 11% plants, 7% molluscs and 7% annelids.

The fish consumed were mostly neonate mosquito fish, Gambusia affinis, but young sailfin mollies, Poecilia latipinna, had been eaten as well, and there had been some cannibalism. The only other vertebrate material found in the guts of Fundulus confluentus was fragments of tailless amphibians too few to be of much significance.

The volumetric contributions of crustaceans (21%) consisted of six major categories: 9% caridean shrimp (*Palaemonetes*), mostly adults but also larvae, zoeae and eggs; 6% amphipods, of six families, viz. aorids (3%), corophiids (*Corophium* and *Erichthonius*), gam-

Type, county, and shore (E or W)	: W)	Jan.	Feb.	Mar.	Apr.	May	əunſ	γlul	.guA	Sept.	Oct.	.voV	Dec.	rotals
Impounded marshes, Brevard Co. (E)	Co. (E)	;			2	;	:		96	1		1	•	86
Impounded marshes, Indian River Co. (E)	River Co. (E)	i	i	i	i	į	į	i	į	!	49	į	1	49
Impounded marshes, Indian River Co. (W)	iver Co. (W)	17	14	35	24	30	12	71	7	90	69	2	2	373
Ditched marshes, Indian River Co. (W)	r Co. (W)	111	73	74	142	81	155	47	74	54	14	145	69	1039
Ditched marshes, St. Lucie Co. (E)	o. (E)	į	92	43	2	13	2	82	8	47	i	2	92	386
Standard-length classes	30-39 mm	17	92	88	73	27	93	48	44	44	46	43	28	643
	40-49 mm	63	46	40	51	42	35	84	94	80	58	92	75	744
	50-59  mm	41	38	18	36	39	21	36	39	41	15	25	53	402
	mm 69-09	7	33	2	12	14	18	29	9	26	12	5	9	143
	70-79 mm	i	i	-		7	2	33	7	i		i	-	13
Totals with food		128	179	152	173	124	169	200	185	191	132	149	163	1945
Totals with empty guts		85	23	82	33	66	103	38	35	17	207	125	71	918
Totals examined for food		213	202	234	206	223	272	238	220	208	339	274	234	2863

marids (partly Gammarus mucronatus), talitrids (Orchestia uhleri), amphithoids (Grubia) and ampeliscids; 2% ostracods, mostly cytherids, some cyprids; 2% cheliferans (Leptochelia); 1% brachyurans, including unidentified zoeae and megalopae, plus adult ocypodids (Uca); and 1% copepods, viz. harpacticoid (some Metis), cyclopoid, calanoid (Diaptomus) and caligoid. Chydorid and sidid cladocerans, idotheid (Chirodotea) and armadillidiid (Cubaris) isopods, and astacurans (Procambarus) had been taken only in minute amounts.

The volumetric contribution of insects (18%) was 12% dipterans (2/3 of the total volume of insects), 2% hemipterans, 2% coleopterans, 1% odonates and 1% hymenopterans. In addition, thysanurans (campodeid), collembolans (entomobryid and podurid), ephemeropterans (including the baetid, Caenis), orthopterans (gryllid), thysanopterans, trichopterans (the hydroptilids Ochrotrichia and Oxyethira, and leptocerid, Oecetis) and lepidopterans (pyralid) had been taken in minute amounts. The volumetric contribution of dipterans (12%) was 5% chironomids (½ the total volume of dipterans), 2% ceratopogonids (mostly Dasyhelea, some Atrichopogon and Culicoides), 1% stratiomyiids (mostly Odontomyia, some Hermetia and Stratiomys) and 1% tipulids; the remaining 2% (cf. Fig. 1) was comprised of dolichopodids (Hydrophorus), syrphids, ephydrids, chaoborids (Chaoborus), psychodids, tabanids (Chrysops and Tabanus), culicids (Aëdes and Anopheles), cecidomyiids and phorids. The volumetric contribution of hemipterans, although only about 2%, included a wide diversity of forms. Less than 2/10 of it was contributed by homopterans, viz. cicadellids, fulgorids, aphidids and coccoids, and over 8/10 by heteropterans, viz. corixids (Trichocorixa), notonectids (Buenoa), mesoveliids (Mesovelia), belostomatids (Lethocerus), pentatomids, nepids

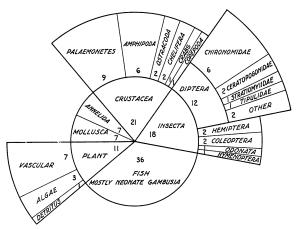


Fig. 1.—Percentage volumes of the major categories of food taken collectively by 1945 female marsh killifish, *Fundulus confluentus* Goode and Bean. See text for the breakdown of each of these categories into subordinate ones

(Nepa), gerrids (Limnogonus and Rheumatobates), naucorids (Pelocoris), hebrids (Hebrus and Merragata), veliids and mirids. The volumetric contribution of coleopterans, also about 2%, was represented by an even greater diversity of forms, viz. hydrophilids (Berosus, Enochrus, Helophorus, Hydrobius, Hydrochus, Paracymus and Tropisternus), heterocerids (Heterocerus), dytiscids (Bidessus, Copelatus, Cybister, Derovatellus, Hydroporus and Hydrovatus), haliplids (Haliplus and Peltodytes), chrysomelids (Galerucella), curculionids (Phytobius), cicindelids, hydraenids (Hydraena and Ochthebius), gyrinids, staphylinids, ptilids and tenebrionids. The volumetric contribution of odonates was about 1% and included libellulids (Erythemis, Erythrodiplax, Nannothemis and Perithemis), coenagrionids and agrionids (Enallagma). Hymenopterans also contributed about 1%, including formicids (Formicoidea), braconids (Ichneumonoidea) and mymarids (Chalcidoidea).

The volumetric contribution of plants (11%) was more than 2/3 vascular, including fresh tissues of *Salicornia perennis* Mill., seeds of *Suaeda linearis* (Ell.) and detritus, and less than 1/3 algae, including cyanophytes (*Oscillatoria*), chlorophytes (*Spirogyra*, desmids and

Chara) and chrysophytes (Pleurosigma).

Annelids and molluscs each contributed about 7% to the total food volume. The annelids were almost all polychaetes, including the nereid, *Laeonereis culveri*, eunicids (*Marphysa*) and arenicolids, with only a trace of oligochaetes. The molluscs included some pelecypods, but were mostly gastropods, predominantly the hydrobiid, *Littoridinops tenuipes*, plus truncatellids (*Truncatella*) and doridids.

The following items, not mentioned above, were taken in insignificant amounts, probably incidentally: rhizopod protozoans, viz. foraminiferans (Elphidium and Rotalia), testaceans (Arcella, Centropyxis and Difflugia) and ciliates (tintinnid and folliculinid); brachionid rotifers; statoblasts of the bryozoan, Plumatella repens; chilognath diplopodans; unidentified invertebrate eggs; and among arachnids, theraphosid (Orthognatha) and dictynid (Labidognatha) spiders (Araneida), oribatid mites (Acarina) and a pycnogonid. There was also a small residue of shell, sand and organic matter.

The percentage volume of a particular taxon consumed probably indicates its relative importance as food more accurately than the percentage frequency with which it was taken, but the latter may serve as a corrective of the former, besides giving some indication of the prevalence and availability of the taxon. It is therefore pertinent to single out the major categories of food (Fig. 1) for a comparison of their percentage volumes and frequencies of occurrence. As the ratios in Table 2 show, the percentage frequencies of occurrence exceeded the percentage volumes of all but three major categories of food, viz. fishes, Palaemonetes shrimp and tipulids. In the cases of fishes and shrimp this is attributable in part to the fact that smaller marsh killifish ate less of these two items (see below, esp. Table 3). Tipulids were present only in guts of the three smaller size classes

(Table 1) of *F. confluentus*, in the following percentage volumes and frequencies of occurrence (the latter in parentheses), 1 (1), 4 (2) and 1 (1), but these three size classes made up 95% of the fish sampled, so that tipulids may be supposed to have been less readily available than other major items, as is indicated also by their overall percentage frequency of occurrence (1.13), which is the lowest one among the major food categories. The percentage frequencies of the remaining major food categories (Fig. 1 and Table 2) were 2 to 7 times their percentage volumes, except for ostracods (17.7), copepods (33.8) and vascular-plant detritus (10.5).

### Effects of Predator Size on Food Selection by Marsh Killifish

Fishes constituted the only food item taken in consistently greater percentage volumes and with increasingly greater percentage frequency by larger than by smaller marsh killifish (Table 3). Consumption of fresh vascular-plant tissue, molluscs, annelids, and of crustaceans as a category showed no correlation with size of predator. This lack of correlation in the case of crustaceans reflected the lack of correlation with predator size in the consumption of amphipods and Palaemonetes shrimp, the larger crustaceans concerned, whereas the other and smaller important crustaceans, ostracods, copepods and cheliferans, were taken by larger marsh killifish in smaller amounts and less often. Consumption was negatively correlated with size of predator in the cases of the remaining major food categories, viz. plant material in general, vascular-plant detritus, algae, arthropods in general, insects in general, hemipterans, dipterans in general, ceratopogonids and chironomids and coleopterans in general. The incidence in fish guts of sand and shell, as a category, consistently decreased in percentage volume and frequency with increase in predator size, suggesting that marsh killifish feed on the bottom decreasingly as they grow larger.

Table 2.—Percentage frequency of occurrence and ratio of percentage frequency of occurrence to percentage volume of each major food category consumed by 1945 female marsh killifish, *Fundulus confluentus*. Compare with Figure 1

Food category	% Freq.	Ratio	Food category	% Freq.	Ratio
Fishes	20.82	0.6	Stratiomyiids	2.62	2.4
Crustaceans	<b>6</b> 2.00	3.0	Tipulids	1.13	0.8
Palaemonetes	3.34	0.4	Hemipterans	7.81	4.7
Amphipods	9.77	1.8	Coleopterans	9.46	5.1
Ostracods	31.67	17.7	Odonates	3.14	3.5
Cheliferans	10.44	4.6	Hymenopterans	2.37	2.8
Brachyurans (crabs)	3.24	3.4	Plants	42.78	3.9
Copepods	27.37	33.8	Vascular, fresh	35.22	5.1
Insects	52.75	3.0	Algae	16.20	6.0
Dipterans	44.52	3.9	Detritus, vascular	15.27	10.0
Chironomids	32.08	5.5	Annelids	18.15	2.7
Ceratopogonids	15.84	7.2	Molluscs	22.93	3.5

### SEASONALITY OF FOOD SELECTION BY MARSH KILLIFISH

There was no evidence of seasonal changes in the consumption of any category of food organism except fishes. The annual curves of both percentage volumes and frequencies of occurrence of fishes in guts of F. confluentus had two major peaks, a smaller, blunt peak (May-June) and a larger sharp peak (September). The depressions before and after these twin peaks plausibly reflect a low incidence of neonate mosquito fish, Gambusia affinis, October through April, but the variable percentages of marsh killifish of the six size classes (Table 1) available from month to month for food analysis make these peaks and the trough between them suspect as artifacts of sampling error as to predator size (cf. Table 3). However, the possibility cannot be ruled out altogether that they reflect in part the spring and autumn peaks of breeding intensity by marsh killifish, to be reported later in a separate publication, which might have influenced their feeding preferences. Some other fishes of the Florida region also have spring and autumn reproductive peaks, which will be examined in another publication. Whether mosquito fish also exhibit two such peaks of reproductive intensity within their overall spawning season, so that their neonates would have two peaks of abundance, is not known and would

TABLE 3.—Food of Fundulus confluentus of different standard lengths. The percentage of the total volume per size class contributed by each item, and in parentheses, the percentage of the fish that ate the item. With increase in size of killifish, consumption of fish tended to increase, and of unstarred items, to decrease, in either or both percentage volume and frequency of occurrence. Trace (t) means less than 1%

Number of fish 1945 643 744 40   S. L. class, mm 29-79 29-39 40-49 50-1   Item   Sand and shell 0.4(33.7) 1(38) 1(35) t(2   Plant 11.1(42.8) 19(46) 15(44) 8(3	59 60-69 70-79 9) t(22) t(15) 9) 8(34) 3(46) 4) 8(35) 3(38)
Item Sand and shell 0.4(33.7) 1(38) 1(35) t(2	9) t(22) t(15) 9) 8(34) 3(46) 4) 8(35) 3(38)
Sand and shell 0.4(33.7) 1(38) 1(35) t(2	9) 8(34) 3(46) 4) 8(35) 3(38)
Sand and shell 0.4(33.7) 1(38) 1(35) t(2 Plant 11.1(42.8) 19(46) 15(44) 8(3	9) 8(34) 3(46) 4) 8(35) 3(38)
Plant 11.1(42.8) 19(46) 15(44) 8(3	4) 8(35) 3(38)
Vascular* 6.9(35.2) 5(35) 8(36) 7(3	0) 4/10) 4 /0)
Detritus $1.5(15.3)$ $4(18)$ $3(15)$ $t(1)$	(2) $t(18)$ $t(8)$
Algae $2.7(16.2) 10(20) 4(18) 1(1$	1) $t(5)$ $t(8)$
Mollusca* $6.6(22.9)$ $3(13)$ $10(30)$ $8(2)$	3(22) 14(31)
Annelida* 6.8(18.2) 9(13) 12(20) 9(2	(3) 1'(17) t(15)
Arthropoda 38.5(81.9) 58(92) 48(83) 40(7	
Crustacea* 20.6(62.0) 18(71) 20(63) 29(5	3) $15(45)$ $20(23)$
Ostracoda $1.8(31.7)$ $5(41)$ $4(34)$ $1(2)$	
Copepoda $0.8(27.4)$ $4(37)$ $1(29)$ $t(1)$	7) $t(10)$ 0 (0)
Chelifera $2.3(10.4)$ $5(10)$ $4(8)$ $2(1)$	4) 1(16) 1 (8)
Amphipoda* 5.6 (9.8) 4 (5) 5(11) 5(1	2) 7(20) 2 (8)
Palaemonetes* 8.8 (3.3) 0 (0) 5 (2) 19 (	7) 7 (9) 15 (8)
Insecta $17.6(52.8) 39(65) 28(52) 11(4)$	(2) 6(36) 2(31)
	5) t (4) 1 (8)
Diptera $11.5(44.5)$ $28(58)$ $19(43)$ $7(3)$	(34) $3(24)$ $t(15)$
Ceratopogonid 2.2(15.8) 11(29) 2(13) 1 (	(5) t $(4)$ t $(8)$
Chironomid $5.9(32.1) 13(34) 8(35) 4(2)$	
Coleotera $1.8(9.5) 5(14) 2(9) 1'$	
Fishes $35.9(20.8)$ $8(11)$ $13(17)$ $35(3)$	

be difficult to establish. In sum, the ostensible seasonality of the consumption of fishes by marsh killifish is best regarded as an inadequately established but interesting possibility.

## Discussion

The diet of marsh killifish is further illuminated by a comparison of the present voluminous data with data less copious but obtained (a) under well-recorded dynamic conditions in an unimpounded high salt marsh, viz. during and after the progress of an unusually well-synchronized and massive mosquito brood and for the overall time interval concerned, regarded as a unit (Harrington and Harrington, 1961), and (b) under the static and otherwise different conditions in the same marsh after it had long been impounded. The data described by Odum (1970) may be dismissed with a brief summary since they were neither volumetric nor correlated with interim environmental conditions and thus less informative in the present context.

Odum reported as most frequently taken by 77 marsh killifish 29-88 mm long, chironomid larvae, adult insects, amphipods, small bivalves, a few isopods and, by those over 55 mm long, especially above 70 mm, fishes (primarily Gambusia affinis). Four (15-18 mm) contained small chironomid larvae and small amphipods, and three of unspecified sizes, 30% detritus and algae. The percentage volumes in the guts of the 88 marsh killifish sampled in the unimpounded marsh during the 6 weeks following its inundation and invasion by fishes, and the hatching of Aëdes mosquitoes (cf. Harrington and Harrington, 1961, esp. Figs. 5-6) were as follows, 1st week (12 guts): Aëdes (100%); 2nd week (33 guts): Aëdes (79%), Palaemonetes (1%), fishes (7%), other items (13%); 3rd week (17 guts): Aëdes (15%), plant (2%), copepods (1%), Palaemonetes (66%), fishes (10%), other (6%); 4th week (20 guts):  $A\ddot{e}des$  (10%), plant (2%), other (88%); 5th week (5 guts):  $A\ddot{e}des$  (2%), plant (8%), copepods (43%), other (47%); 6th week (1 gut): Aëdes (2%), plant (2%), copepod (14%), other (82%). The percentage volumes contributed to the total food taken collectively by all 88 killifish were: Aëdes (54%), Palaemonetes (19%), fishes (8%), annelids (4%), gammarids (3%), dolichopodids (3%), plant (1%), isopods (1%), coleopterans (1%), residue (2%), all other items (4%). The percentage volumes contributed to the total food taken collectively by the 41 marsh killifish from the same marsh after it had been impounded were: Palaemonetes (44%), gastropods (20%), fishes (19%), annelids (6%), chironomids (5%), coleopterans (3%), ostracods (1%), odonates (1%), all other items (1%).

The changes in the percentage volumes of the constituents of the potential overall diet of marsh killifish taken in response to intraseasonal fluctuation in the abundance of  $A\ddot{e}des$  mosquitoes demonstrate that small samples, especially if isolated from the temporal context of interim biotic and environmental changes, can give distorted pictures of the scope, flexibility and long-term configuration

of the diet. We find no reason to amend our appraisal (Harrington and Harrington, 1961) of the food habits of small brackish-water cyprinodontoids, including Fundulus confluentus, as characterized by "plasticity in food selection, omnivorous diets, sharing of common food resources among species, quick changeover to alternative diets, ontogenetic food progression in young of larger species, and short food chains," to paraphrase remarks of Larkin (1956) concerning freshwater fishes. This does not invalidate the classification of Fundulus confluentus in the context of energy flow as a "middle carnivore" (Odum, 1970), even though one of Odum's criteria was the ingestion of plant materials in amounts less than 5% of the total food volume, whereas these comprised 11% of the total food volume consumed by the marsh killifish of present report, i.e., more than can be dismissed as "probably the result of accidental ingestion during capture of benthic animals" (Odum, 1970: 124). On the other hand, marsh killifish manifestly are preferential carnivores, as the percentage volumes of plant materials taken by them in the same marsh before (1%) and especially after it had been impounded (less than 1%) indicate. The invertebrate fauna of the marsh had been markedly impoverished by impoundment, such that Gambusia affinis, typically an omnivore with a strong predilection for animal food and outstanding food-searching ability, was subsisting on 70% plant materials, and the other species in the impoundment except Fundulus confluentus, on 92% or more plant materials. After the marsh was impounded, however, fresh vascular plant tissue became virtually unavailable and the total volume of plant materials taken in the impoundment by all fish regardless of species was 53% vascular plant detritus and 46% algae. Since the 11% plant materials consumed by the 1945 marsh killifish comprised 7% fresh vascular tissue, 3% algae and 1% vascular detritus, the failure of the marsh killifish in the impoundment to ingest plant materials must be attributed largely to the destruction of vascular plants that resulted from impoundment, and it cannot be inferred that marsh killifish only ingest plant materials incidentally to feeding on benthic organisms. Odum (1970) lists bivalves and adult insects among items most frequently taken by marsh killifish, but neither was prominent among the major categories of food consumed by the marsh killifish sampled by us (Fig. 1). Bivalves (pelecypods) made up 0.02% and gastropods 6.53% of the 6.55% contributed by molluscs to the total food volume. Adult insects, comprising no more than half the coleopterans and fewer of the heteropterans, made up less than 2% of the 18% contributed by insects to the total food volume.

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