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The Importance of an Infrequently Flooded Intertidal Marsh Surface as an Energy Source for the Mummichog *Fundulus heteroclitus:* An Experimental Approach

S. B. Weisberg * and V. A. Lotrich

School of Life and Health Sciences, University of Delaware; Newark, Delaware 19711, USA

Abstract

Fundulus heteroclitus is known to ascend onto the marsh surface to feed. Our study investigated whether the marsh surface food items are a necessary source of caloric intake for the Canary Creek, Delaware, USA population of this species. Enclosure techniques were used to restrict mummichogs from the marsh surface and the growth rates of these fish were compared to those having access to the marsh surface. Growth rates were significantly higher for mummichogs allowed access to the marsh surface. Food addition and density reduction experiments showed that food availability per fish, rather than behavioral responses due to fish crowding, was responsible for the increased growth. Although food was available in the subtidal portion of the habitat, it was of insufficient quantity for fish at natural density to grow at a normal rate, and mummichogs must utilize the marsh surface for at least a portion of their energy intake.

Introduction

Many fish feed at times of the day when prey are most abundant or most vulnerable (Helfman, 1978). The mummichog *Fundulus heteroclitus,* an abundant resident fish in Atlantic tidal marshes, feeds primarily during daytime high tides (Butner and Brattstrom, 1960; Weisberg *et al.,* 1981), when the marsh is flooded and it has access to prey on the intertidal marsh surface. *F. heteroclitus* ingests a variety of marsh invertebrates (Schmelz, 1964; Kneib and Stiven, 1978), and influences prey distribution and abundance by its consumption (Vince *et al.,* 1976; Kneib, 1980). Because *F. heteroclitus* feeds at high tide on intertidal organisms, Valiela *et al.* (1977) have suggested that mummichogs are an important energy link between the marsh surface and subtidal food webs. Although the impact of its feeding rhythm on prey organisms has been considered, any advantage gained by *F. heteroclitus* in employing a high tide feeding strategy remains uninvestigated.

Mummichogs have three potential sources of available food: (1) the water column organisms, (2) the subtidal benthos, and (3) the intertidal benthos, all of which are utilized to some degree by *Fundulus heteroclitus* in Canary Creek Marsh, Delaware (Schmelz, 1964). The first two sources are constantly available, though the composition of the plankton and nekton changes with the stage of tide. In contrast, the marsh surface is sufficiently flooded to allow access by fish to the intertidal benthos only during tides which exceed mean high water. In Canary Creek, the marsh surface may remain unavailable for periods of up to a week during the neap tide period, during which time the other two food sources must be utilized. Subtidal food sources may be sufficient for normal fish growth. Alternatively, they may provide a subsistence, or less than subsistence, diet during neap periods. In this study we experimentally restricted fish from the marsh surface, and compared their growth with fish allowed normal access to the marsh surface, to determine if food items found on the marsh surface are necessary for normal mummichog growth at the population density found in Canary Creek Marsh, or if subtidal food sources are of sufficient quantity and quality to render marsh surface foods an unnecessary supplement in a food-rich environment.

Materials and Methods

The study site was in Canary Creek Marsh, Lewes, Delaware, USA, a 190 ha *Spartina alterniflora* marsh with a mean tidal range of 1.3 m. Salinity normally ranges between 10–28 ppt at low and high tide, respectively. Meredith and Lotrich (1979) give a further description of the site.

* Present address: Environmental Center, Martin Marietta Corp.; 1450 South Rolling Road, Baltimore, Maryland 21227, USA

Caging techniques were used to manipulate density, food supply, and area to which fish were allowed access. Pens of two different sizes were constructed. One kind, called the restricted type, enclosed an area of 23.6 m^2 (7.6 m × 3.1 m) entirely within the subtidal channel, denying fish access to the marsh surface. The other kind of pen, called the unrestricted type, measured 7.6 m × 19.7 m and contained a subtidal channel area of 23.6 m^2 (7.6 m × 3.1 m) and an intertidal marsh surface area of 126.1 m^2 (7.6 m × 16.6 m).

Pens were constructed of galvanized hardware cloth (7 mm mesh). This size mesh prevented fish escape and altered flow rate through the pens by less than 10%. The mesh was periodically cleaned with a brush to prevent clogging and attachment of fouling organisms. On the marsh surface 0.61 m fencing was secured to 51 mm × 76 mm × 1.2 m wooden stakes placed every 1.4 m. Fencing was buried below ground prior to its being nailed to the stakes. A similar procedure was followed at low tide in the subtidal portion of the habitat, except these stakes were 2.4 m long and wider hardware cloth was used so that the subtidal portion of the cage was the same height as the fence on the intertidal marsh surface. To prevent scour-induced fish escape, a 0.6 m-wide apron, consisting of 7 mm mesh nylon netting with a lead line, was sewn near the bottom of the subtidal fencing. To prevent predation by birds, 51 mm mesh netting was draped over the enclosed subtidal area where the fish could be particularly vulnerable at low tide.

Following construction, fish enclosed in each pen were removed using minnow traps (Nylon Net Co. No. G-40) over a period of several days. At that time twenty fish, marked with acrylic paint using the technique of Lotrich and Meredith (1974), were placed in each pen. The fraction of marked individuals in further recaptures over the next several days was used to assess when the remaining number of unmarked fish had declined to less than ten individuals. This period also served to test for ability of each pen to retain marked fish and exclude unmarked fish.

On 2 July 1979, two restricted and two unrestricted type pens were each stocked with 180 *Fundulus heteroclitus*, which is the normal density for a 23.6 m^2 section of tidal creek (Meredith and Lotrich, 1979). Fish used in stocking the pens were seined from a nearby area in the creek and represent the natural size distribution of fishes present in the creek. Sixty of these 180 fish were individually measured for total length (TL), weighed, and marked with acrylic paint. Marked fish were selected in equal sex ratio and ranged in size between 50–100 mm (TL). After a 9-wk experimental period, the marked fish were recaptured, measured, and weighed to determine growth per individual. No attempt was made to recapture all marked fish.

During 1980 three pens of the restricted type and two pens of the unrestricted type were constructed. One pen of each type was stocked on 10 June 1980 with 180 fish in a repetition of the 1979 experiment. Since differences in growth rate between fish in the two pen types were evident in 1979, one pen of each type was stocked with 1/8 the normal density (23 fish, all of which were individually marked) on 19 June 1980 to determine if the observed effect of access to the marsh surface was density dependent. To determine if growth differences were related to marsh surface access or to food supply, one restricted pen was stocked on 11 June 1980 with 180 fish and given a supplemental ration of food. Every 2 to 3 d, three 0.5 kg pieces (an *ad libitum* portion) of bluefish (*Pomatomus saltatrix*) were each tied to a nylon line and added to this pen. Experimental conditions were maintained for 1 month during 1980, after which marked fish were recaptured, measured, and weighed.

All weights were wet weight taken by placing fish on a weighing chamber consisting of two sponges glued together. The top sponge had the center removed, forming a pocket for the fish. The sponge chamber and fish were weighed to the nearest 0.1 g. Fish were removed and the sponge reweighed. Fish weight was calculated as the difference between the two measures. The mean difference between replicate weighings using this method was 0.022 ± 0.017 (95% C.I.) g. Individual growth rates were calculated from weight as percentage of body weight per day using the following formula: $G = [(W_F - W_I)/W_I/t]$ where W_I and W_F are the initial and final weight, respectively; and t is the time period between weighings. All statistical comparisons of mean growth rates between pens were made using arcsin transformation of the individual growth rates.

Results

No significant differences were found comparing the mean growth rates between the three unrestricted pens where fish were kept at normal density (Table 1) (ANOVA, $P > 0.05$). There were also no differences in growth rate between replicates where fish were kept at normal density in restricted pens (ANOVA, $P > 0.05$). Thus, data from each set of replicate pens were pooled for all comparisons between treatments.

Growth rate of fish in the restricted and unrestricted type pens were significantly different (Student's *t*-test, $P < 0.001$). Fish held in pens that allowed access to the marsh surface gained weight at a rate not significantly dif-

Table 1. Weight gain (as percent of body weight d^{-1}) for fish at normal density when access is allowed to or restricted from the marsh surface. Each value represents one replicate pen. Number of fish measured from each pen is in parentheses. + = 1979; * = 1980

	$\bar{X} \pm 95\%$ C.I.
Restricted	−0.072 ± 0.067 (21)*
	−0.090 ± 0.091 (25)+
	−0.037 ± 0.084 (21)+
Unrestricted	0.374 ± 0.178 (17)*
	0.307 ± 0.050 (40)+
	0.346 ± 0.172 (9)+

Table 2. Weight gain (as percent of body weight d^{-1}) of fish when kept below normal density or when food was added. Number of fish measured is in parentheses

	$\bar{X} \pm 95\%$ C.I.
1/8 Normal density Restricted pen	0.974±0.170 (17)
1/8 Normal density Unrestricted pen	1.028±0.187 (14)
Normal density Restricted pen Food added	1.153±0.128 (19)

ferent from the rate (Student's *t*-test, $P > 0.05$) for mummichogs from the uncaged natural population (Meredith and Lotrich, 1979). When mummichogs at normal density were restricted from the marsh surface, they had a growth rate not significantly different from zero (Student's *t*-test, $P > 0.05$). When fish restricted to the subtidal channel were examined in 10 mm size classes, no size group was observed to grow.

At the 1/8 normal density, mummichogs in the restricted type pen showed no difference in growth from fish at the same density in the unrestricted type pen (Table 2) (Student's *t*-test, $P > 0.05$). Growth rates at the lower density were more than three times the growth rate of fish held in the unrestricted pen at normal density.

When fed the supplemental ration, fish at the normal density in the restricted type pen grew at a greater rate than unfed fish enclosed at the normal density in an unrestricted type pen (Tables 1 and 2). Fish fed the supplemental ration at normal density grew no faster (Student's *t*-test, $P > 0.05$) than fish that were maintained in either pen type at the lower density without added food.

Discussion

The growth rate we report for *Fundulus heteroclitus* kept at normal density in an unrestricted type pen ($\bar{X} = 0.342$) is not significantly different (Student's *t*-test, $P > 0.05$), from the growth rate calculated using the data of Meredith and Lotrich (1979) ($\bar{X} = 0.331$) for fish of similar size from the natural Canary Creek population. Thus, *F. heteroclitus* is a good organism with which to conduct enclosure experiments because mummichogs normally maintain a limited home range (Lotrich, 1975) and changes in their growth due to caging appear to be insignificant.

When *Fundulus heteroclitus* is allowed access to the marsh surface it grows at a faster rate than when it is restricted to the subtidal portion of the habitat. Since the growth rate of restricted fish increased substantially when fed a supplemental ration, and was even higher than the growth rate of unfed unrestricted fish, availability of food, and not behavioral responses due to release from crowding, must be responsible for increased growth when mummichogs are allowed marsh surface access. Improvement in growth rate with access to the marsh surface was independent of fish size in the range examined, despite the fact that some of the marsh surface invertebrates are uningestible by smaller size mummichogs (Vince *et al.*, 1976).

While it is apparent that the intertidal marsh surface contains food resources necessary for the natural mummichog population, the value of the subtidal food resources should not be overlooked. Food of acceptable quality is certainly available in the subtidal portion of the habitat since fish restricted to the Creek at the 1/8 normal density grew at the same rate as unrestricted mummichogs at 1/8 x density and grew faster than mummichogs in the laboratory fed *ad libitum* portions once per day of either *Nereis* sp. or *Palaemonetes* sp. (Weisberg and Lotrich, in press). Food of considerable quantity must be consumed from subtidal areas since fish restricted to the subtidal habitat at normal density did not lose weight at the rate reported by either Prinslow *et al.* (1974) or Weisberg (unpublished data) for mummichogs starved under laboratory conditions. Mummichogs starved at 20 °C in the laboratory lose weight at the rate of 1.12% of body wt d^{-1} (Weisberg, unpublished data). Fish in the restricted type pens ingested enough energy to avoid this weight loss. Therefore, marking the conservative assumption of no processing costs, the minimum daily energy assimilated by a representative 1 g dry wt fish in a restricted pen is 11.2 mg ($= 1\ g \times 1.12\%$) times 4 769 cal g dwt^{-1} (Weisberg, unpublished data) equal to 53 calories. Fish in the unrestricted type pen grew at a rate of 0.342% of body wt d^{-1}. The minimum daily energy assimilated by these fish is ($11.2\ mg \times 4\ 769$ ca g dwt^{-1}) + [3.42 mg (from $0.342\% \times 1$ g) $\times 4\ 769$ cal g dwt^{-1}] equal to 69 calories. Dividing the minimum energy uptake of restricted fish by the minimum energy uptake of unrestricted fish (53 divided by 69) shows that as much as 75% of the energy uptake of the natural population could possibly be gathered in food taken from the subtidal portion of the habitat. The relatively higher metabolic rates of fish under natural conditions, as compared to laboratory conditions, probably means that the restricted fish are processing more than 1.12% body wt d^{-1} from subtidal resources to meet metabolic demand, and that percentage of total energy potentially procured from the subtidal portion of the habitat could exceed the 75% estimate.

Despite the significant contribution of the subtidal food resource, the Canary Creek population of *Fundulus heteroclitus* at its present population density has exceeded the capacity at which growth is possible using only subtidal food resources. Since the fish in 1/8 x density pen exhibited a higher growth rate than 1x density fish in the unrestricted pen, it is quite probable that a lower density population could be supported if fish were denied access to the marsh surface; however, food taken from the marsh surface is a necessary resource for the Canary Creek mummichogs if the present population size and individual growth rates (Meredith and Lotrich, 1979) are to be maintained.

The Canary Creek population of *Fundulus heteroclitus* has a tidal feeding rhythm (Weisberg *et al.*, 1981). Feeding principally at high tide allows the fish to maximize their intake of marsh surface prey. The energy contained in prey taken on the marsh surface egresses with the fish on ebbing tides to the subtidal portion of the habitat. These fish in turn may be eaten by subtidal predators or scavengers. This method of energy transfer from the highly productive marsh surface is potentially important to the subtidal food web.

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