

Growth, Production and Energy Transformations in the Salt-Marsh Killifish *Fundulus heteroclitus**

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Abstract

Populations of *Fundulus heteroclitus* (L.) at the beginning of a growth season in a New England salt marsh consist of 3 yearly age classes, with the 1-year-old class contributing most of the biomass. Calculation of production rates revealed that the young fish were the most active part of the population and that females were more productive than males. The entire population spent equal amounts of energy in growth and in metabolism. Including the young of the year, we obtained total production of 160 kg dry weight/ha, a value among the highest obtained for natural fish populations. About 5 to 15% of the production is available to predators. Rates of food consumption by *F. heteroclitus* are high enough to turn over the population of prey relatively often. Populations of *F. heteroclitus* are thus capable of exerting an important influence on the abundance and distribution of their prey.

Introduction

Fundulus heteroclitus (L.), the salt-marsh killifish, is the most common fish in tidal marshes of New England. In Great Sippewissett salt marsh near West Falmouth, Massachusetts, USA, feeding activity of the overwintering *F. heteroclitus* begins about the first week in April and small fry can be observed during the second week of June. Fry are present throughout the summer, a last group appearing sometime in August. Fish smaller than 3 to 4 cm in length tend to remain in the tidal creeks. Adult killifish (greater than about 4 cm in length) follow flooding tides into tidal creeks of the salt marsh and, if the tide is high enough, move onto the marsh surface to feed. As the tide ebbs, adult fish return to the central pools and deeper parts of the estuary. Darnell (1964) and Jeffries (1972) reported detritus to be the major component of the diet, but Prinslow *et al.* (1974) found that detritus did not contribute to fish growth. The fish would seem to be mainly carnivorous, although algal filaments and detritus are common in gut contents.

The goals of this study were to obtain estimates of the production and food consumption of an adult population of *Fundulus heteroclitus* over a growing season. The calculations were based on estimates of population density, rates of growth and mortality and mean biomass for each of the three age classes of male and female killifish.

Materials and Methods

Mark-Recapture Procedures

Monthly censuses of the adult *Fundulus heteroclitus* (L.) population were carried out from June to November, 1971. The fish were caught in 4 commercially available minnow traps (mesh opening 4.5 mm) placed across the mouth of each of 8 tidal creeks on the flooding tide. The trapped fish were measured to the nearest centimeter, sexed, dyed red with rhodamine B, and released at the head of the creek before peak high water. The traps were reset before high tide to capture the fish leaving the marsh on the ebbing tide. After 4 to 6 h, the traps were collected again and the recording procedure repeated, noting marked individuals. The killifish left the marsh surface soon after the peak

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high water. This entire procedure was repeated monthly from June to November. Fish smaller than about 4 cm in total length were able to pass through the mesh of the traps, so their numbers were not estimated.

The population size was calculated as

$$\bar{N} = \frac{m(c + 1)}{r + 1} \quad (\text{Bailey, 1951}),$$

where, out of a population of \bar{N} individuals m are marked, and c is the number of fish in a recovered sample, of which r are marked.

The assumptions involved in the procedures were met fairly well in this study (Jones, 1964; Eberhardt, 1969). The marked fish were visible in the small creeks, so that it was fairly obvious when random mixing of marked fish did not take place. There was no difference in behavior of marked and unmarked fish entering traps. Male and female fish of various sizes were brought into the laboratory, dyed with rhodamine B and placed in 4-l jars. The dye remained distinct for 24 to 36 h, and no mortality of stained fish occurred over a period of 2 weeks.

Age-Structure Determination from Scale Readings

Scales from fish obtained in the monthly collections were examined to age the catch. A selected subsample of 20 to 25 male and 20 to 25 female fish was taken so that the entire size spectrum of the preserved collection was represented. Three scales were examined from the mid-lateral region of each fish and the age class assigned accordingly.

Measurement of Growth

Preserved samples of male and female killifish collected in May, 1971 were measured to the nearest 0.1 cm, dried in an oven for at least 48 h at 60°C, and weighed. Length-weight relationships were determined for both male and female fish to permit estimates of individual dry weights from total length, using the allometric formula $w = aL^b$. (w = weight, L = length, a and b are fitted constants).

The raw data from all 8 creeks were pooled for each month and the numbers (\bar{N}) of male and female fish in each size class were calculated. The histograms of the data suggested that the length-frequency distribution was lognormal (Fig. 2). Cumulative frequency plots yielded monthly estimates of the mean length and standard deviation of each age class of adult male

and female killifish. The methods for the use of probability paper in the analysis of normally distributed size-frequency distributions (Harding, 1949; Cassie, 1954) were adapted to the log transformation (Aitchison and Brown, 1969).

The youngest age class of adult fish were those in their second season of growth during 1971. We truncated this class, referred to as Age 1, to below 4.0 cm in June and July and 5.0 cm thereafter due to the presence of young-of-the-year fish. Since the Age 1 group extended to two or three size classes (Fig. 1), it was impossible to obtain a direct estimate of the amount of upper truncation of this age group. Therefore, the percentage of truncation was determined by the method outlined by Hald (1949, 1967), adapted for the log transformation (Aitchison and Brown, 1969), for the entire distribution. The percentage of truncation (T_1) of the Age 1 group was then determined as $T_1 = 100 T/P$, where T was the percentage of truncation of the whole distribution and P was the percentage of the whole distribution represented by Age 1 fish.

The number of fish in each age class was calculated by summing the frequencies for each size class up to the cut-off point of the cumulative frequency distribution. The number thus obtained for the Age 1 group was increased to make up for the percentage of truncation. No estimate was made of the amount of overlap in numbers between the Age 1 and Age 2 groups or between the Age 2 or Age 3 groups. This resulted in somewhat of an overestimation of the numbers of Age 1 fish, and underestimated the number of individuals in the Age 2 and Age 3 groups.

Growth, mortality and production rates and stock biomass were estimated according to Ricker (1946), Allen (1950) and Chapman (1967, 1968).

Production was computed as $P_i = G_i \bar{B}_i$, where B is stock biomass, and $\frac{dB_i}{dt} = B_i(G_i - Z_i)$, $B_{2i} = B_{1i} e^{(G_i - Z_i)t}$, and mean biomass was obtained both by using an exponential model, $\bar{B}_{e_i} = \frac{B_{1i}(e^{G_i - Z_i} - 1)}{G_i - Z_i}$, and with a linear model, $B_{1i} = \frac{B_{2i} - B_{1i}}{2}$.

Instantaneous growth was obtained as

$$G_i = \frac{\ln \bar{w}_{2i} - \ln \bar{w}_{1i}}{t_2 - t_1},$$

where \bar{w}_{1i} is mean weight of fish of i th age at time t_1 . The calculation of G_i is based on observed increases in the aver-

age weight of individual fish, not on total biomass. If total biomass were used, mortality would be included twice, once in the observed data and again in $e^{(G_i - Z_i)}$.

Mortality was calculated as

$$Z_i = \frac{\ln N_{1i} - \ln N_{2i}}{t_2 - t_1},$$

where N is the number of fish of i th age at time t .

To measure what fraction of total growth was devoted to egg production, we weighed ovaries of a sample of fish collected in May, a time of peak gonad development, and in October, when reproduction had ceased and gonads were spent.

Metabolic Expenditures and Food Consumption

The rate of resting metabolism (R) is usually calculated as $R = aW^b$, where a and b are constants for a given species and W is the weight of an individual. Hoss (1967) obtained values of $b = 0.568$ and $a = 0.339$ for *Fundulus heteroclitus* in a size range from 2 to 18 g at 20°C. We have obtained measurements of respiration rates of killifish similar to those of Nixon and Oviatt (1973), and will therefore use their equation for respiration of killifish at different temperatures (T), $R = 0.12 T + 0.42$. R is expressed in $\text{mgO}_2 \text{ g dry weight}^{-1} \text{ h}^{-1}$. Mann (1965, his Table 4) presents data where a is shown to be linearly dependent on temperature. We calculated a regression, $a = 0.0433 + 0.016 T$, $r = 0.95$, and then obtained $R = (0.0433 + 0.0161 T) W^b$. We assumed that there was no interaction between size of fish and the effect of temperature on respiration, which seems reasonable from Figs. 6-10 in Mann (1965). This calculation enabled us to consider both the effects of temperature and size of fish on respiration.

Records of seawater temperature were used to calculate the respiration rate at the time of sampling. Two successive rates were averaged and used to calculate the respiration for the interval between the two fish sampling dates.

The total potential energy of food consumed (C_1) by an average fish of age i is

$$C_i = F_i + U_i + B_i + R_i,$$

where C = total energy of the ration, F = energy value of the feces, U = energy value of materials excreted in the urine or through the body surface, B = total change in the energy value of body materials, i.e., the energy invested in growth and reproduction, and R = total energy of metabolism.

We did not measure waste products, but after considerable discussion Winberg (1956) and Mann (1965) conclude that $F + U$ is about 20% of C , so that

$$C_i = 1.25 (\Delta B_i + M_i),$$

where M_i is the total energy of metabolism of an average fish of age i in nature taken as twice the resting level. ΔB_i , the increase in biomass during the growing season, was calculated from

$$N_i = N_{0i} e^{-Z_i t} \quad \text{and} \quad W_i = W_{0i} e^{G_i t}.$$

Biomass and production were expressed on an areal basis by calculating the area flooded by a mean high tide from an air photo. The sampling area was thus estimated to be about 8000 m^2 .

Results

Fig. 1 shows total body length plotted against age for *Fundulus heteroclitus*, as determined from scale readings. Three age classes were present in June-July, while the young-of-the-year (Age 0) entered our population by the end of August. The 3-year-old fish disappeared by October and were absent in November.

The percent recaptures averaged 12% of those marked over each of the 5 dates (range 4 to 24%). The overwintered population consists mainly of 4 to 5 cm length fish (cf. June, Fig. 2). These fish grow to 6-7 cm by September, when the young spawned earlier in the summer begin to enter our samples. In November the 4 to 5 cm class again dominate the population about to overwinter.

The mean length of female fish of a given age was consistently greater than that of male fish of the same age (Table 1), but the numbers of males and females were roughly equal. There were very few Age 3 fish present in October and November (Fig. 1), implying significant mortality rates for the larger fish.

The regression of dry body weight on length for males was $W = 1.23 L^{3.45}$, for females $W = 1.41 L^{3.45}$. A female fish of a given length was slightly heavier than a male of the same length. These formulas should give near maximum values of dry weight for a given length of fish because the collections were made in May, a time near peak gonadal development (Mathews, 1938).

The seasonal trend in the instantaneous coefficient of growth was similar for all three age classes of male and female killifish. Growth was slightly higher early in the growing season (June-July), decreasing thereafter (Table 2). Mortality was variable with a

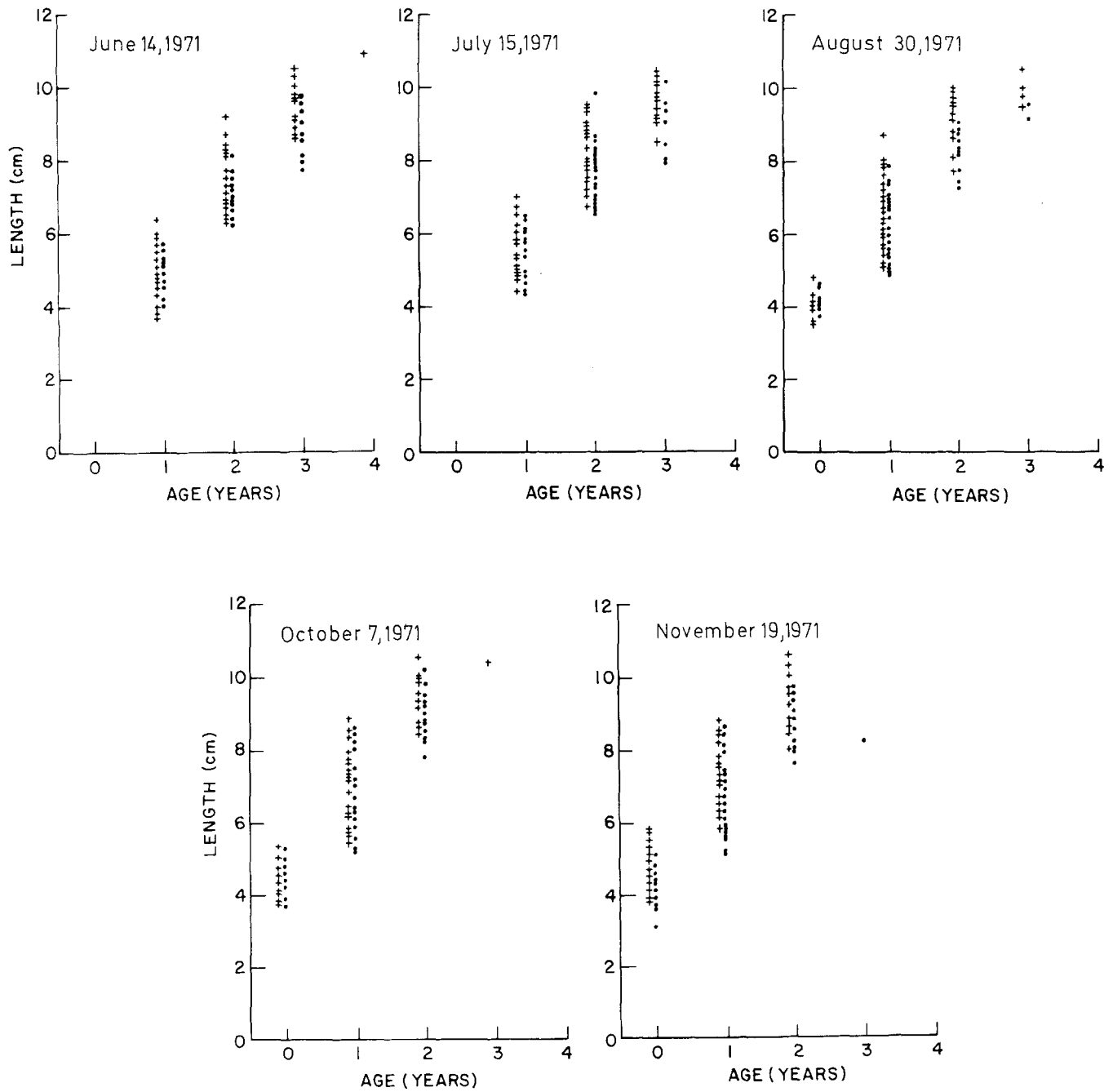


Fig. 1. *Fundulus heteroclitus*. Size of fish of various year classes as determined by scale rings. Dots: males; crosses: females

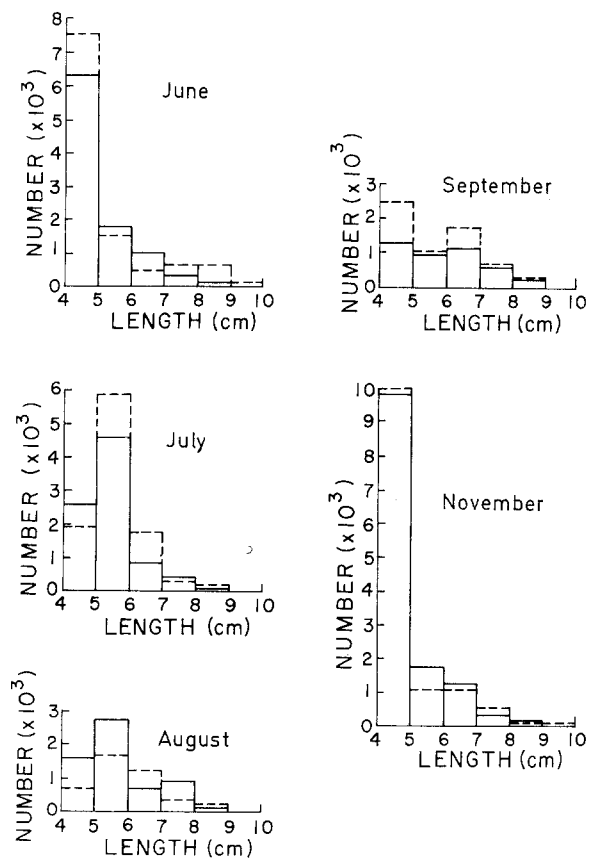


Fig. 2. *Fundulus heteroclitus*. No. estimated by capture-recapture procedure. Continuous lines: males; dashed lines: females

suggestion of a decrease as the season progressed, particularly in females (Table 2). The Age 3 individuals suffered the highest mortalities, disappearing after July.

Very similar values were obtained from the linear and exponential models of mean stock biomass (Table 3). All age groups and both sexes showed an early period of high production and reduced production later in the growing season. Over the entire growing season, females contributed more to production than did males (Table 4). The 1-year-old class was the main source of biomass for both sexes (Table 4).

Mann (1965) added an amount due to reproduction to obtain total production. It seems, however, that at least part of the reproductive effort has already been accounted for in the calculations for growth, so that addition of reproductive products would overestimate total production. In any event, the amount of biomass involved in reproduction was small. The total weight of eggs released, calculated on the basis that ovaries develop once each season and that every female captured had reproduced, was 533 g (Table 5). Males spend a smaller fraction of body weight in reproduction than females (Mann, 1965), but even assuming equal expenditures, the total gonadal products would be about 1.5% of

Table 1. *Fundulus heteroclitus*. Age breakdown of mark-recapture estimates for 1971 based on total length. sd: standard deviation. Age 3 fish were not found during September - November

Date	Mean length \pm sd (cm)			Number		
	Age 1	Age 2	Age 3	Age 1	Age 2	Age 3
Males						
16 June	4.5 \pm 1.1	6.3 \pm 1.1	7.8 \pm 1.1	10580	2009	201
14 July	5.0 \pm 1.1	6.6 \pm 1.1	8.4 \pm 1.0	7122	1738	89
20 Aug.	5.5 \pm 1.1	7.0 \pm 1.0	9.0 \pm 1.1	5246	1382	67
25 Sept.	5.8 \pm 1.1	7.6 \pm 1.1		2945	695	
10 Nov.	6.3 \pm 1.1	7.8 \pm 1.1		2548	462	
Females						
16 June	4.8 \pm 1.1	6.8 \pm 1.1	8.8 \pm 1.0	10073	1938	379
14 July	5.3 \pm 1.1	7.2 \pm 1.1	9.2 \pm 1.1	8363	1568	114
20 Aug.	5.9 \pm 1.2	7.7 \pm 1.1	9.6 \pm 1.1	3746	1257	86
25 Sept.	6.2 \pm 1.1	8.2 \pm 1.1		2682	1036	
10 Nov.	6.6 \pm 1.1	8.5 \pm 1.1		2061	792	

Table 4. *Fundulus heteroclitus*. Seasonal production (g/m^2) for killifish of different ages and sexes. Production estimates are based on linear model described in text

Age	Males	Females	Total
1	2.64	3.48	6.12
2	1.00	1.66	2.66
3	0.12	0.18	0.30
Total	3.8	5.3	9.1

Table 5. *Fundulus heteroclitus*. Weight of gonads and eggs for various-sized females. Numbers in parentheses are numbers of fish involved

Total length (cm)	Weight of gonads (mg)		Weight of released eggs (mg)	Weight of eggs released by population (g) ^b
	Mature gonads (17 May 1972)	Spent gonads (20 Oct. 1972)		
3-4	18.7± 4.8 (3)	2.0±0.3 (4)	16.7	0
4-5	47.8± 3.5(10)	- -	42 ^a	105.0
5-6	93.2±10.7(10)	4.5±0.2 (5)	88.7	88.7
6-7	131.8±14.0(10)	7.5±0.5 (5)	124.4	211.5
7-8	140.2±10.1 (9)	11.1±1.1 (5)	129.2	77.5
8-9	218.4±26.5 (8)	16.7±1.5 (5)	201.7	50.4
9-10	409.6±45.6 (5)	26.3±3.7 (5)	383.3	0
10-11	457.1±39.8 (5)	36.7±5.6 (4)	420.4	0
			Total	533.1

^aObtained by interpolation.

^bFor population of females present in September.

total production, or 0.13 g/m^2 out of a total production of 9.1 g/m^2 (Table 4).

The temperature of tidal water varies seasonally and with the direction of the tidal flow (Fig. 3). As a best estimate we took the average temperature during the course of a tidal cycle when the fish were being sampled, and used this average calculation of respiratory rates. Most of the energy involved in growth and metabolism was processed by younger fish, with females more active than males (Table 6). Resting metabolism was less than half the energy spent in growth and reproduction. If active metabolism is taken to be twice resting (Winberg, 1956), there were about equal investments in growth and metabolism.

Discussion

The dry weight biomass of *Fundulus heteroclitus* in Great Sippewissett marsh (Table 7) was similar to that in a Rhode Island marsh (Nixon and Oviatt, 1973) and to fish biomass in some rivers and lakes (Mann, 1965).

The production by *Fundulus heteroclitus* for the entire growing season (Table 4) was $91 \text{ kg dry weight/ha}$ not including the 0 class. To get an estimate of total production we considered the 0 age-class production to equal the biomass of fish in the year-one class at the beginning of the sampling period in the spring. This is a recruitment measure, and underestimates production by an amount de-

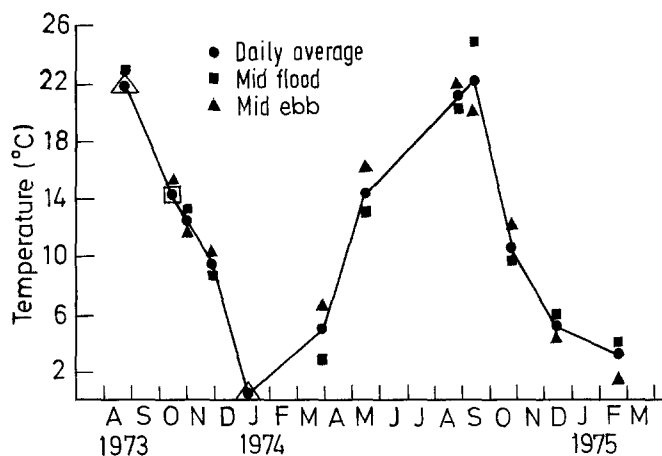


Fig. 3. Temperature of tidal water entering and leaving Great Sippewissett marsh. (Data partly obtained by E.C. Carpenter and associates)

Table 6. *Fundulus heteroclitus*. Calculated values (kcal/m^2) for resting metabolism, growth, and food consumption for growing season

Age	Total resting metabolism	Reproduction and growth	Consumption
Males			
1	5.3	11.3	27.5
2	2.1	4.3	10.7
3	<u>0.1</u>	<u>0.5</u>	<u>0.9</u>
Total	7.5	16.1	39.1
Females			
1	6.0	16.0	35.0
2	2.9	7.7	16.8
3	<u>0.2</u>	<u>0.8</u>	<u>1.6</u>
Total	9.1	24.5	53.4
Total both sexes	16.6	40.6	92.5

Table 7. *Fundulus heteroclitus*. Summary of biomass, production and consumption of population for each month

Date	Biomass (g/m^2)	Production during time interval (g/m^2)	Consumption during time interval (kcal/m^2)	Ecological efficiency
16 June	12.8	3.8	32.3	11.8
14 July	59.6	2.8	29.1	9.6
20 Aug.	10.8	1.6	18.5	8.6
25 Sept.	8.3	1.0	12.8	7.8
10 Nov.	7.8	—	—	—
	sum	9.2	92.7	
	Recruitment of 0 age class	<u>6.9</u>	<u>23.0^a</u>	
	Annual total	16.1	115.7	

^aOn basis of respiration at 4°C for 8 winter months and no mortality.

pendent on the intensity of predation on these youngest fish. Predation is certainly small over the winter, since the estimate of their numbers at the beginning of the sampling year is nearly identical to that of the subsequent 0 class in the following fall. From Table 3 we calculate a production of the 0 class to be at least 70 kg/ha, which gives a total *F. heteroclitus* production of 160 kg dry weight/ha (ca. 640 kg wet weight/ha or 64 kcal/m^2). This value is comparable to production by an assemblage of species in the River Thames in England and trout in the Horokiwi Stream in New Zealand, the most productive, relatively

unfertilized systems studied (Mann, 1965). Small, intensively managed ponds have higher production. Our calculation does not include the contributions of other fish species that were also abundant in the tidal creeks (*Menidia menidia*, *Anguilla rostrata*, *Gasterosteus aculeatus*, *Brevoortia tyrannus* and *Cyprinodon variegatus*).

Populations of salt-marsh killifish are very dense relative to most other fish, similar to bleak or roach in the River Thames (Mann, 1965). In the marsh, the ratio of production to winter standing crop is over 2 (Table 7), in contrast to the 0.65 for the Thames or the 0.5 given by Huet (1964) as a typical

freshwater value. This semiannual turnover in a fish with at least a 3-year life span indicates intense predation upon *Fundulus heteroclitus*. This is consistent with our knowledge of the large number of species of fish and birds that feed on small marsh fish.

The amount of energy consumed by the killifish is greatest during the early growing season and decreases thereafter (Table 7). The total annual consumption was at least 120 kcal/m² (this value includes a very conservative estimate for 0 class fish based on respiration at 4°C from November to June and ignoring metabolism from hatching until November). Birkett (1970) obtained a similar value for marine fish on Dogger Bank. Mann (1965) calculated that the 5 species in the Thames consumed 704.5 kcal/m².

Supposing that the entire fish production is vulnerable to predation by striped bass, bluefish, herons, egrets, terns and gulls, we can calculate the ecological efficiency from the production and consumption values of Table 7. The efficiencies are in the expected range (5 to 15%), and fall as the growing season progresses.

We have an as yet unpublished series of samples of invertebrates from the tidal creeks and the marsh surface. The biomass densities in these samples show strong seasonal trends, but range between 50 and 1000 mg dry weight/m². These could provide about 3 to 52 kcal/m² if all invertebrates were acceptable food items. We know this is not the case from gut analysis and prey-preference experiments. During spring and early summer (Table 7), prey consumption was about 1.2 kcal/m² day. Towards fall, only about 0.3 kcal/m² day were used. The prey standing crops would then last about 2.5 to 43 days during the spring, and 10 to 173 days during the fall. In subsequent papers, we will work out this relationship in more detail incorporating production by prey and prey-selective behavior by the fish, but the present estimates of duration of food supply available to predators agree well with that calculated from data on food consumption in the laboratory (Prinslow et al., 1974). We also have data showing that *Fundulus heteroclitus* feed mainly in the marsh surface, corroborating the results of Butner and Brattstrom (1960). Killifish have the potential to influence the abundance of prey species in a salt marsh. We have experimental data (Vince et al., 1976) demonstrating that the prey-selection behavior, mediated by the physical characteristics of salt-marsh habitats, determines the abundance

and spatial distribution of salt-marsh invertebrates.

Killifish are obviously a key species in the functioning of the salt-marsh ecosystem. Their very high populations and production rates as well as their selective feeding behavior are critical in determining qualitative and quantitative aspects of the distribution of their prey. Their movements on and off the marsh surface must be an important aspect in the export of organic materials from the marsh surface.

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