

12-1991

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Consumption Rates, Evacuation Rates, and Diets
of Pygmy Killifish, *Leptolucania ommata*, and
Mosquitofish, *Gambusia affinis* (Osteichthyes: Atheriniformes)
in the Okefenokee Swamp

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ABSTRACT.— I studied feeding dynamics of *Leptolucania ommata* and *Gambusia affinis* in the Okefenokee Swamp. Both fishes mainly ate insect larvae (such as Chironomidae) and Cladocera. Evacuation rates ranged from 0.143 (*L. ommata* in winter) to 0.279/hour (*L. ommata* in summer). Daily food consumption (dry weight) ranged from 24.2 (*L. ommata* in winter) to 148.3 mg/g/day (*G. affinis* in summer). Maximum consumption by both species was estimated at 26.31 mg/m²/day, in summer. These values are consistent with other observations supporting a hypothesis that invertebrate prey production is substantial in these blackwater wetlands.

Relatively little is known about the diets and feeding dynamics of fishes of freshwater wetlands (Weller 1981). Studies of the diets of wetland fishes have concerned those in salt and estuarine marshes (e.g. Harrington and Harrington 1961, Wetzel 1971, Kjelson et al. 1975). I do not know of a previous study on consumption or evacuation rates of any fish in any saltwater or freshwater wetland.

This study was based on field data from the Okefenokee Swamp, Georgia-Florida, the largest entirely freshwater wetland in the United States (1800 km²). My objectives were to determine the diets and rates of consumption and evacuation under field conditions of two of the most abundant fishes in a marsh on the west side of the Okefenokee Swamp: that is marsh C, the "Control" marsh of Stinner (1983) and Oliver and Schoenberg (1989). To quantify dynamics at the ecosystem level and to estimate minimum invertebrate prey production, I then used measures of daily food consumption to estimate area-based consumption (consumption per m²) by these fish. These invertebrate production estimates may help to resolve whether blackwater habitats have low secondary productivity, as suggested for tropical blackwaters (Janzen 1974, Fittkau et al. 1975, Araujo-Lima et al. 1986), or substantial productivity (Freeman and Freeman 1985). Methods are field-based to obviate elaborate laboratory feeding studies and to obtain data under natural conditions.

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The two fishes examined were *Leptolucania ommata* Jordan, the pygmy killifish, and *Gambusia affinis* Baird and Girard, the mosquitofish, small members of the order Atheriniformes. *Leptolucania ommata* lives in quiet, densely vegetated fresh waters from southern Georgia and Alabama to Florida (McLane 1955, Laerm et al. 1980). *Gambusia affinis* is native from southern Illinois to Texas and Georgia, and it has been introduced to warm waters around much of the world, primarily to consume mosquito larvae (Hess and Tarzwell 1942, Krumholz 1948, Hurlbert and Mulla 1981). In marshes on the west side of the Okefenokee Swamp, *L. ommata*, *G. affinis*, *Enneacanthus gloriosus* Holbrook, and *Elassoma okefenokee* Böhlke are by far the most numerous fishes (in that order at C and R sites, Oliver and Schoenberg 1989). The individuals used in this study were adults that came within the common distributions of length (*L. ommata* of 13-20 mm, *G. affinis* of 15-25 mm standard length). Both species were studied in the field for a 24-hour period in the summer and in the winter.

The study site is a subtropical marsh that has large daily temperature fluctuations. It lies approximately 200 m E of the entrance to the Suwannee River sill (an earthen dam that borders the west side of the Okefenokee Swamp). This blackwater area (mean depth 43-113 cm) had floating and submersed macrophytic vegetation (mainly *Nuphar luteum* and *Utricularia* spp.). Daily water temperature ranges were 4-20°C during winter observations, and 26-37°C during summer observations. The site differed from the Okefenokee LCP site of Freeman and Freeman (1985) in that the latter was shallower (10-55 cm) and was dominated by floating, submersed, and emergent macrophytes (*Nymphaea odorata*, *Eriocaulon compressum*, and *Rhynchospora inundata*).

METHODS

I obtained evacuation rates by two related methods done simultaneously, which allowed comparison of results (compare with single-method analysis, e.g. Sainsbury 1986). In the "tank" method, the decline in gut contents of fish held without food was converted to an evacuation rate (Staples 1975, Garcia and Adelman 1985). Clear immersed tanks at the edge of the marsh were used to track natural light levels and water temperatures (measured by a standard mercury thermometer). Okefenokee water was filtered into tanks through a screen (<63 µm mesh) to remove potential food items. At approximately 4-hour intervals, large fish captured by seine were placed into two tanks and smaller fish into two other tanks, so that the larger fish would neither consume nor frighten the latter. I preserved about half the seined fish immediately in buffered formalin and preserved the rest

approximately 4 hours after they were put in the tanks, for comparison of gut contents. In the "field" method, the decline in gut contents between field samples taken at intervals during non-feeding times of day yielded a second measure of evacuation rates. (See the section on Feeding Dynamics for an example of evacuation analyses.)

In the laboratory, lengths of foods in foreguts were converted to weights. Foreguts were analyzed because their contents declined consistently with time in tanks, whereas hindguts continued to receive food from foreguts in some cases. I examined foregut contents under a dissecting microscope and measured lengths of food items. Length-weight regressions in Dumont et al. (1975) were used to calculate dry weights of Ostracoda, Harpacticoida, nauplii, and most Cladocera. Hall et al. (1970) gave macrothricid weights. Insect head-capsule widths were converted to weights (Smock 1980). Ruttner-Kolisko (1977) and J. Gerritsen and H. S. Greening (personal communication) gave rotifer length-weight conversions. A regression by Gerritsen (personal communication) for the Okefenokee Swamp was used to derive cyclopoid weights. Maximum carapace widths of araneids were converted to weights (Edgar 1971, Barber 1983). Weights of Acari were estimated from the regression of Oribatei by Persson and Lohm (1977).

I calculated a length-weight regression to yield weights of *Gambusia affinis* within *Gambusia* foreguts. Foregut content (S) was expressed in relative units, i.e. mg dry food/g dry fish, assuming 20% dry to wet weight conversion for fish (e.g. Lagler et al. 1977).

Evacuation rates, daily food consumption, and area-based consumption were calculated for both fishes. Area-based consumption equals the dry weight equivalent of fish density (Oliver and Schoenberg 1989, method of density measurement adapted from Freeman et al. 1984) times calculated daily food consumption (Staples 1975, adjusted in Elliott and Persson 1978; Persson 1982; Garcia and Adelman 1985). Results are based on collections of fish at about 4-hour intervals for 24 hours, in summer (*L. ommata* and *G. affinis*, 19-20 August 1984) and winter (*L. ommata* on 7-8 March 1984, and *G. affinis* on 16-17 February 1985, when it was common).

ANALYSES AND RESULTS

DIETS

Chironomids and Cladocera dominated the diet of *Leptolucania ommata*. Major prey types were Chironomidae, unidentified Insecta, and Cladocera (Table 1). Oribatid mites, not usually found in fish guts (B. J. Freeman, personal communication), were eaten by both *L. ommata* and *G. affinis*.

Table 1. Percent of relative foregut content (and SE) attributable to various foods in winter and summer^a.

Food category	<i>Leptolucania ommata</i>				<i>Gambusia affinis</i>			
	March 1984 [27]		August 1984 [30]		February 1985 [12]		August 1984 [23]	
Chydoridae	4.66	(1.54)	2.23	(0.53)	0.02	(0.01)	0.29	(0.11)
Macrothricidae	1.06	(0.45)	0.52	(0.21)	0.02	(0.02)	0.20	(0.08)
Other Cladocera	9.44	(3.04)	5.71	(2.39)	0.10	(0.06)	1.51	(0.63)
Ostracoda	0.00	(0.00)	0.00	(0.00)	0.00	(0.00)	0.05	(0.02)
Harpacticoida	0.30	(0.16)	0.00	(0.00)	0.00	(0.00)	0.00	(0.00)
Cyclopoida	0.61	(0.56)	1.26	(0.47)	0.00	(0.00)	0.76	(0.27)
Nauplii	0.05	(0.05)	0.01	(0.01)	0.00	(0.00)	0.00	(0.00)
Rotifera	0.00	(0.00)	0.02	(0.01)	0.00	(0.00)	0.00	(0.00)
Non-tanypode Chironomidae	46.56	(20.64)	43.63	(23.20)	4.76	(4.76)	9.73	(4.96)
Tanypodinae	35.67	(21.92)	20.72	(14.65)	0.00	(0.00)	13.59	(7.80)
Hemiptera	0.00	(0.00)	3.67	(3.67)	0.00	(0.00)	3.44	(1.30)
Odonata	0.00	(0.00)	0.00	(0.00)	0.00	(0.00)	15.50	(12.00)
Unidentified Insecta	1.65	(1.65)	21.87	(19.23)	94.25	(55.05)	35.44	(14.13)
Araneae	0.00	(0.00)	0.00	(0.00)	0.00	(0.00)	15.91	(7.72)
Oribatei	0.00	(0.00)	0.35	(0.29)	0.84	(0.57)	0.61	(0.28)
Other Acari	0.00	(0.00)	0.00	(0.00)	0.00	(0.00)	0.02	(0.01)
Fish (<i>G. affinis</i>)	0.00	(0.00)	0.00	(0.00)	0.00	(0.00)	2.94	(2.94)
TOTAL	100.00		100.00		100.00		100.00	

^aNumbers of foreguts (in square brackets following dates) are about equally represented from all parts of the diel cycle.

In *Gambusia affinis*, insects were dominant in the diet, but other arthropods and some mosquitofish were also eaten. In summer, Tanyptodinae and odonate nymphs were quantitatively significant foods (Table 1). Cladocera, Cyclopoida, and Araneae composed more of the diet in summer than in winter. In both winter and summer, non-tanyptode Chironomidae and unidentified Insecta were dominant food items. *Gambusia affinis* showed some cannibalism (in summer, about 3%).

FEEDING DYNAMICS

Gambusia affinis. The balance between consumption and evacuation may be inferred from diel changes in foregut content (solid lines on Fig. 1). When the slope of the line is positive, consumption rate is greater than evacuation rate during the specified time period; when negative, consumption is less than evacuation.

Analysis of evacuation rates is based on comparisons of gut-content trends obtained by field and tank methods, i.e. the solid versus the dashed lines of Fig. 1 and 2. During certain periods (e.g. 1055 to 1455 hours), fish in the field actively fed, which resulted in an increase in the foregut content (Fig. 1). For such periods, it is necessary to use the fish held in food-free tanks (dashed lines) to calculate evacuation rates. At other times (e.g. 1850 to 2250 hours), the foregut content declined in both field fish and tank-held fish. For these periods, I considered field fish, which were unconfined and egesting in their natural environment, to provide the better estimate of natural evacuation rate. The evacuation rate is computed by

$$r = \frac{\ln(S_0+1) - \ln(S_t+1)}{t}$$

in which S_0 is relative foregut content before and S_t is relative foregut content after time t (adapted from Elliott and Persson 1978; 1 is added to allow logarithmic transformation of zeros). The same equation applies for determining evacuation in tank-held fish. When evacuation data were missing for a period, evacuation rate was presumed to be an average of rates before and after that period. Finally, the various rates during the day were weighted by time to produce an average evacuation rate (Table 2).

Evacuation rates for each of the time periods were used in calculating consumption over each of these periods. Each such evacuation rate was combined with average foregut content before and after the period

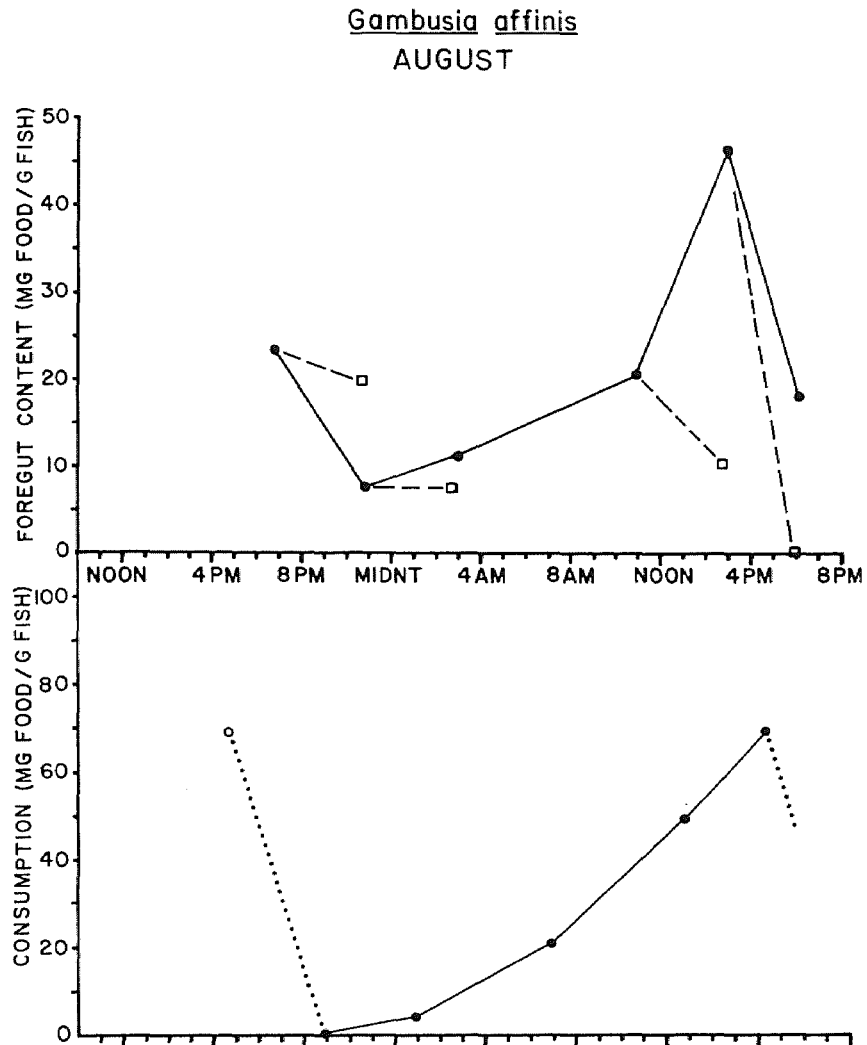


Fig. 1. Foregut content of and food consumption by *Gambusia affinis* in summer. In the upper panel, filled circles and solid lines show diel content trends in field fish; open squares and dashed lines show changes in content of fish held in food-free tanks. In the lower panel, filled circles and solid lines show trends in consumption during each time period; the open circle and dotted lines show the presumed trend based on difference between the final (1630 hours) and initial (2050 hours) consumption values.

Leptolucania ommata
AUGUST

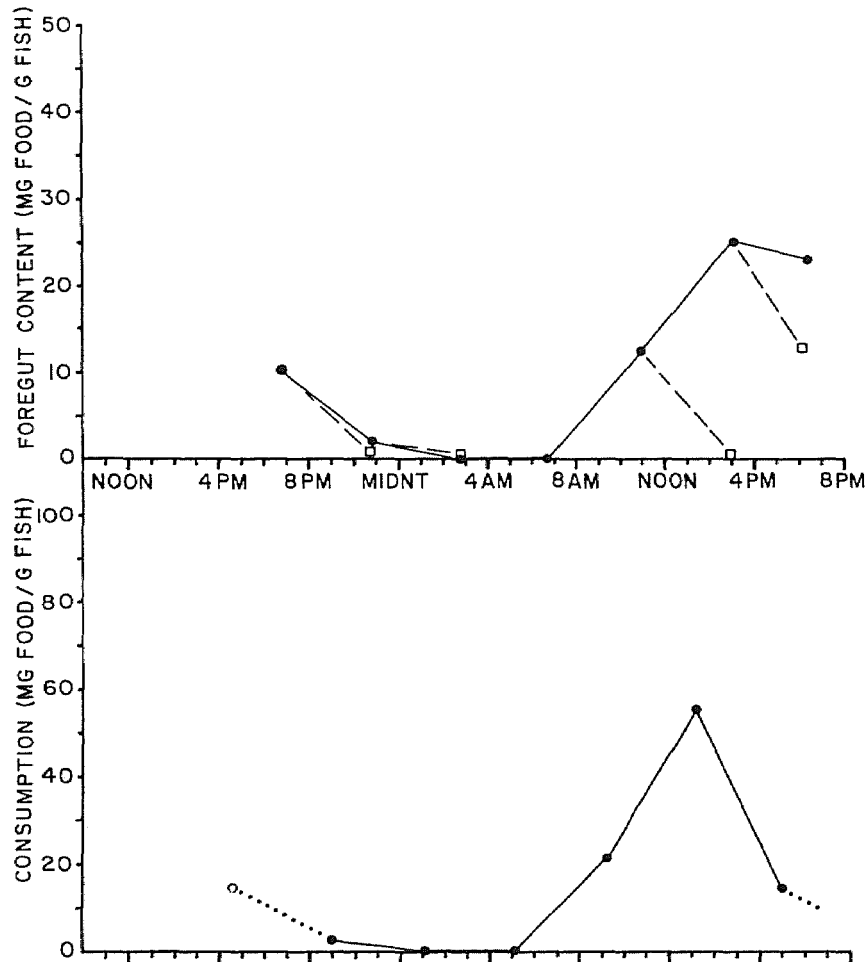


Fig. 2. Foregut content and food consumption of *Leptolucania ommata*. (See Fig. 1 legend for details.)

Table 2. Evacuation rates and food consumption. Food in mg, fish in g dry weight.

Species	Season	Sampling dates	Foregut evacuation rate, r (per hour)	Daily food consumption ΣC_t (mg/g/day)	Fish biomass (g/m ²)	Area-based consumption (mg/m ² /day)
<i>Leptolucania ommata</i>	Winter	11 February 1983 7-8 March 1984	0.143	24.2	0.0292	0.71
	Summer	29 August 1983 19-20 August 1984	0.279	93.1	0.2468	22.99
<i>Gambusia affinis</i>	Winter	4-5 January, 11 February 1983 ^a 16-17 February 1985	0.157	32.1	0.0103	0.33
	Summer	29 August 1983 19-20 August 1984	0.262	148.3	0.0224	3.32

^aBecause no *G. affinis* were captured in February 1983, biomass is averaged over January and February.

to yield consumption during the period (adapted from Elliott and Persson 1978):

$$C_t = \frac{((S_t+1) - (S_0+1)e^{-rt})}{1-e^{-rt}}$$

Daily food consumption, ΣC_t , is the sum of consumption rates over each period. For *G. affinis* in summer, the graph of consumption versus time (bottom panel of Fig. 1) indicates that peak consumption occurred in the afternoon.

Gambusia affinis in winter samples showed feeding trends similar to those in summer but at lower levels. Evacuation rate and daily food consumption were lower in February than in August (Table 2). There was a single feeding peak in late afternoon, as in summer. Low daily food consumption combined with low fish biomass to produce very low area-based consumption.

Leptolucania ommata. *Leptolucania ommata* showed diel feeding patterns similar to those of *G. affinis*. Foregut content in summer peaked in late afternoon (Fig. 2). Consumption showed one daily peak, in the afternoon. In winter (March 1984), *L. ommata* also consumed maximally in the afternoon, as other species-season combinations had done.

Leptolucania ommata had seasonal feeding dynamics similar to those of *G. affinis*. The evacuation rate in summer was 0.279/hour, similar to the 0.262/hour calculated for *G. affinis* in summer (Table 2). The evacuation rate in winter was also similar in the two species, 0.143 and 0.157/hour, respectively. In both species, daily food consumption increased from winter to summer by a factor of about 4 (3.85 for *L. ommata*, 4.62 for *G. affinis*). This increase might be largely a result of temperature-dependent feeding: If the " Q_{10} " for food consumption were about 2, the approximately 20° C difference from winter to summer would give an increase of about 4 times. Such a doubling of feeding for every 10° C is consistent with the results of Salvatore et al. (1987), who found that the feeding rate of *Dorosoma cepedianum* Lesueur approximately doubled when laboratory water temperature increased from 10 to 20° C. Thus such differences in feeding rates may be largely attributed to the environmental temperature.

DISCUSSION

The two fishes fed on similar kinds of foods. This should not be surprising, because I captured them in the same areas and observed them feeding at about the same depth (near the surface). Diets, evacuation, and consumption in this study were similar to values

reported for fishes in other types of habitats (see comparisons in the following discussion).

The diet of *L. ommata* in the Okefenokee marshland was mainly chironomid larvae and other insects, as well as Cladocera. Similarly, in the St. Johns River system of north Florida, *L. ommata* ate mainly chironomids, Cladocera, and Copepoda (McLane 1955). In the Okefenokee, *Gambusia affinis* consumed mainly chironomids, odonates, other insects, and Cladocera (Table 1). Similarly, *G. affinis* in shallow areas of Wheeler Reservoir, Ala., ate mostly Entomostraca (presumably Cladocera or Copepoda), Chironomidae, and other juvenile insects (*Anopheles*, Hess and Tarzwell 1942). In California rice fields, *G. affinis* ate mostly Cladocera and immature Chironomidae (Washino and Hokama 1967) and some Ostracoda (Farley 1980). Those in California ponds ate mostly Cladocera (Miura et al. 1979). Thus, in Okefenokee marshes, the fishes fed primarily on the same kinds of foods that they ate in other localities and in different habitats. The two fishes in the Okefenokee freshwater marsh ate oribated mites, which are often associated with an algal, detrital system of this kind (Pennak 1978), but Oribatei were a minor component of their diets (Table 1).

Both fishes showed peak consumption rates at about the same time of day, the afternoon. The afternoon had bright sunlight and the highest temperatures of the day, and these factors may have contributed to increased consumption by fish (Reddy 1975, Mann 1978, Smagula and Adelman 1982, Garcia and Adelman 1985), and high illumination may make foods more conspicuous, particularly in a vegetated blackwater environment.

Evacuation rates of the two fishes were alike, and similar to rates reported for other fishes. Foregut evacuation rates were 0.143 and 0.279/hour for *L. ommata* in winter and summer, respectively. Similarly, rates for *G. affinis* were 0.157 and 0.262/hour. Doble and Eggers (1978) reported rates of 0.109 and 0.267/hour for small juvenile *Oncorhynchus nerka* Walbaum in winter and summer. Ruggerone (1989) measured evacuation of 0.274 to 0.329 for *Oncorhynchus kisutch* Walbaum at 13° C. Persson (1982) found rates of 0.129 and 0.499/hour for *Rutilus rutilus* L. held at 12 and 24° C in the laboratory. Amundsen and Klemetsen (1988) reported rates of 0.08 to 0.16/hour for *Salvelinus alpinus* L. at 13° C. Thus, evacuation rates for *L. ommata* and *G. affinis* appear to be well within the range of values reported for various fishes.

Because evacuation rates are similar to rates of other fishes, consumption measures of *Gambusia* and *Leptolucania* in the Okefenokee Swamp are in the same range as estimates for other species. Daily food consumption by *L. ommata* was 24.2 and 93.1 mg/g/day (dry weights), in winter and summer, respectively. Values for *G. affinis* were 32.1 and

148.3 mg/g/day. Doble and Eggers (1978) found that *Onchorhynchus nerka* juveniles ate 15.3 and 44.1 mg/g/day in Lake Washington in winter and summer, respectively. Garcia and Adelman (1985) reported that *Cyprinus carpio* L. in the Mississippi River consumed 204 mg/g/day in summer (assuming a fish dry to wet ratio of 20%). Cech et al. (1981) stated that in the laboratory, newborn *G. affinis* ate from 70 to 820 mg/g/day at 10-35°C. Thorpe (1977, in Elliott and Persson 1978) reported summer consumption by *Perca fluviatilis* L. in Loch Leven to be 54 mg/g/day (dry weights, assuming fish dry to wet ratio of 20% and prey wet to dry ratio of 6; Freeman and Freeman 1985), but this was an underestimate according to Elliott and Persson (1978). Basimi and Grove (1985) reported that summer consumption by small *Pleuronectes platessa* L. off the coast of Wales was 43 mg/g/day (assuming the same ratios). Sagar and Glova (1988) found that juvenile *Oncorhynchus tshawytscha* Walbaum in the Rakaia River, New Zealand, ate 83 mg/g/day at a mean temperature of about 15°C. Consumption by *O. kisutch* ranged from 21 to 44 mg/g/day at 5.8-7.5°C (Ruggerone 1989). Food consumption rates of *L. ommata* and *G. affinis* from the Okefenokee wetland clearly fall within the range of fish in other types of environments.

As expected, area-based consumption by the two fishes was low in winter and higher in summer. *Leptolucania ommata* in the Okefenokee marsh consumed 0.71 and 22.99 mg/m²/day in winter and summer, respectively. *Gambusia affinis* ate less, presumably because of their lower biomass; they consumed 0.33 and 3.32 mg/m²/day in winter and summer, respectively. In comparison, in a small New Zealand lake with only one fish species, Staples (1975) reported that *Philypnodon breviceps* Stokell in summer consumed 203 mg/m²/day (assuming a wet to dry ratio of 6); this value was an underestimate according to Elliott and Persson (1978). In a New Zealand stream where trout and eels were also present (Hopkins 1970, in Staples 1975), the maximum reported area-based consumption by *P. breviceps* was equivalent to 74 mg/m²/day.

Consumption data are consistent with a hypothesis that invertebrate prey production in Okefenokee blackwater marshes is substantial. Consumption values in spring and fall are usually between winter and summer values, rising in a nonlinear manner as a function of temperature (see Feeding Dynamics above; Staples 1975, Doble and Eggers 1978). Thus, the geometric mean of winter and summer consumption values may give a reasonable estimate of mean daily food consumption for the whole year. Calculating the geometric mean of consumption values (from Table 2) yields estimates of 47.5 and 69.0 mg/g/day for *L. ommata* and *G. affinis*, respectively. When each of these values is multiplied by average dry biomass per m² (from Oliver and Schoenberg

1989) for each of these fishes, consumption by both *L. ommata* and *G. affinis* is calculated to be 5.88 mg/m²/day. Assuming a wet to dry conversion of 6, invertebrate prey production would have to be at least 130 kg/ha/year (wet weight), just to meet consumption needs of these fish. At a recently abandoned bird rookery on the west side of the Okefenokee, guano fertilization apparently increased standing stocks of several trophic levels, including fish (Oliver and Schoenberg 1989): Average annual biomass estimates of *L. ommata* and *G. affinis* were elevated to 4.5 times the levels of the present study. Invertebrate production may have been about 580 kg/ha/year, just to meet consumption by these fish. At the same site, I measured fish production directly by the size-frequency method (Hynes and Coleman 1968, Freeman and Freeman 1985) and made a second estimate of prey production: Based on a combined production for *L. ommata* and *G. affinis* of 89.8 kg/ha/year (wet weight, unpublished data) and a gross conversion efficiency of $\leq 25\%$ for fish (Brett and Groves 1979), production of invertebrate prey would have to be at least 360 kg/ha/year, just to meet consumption requirements of the two fishes. These values are within the range of estimates of production for the total zoobenthos in non-blackwater systems given by Waters (1977), and they are consistent with the findings of Freeman and Freeman (1985) that indicated substantial productivity of another Okefenokee blackwater ecosystem.

ACKNOWLEDGMENTS.— I thank Robert E. Reinert and Steven A. Schoenberg, of the University of Georgia, and Tom Richards for their valuable help and ideas. This research was supported by National Science Foundation grants BSR 8114823 and BSR 82155587. Paper No. 63, Okefenokee Ecosystem Investigations.

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Accepted June 1991