Estuaries and Coasts (2015) 38:1535–1544
DOI 10.1007/s12237-014-9913-3

NOTE

Size-Selective Foraging of Adult Mummichogs, *Fundulus heteroclitus*, in Intertidal and Subtidal Habitats

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Received: 3 June 2014 / Revised: 27 October 2014 / Accepted: 29 October 2014 / Published online: 11 November 2014

Abstract Intertidal marshes provide an important foraging habitat for resident marsh fishes. However, few studies have considered whether the importance of intertidal foraging is uniform across the adult-size range of marsh fishes or whether size-selective foraging, which has been demonstrated in intertidal habitats, also occurs in subtidal habitats. This study compares diet composition of adult mummichogs (*Fundulus heteroclitus*) in Hoffler Creek, VA, USA, foraging in intertidal salt marshes with the diet of individuals foraging in the subtidal creek and considers the effect of fish size on gut fullness and consumption of major intertidal and subtidal diet items. Gut fullness was significantly greater in the intertidal salt marsh for small mummichogs (40–60 mm total length), and small mummichogs were significantly more likely than larger individuals to consume several major intertidal diet items, including copepods and ostracods. However, gut fullness was greater in the subtidal creek for large mummichogs (70–90 mm total length (TL)) due to consumption of grass shrimp (*Palaemonetes* spp.). This diet item was rarely consumed by large mummichogs in the marsh or by smaller mummichogs in either habitat. Modifications to the marsh landscape that affect prey resources for fishes may, therefore, have differing impacts across adult size classes. Although subtidal habitats are not frequently considered important for foraging of marsh fishes, access to shallow, subtidal water may allow larger adults to take advantage of additional prey resources, such as shrimp.

Communicated by Richard W. Osman

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Keywords Mummichog · *Fundulus heteroclitus* · Salt marsh · Tidal creek · Diet

Introduction

High primary production in salt marshes supports large numbers of invertebrates that consume a combination of marsh grass detritus, microheterotrophic decomposers, microbenthic and epiphytic algae, and phytoplankton (Kreeger and Newell 2000). This dense availability of invertebrates creates a fertile feeding ground for small fishes (Kneib 1997; Deegan et al. 2000), and stable isotope analyses have demonstrated the importance of both *Spartina* spp. detritus and algal resources to production of resident marsh fishes (Kneib et al. 1980; Peterson and Howarth 1987; Currin et al. 1995; Wainright et al. 2000; McMahon et al. 2005). The importance of intertidal foraging is also supported by numerous studies showing that marsh fishes have fuller guts when captured on the ebbing tide as they leave intertidal habitats than when they enter these habitats on the flooding tide. This pattern has been observed for fishes entering and leaving vegetated marshes (Rozas and LaSalle 1990; Fell et al. 1998), intertidal marsh creeks (Kleypas and Dean 1983; Rountree and Able 1992; Laffaille et al. 2001; Hampel and Cattrijsse 2004), and intertidal marsh ditches (Allen et al. 1994). In addition, mummichogs (*Fundulus heteroclitus*) with access to the flooded salt marsh surface grow significantly faster than individuals restricted to subtidal habitats (Weisberg and Lotrich 1982; Javonillo et al. 1997), a pattern that has also been suggested by bioenergetics modeling for California killifish (*F. parvipinnis*; Madon et al. 2001).

In addition to differences in the quantity of food consumed in intertidal and subtidal habitats, comparisons of the diet of resident fishes caught on flooding and ebbing tides have demonstrated differences in some food categories (Rozas and LaSalle 1990; Allen et al. 1994; Fell et al. 1998). However, these studies did not consider the length of time fishes had access to intertidal habitats in order to ensure that food items were accurately assigned to the zone in which they were consumed. A better understanding of the diet composition of resident fishes across the intertidal-subtidal marsh gradient is important considering that changes in fish diet have been used to evaluate impacts of invasive species (Fell et al. 1998; Laffaille et al. 2005), pollution (Goto and Wallace 2011; Schein et al. 2013), and restoration activities (Moy and Levin 1991; Allen et al. 1994; James-Pirri et al. 2001) on the marsh fish community. Such factors may differentially affect intertidal and subtidal habitats, and analysis of changes in fish diet in both zones may be needed to fully evaluate their ecological impacts. In addition, despite evidence that fish size impacts prey selection by resident marsh fishes both in the laboratory (Vince et al. 1976; Smith and Weis 1997) and in the field (Kneib and Stiven 1978; Allen et al. 1994; Smith et al. 2000; Goto and Wallace 2011), a comparison of the impact of fish size on subtidal and intertidal diets is lacking.

The objectives of this study were to compare the diet composition of adult mummichogs foraging in intertidal and subtidal habitats and to examine the influence of fish size on intertidal and subtidal diets. Mummichogs are frequently the numerically dominant fish species in salt marshes along the east coast of the USA, and in most systems, adult mummichogs move into intertidal areas with the flooding tide while moving into adjacent subtidal habitats with the ebbing tide (Kneib 1986; Teo and Able 2003). By feeding in intertidal habitats and then serving as important prey for a diversity of estuarine predators in subtidal habitats, mummichogs' tidal movement may transfer intertidal energy to subtidal food webs (Valiela et al. 1977; Kneib 1986, 1997). Although the importance of mummichogs to estuarine food webs has been recognized for over three decades and much is known about the general diet of these fishes in marsh habitats (Kneib and Stiven 1978; Kneib 1986; Allen et al. 1994; Fell et al. 1998; James-Pirri et al. 2001), previous studies have not comprehensively compared the diet of mummichogs known to be foraging in intertidal marshes with those foraging in subtidal creeks or evaluated the impact of fish size on subtidal and intertidal diets separately.

Study Site

Mummichogs were collected from subtidal and intertidal habitats at two sites along Hoffler Creek, a tributary of the James River in Portsmouth, VA, USA, located approximately 11 km from the mouth of the river at the Chesapeake Bay (Fig. 1). Hoffler Creek is brackish (12–28 ppt salinity) with a mean tidal range of 0.84 m. At site A, the subtidal creek was 45 m across with 61 m of adjacent intertidal habitat, and at site B, the subtidal creek was 33 m across with 29 m of adjacent intertidal habitat (Fig. 1). At both sites, the intertidal habitat closest to the subtidal creek was vegetated with a thick bank of *Spartina alterniflora*, with the exception of several narrow intertidal channels. The interior intertidal habitat included large areas of vegetated marsh composed predominantly of *S. alterniflora* as well as small areas of unvegetated mud flats. Mummichogs are abundant in intertidal habitats along Hoffler Creek when water is present, but adult mummichogs retreat into the subtidal creek at low tide.

Methods

Development of Sampling Protocol

The sampling protocol for diet analysis was designed to ensure that diet items were accurately assigned to the habitat in which they were consumed. Prior to fish collection for diet analysis, I determined the minimum water depth at which adult mummichogs moved into intertidal habitats or retreated to subtidal habitats. On the flooding tide, sampling was conducted in unvegetated, intertidal channels leading to the vegetated marsh to determine when fish moved into the marsh. A seine net (6.4-mm mesh, 6 to 8 m long adjusted to be approximately 1 m wider than channel width) was hauled from the upland edge of the channel to a block net (6.4-mm mesh) at the subtidal creek bank. At the same time, a seine net haul (6.4-mm mesh, 7.6 m long) was conducted in the subtidal creek at the mouth of the intertidal channel to determine whether mummichogs were still located in the subtidal creek as intertidal habitat became available. Intertidal water depth during sampling was measured in the middle of the intertidal channel 3 m upland from the subtidal creek bank. Seine net hauls were repeated at 1-cm water depth intervals (Table 1) with sampling conducted in multiple channels over 6 days so that seine net hauls in a single channel were at least 30 min apart (with the block netting removed during this time) to avoid deterring mummichogs from moving into the intertidal channel at typical water depths. Sampling in the intertidal channel was conducted on the ebbing tide following the same procedure to determine the water depth at which mummichogs were no longer present in the intertidal zone.

Data from this preliminary sampling were used to determine when mummichogs collected in subtidal or intertidal habitats would have been in that habitat for a minimum of 3.5 h prior to collection. Mummichogs do not have a true stomach, so diet items from sections I and II of the gut (the anterior portion up to the second bend of the digestive tract; Babkin and Bowie 1928) were included in the study (see below). Evacuation of ingested food items into section III of the gut takes 2 to 3.5 h at 20 °C (Weisberg et al. 1981). Given that gut evacuation rates increase with increasing temperature

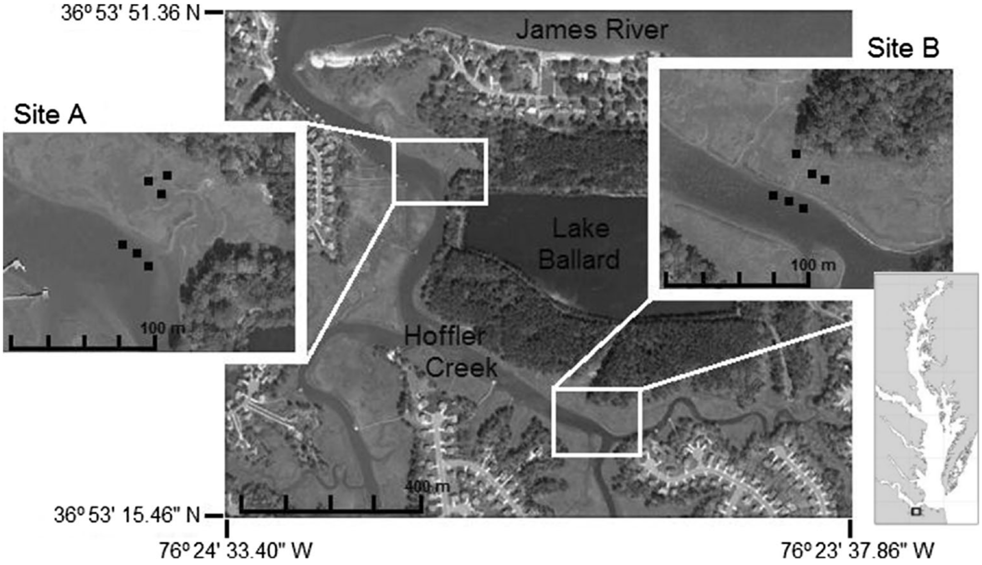

Fig. 1 Study area along Hoffler Creek, Portsmouth, VA, USA. *Black squares* on inset maps of site A and site B indicate locations of minnow traps used to capture mummichogs in subtidal and intertidal habitats, with *each square* representing two traps

(Jobling 1981) and water temperatures were greater than 20 °C in Hoffler Creek on all sampling dates, passage of food items into section III of the gut should have occurred more rapidly than 3.5 h. In the Hoffler Creek system, mummichogs ≥40 mm total length (TL) moved into the intertidal habitat along the advancing flooding tide at a minimum water depth of 5 cm, and few mummichogs were collected in the subtidal creek once intertidal habitat with a minimum water depth of 12 cm was available (Table 1). Extensive vegetated marsh was flooded to a depth of 12 cm (recorded at locations of fish collection for diet analysis) no later than 3 h before slack high tide at both sites on all sampling dates. Fish were collected from the intertidal marsh for diet analysis (see below) beginning 0.5 h after slack high tide. These fish would have had access to and likely occupied the intertidal habitat for a minimum of 3.5 h, assuming that the fish did not move repeatedly between intertidal and subtidal habitats during this time. I believe this is a reasonable assumption given the decreasing number of mummichogs found in subtidal seine net hauls during the flooding tide in this study (Table 1) as well as the rarity of mummichogs in seine net hauls conducted in subtidal habitats at high tide in this system (J.S. Thompson, unpublished data). In addition, collection of fish for diet analysis in the marsh was conducted at least 20 m from the subtidal creek bank, so it would be unlikely that fish that had just moved from the subtidal habitat would be collected.

Table 1 Number of mummichogs (≥40 mm TL) collected in seine net hauls on the flooding and ebbing tides in Hoffler Creek, Portsmouth, VA, USA. Seine net hauls in the intertidal zone were conducted in channels leading to vegetated marsh. On the flooding tide, seine net hauls were also conducted in the subtidal zone at the mouth of intertidal channels. Water depth refers to the depth of the water during seine deployment in the middle of the channel 3 m upland from the bank of the subtidal creek

Water depth (cm)	Flooding tide		Ebbing tide
	Intertidal zone	Subtidal zone	Intertidal zone
1	0	15	0
2	0	13	0
3	0	21	0
4	0	9	1
5	2	18	3
6	1	12	4
7	8	12	7
8	17	7	14
9	13	4	23
10	20	6	19
11	16	4	10
12	8	0	15
13	9	2	7
14	5	0	8
15	3	1	4

On the ebbing tide, no mummichogs were collected in the seine net in the intertidal zone once the water depth dropped to 3 cm (Table 1), which occurred no later than 1.75 h prior to slack low tide at both sites on all sampling dates (water depth recorded at the location of depth measurements during previous seine net sampling, described above). In the subtidal creek, fish were collected for diet analysis beginning 1.75 h after slack low tide to capture mummichogs that had been forced into subtidal habitat by the ebbing tide for a minimum of 3.5 h but before fish began to move back into the intertidal zone.

Diet Analysis

Mummichogs ≥40 mm TL were collected for diet analysis in unbaited, cylindrical minnow traps (22.9 cm diameter, 44.5 cm long, 6.4-mm mesh) in May through August 2008. Intertidal collections were made on a single day each month, with traps set in vegetated marsh areas at sites A and B simultaneously. Subtidal collections were made on a single day no more than 1 week after intertidal sampling, with traps set at the minimum water depth required to cover the trap in order to target high densities of mummichogs observed in shallow water along the bank of the creek. On each sampling date, six minnow traps were set in the appropriate habitat at both site A and site B. All traps were initially set between 1300 and 1330; given that mummichogs are diurnal foragers (Weisberg et al. 1981), capturing fish during daylight hours should ensure that they had been actively feeding in the preceding hours. Fish were removed from the traps every 15 min. After removing the fish, each trap was then repeatedly reset in the same habitat either until 1600 or until a total of 60 fish were collected for that sampling date. Captured fish were immediately anesthetized in a lethal dose of MS-222 to prevent regurgitation of stomach contents. Each fish's total length was recorded, and it was preserved in 10 % buffered formalin.

In the lab, each preserved fish was blotted, weighed (±0.01 g), and its digestive tract removed. Diet items from sections I and II of the gut (hereafter referred to as "gut contents") were weighed, and a gut fullness index (GFI) was calculated for each fish as (gut contents weight/body weight) × 100. This approach allowed gut fullness to be compared between fish of different sizes (Hyslop 1980). All diet items were identified under a dissecting microscope. Because comparisons between groups of fish (by habitat and length) were desired, diet items were not identified to species but rather to general categories that allowed fish to be classified by dominant prey types. Most of these prey categories were groupings of small arthropods (e.g., insects, copepods, ostracods; Tables 2 and 3). Recognizable *Spartina* detritus was also common in mummichog guts, but this detritus was always found in association with attached algae (predominantly diatoms as well as living and dead filamentous algae) so this diet item was classified as detrital-algal complex. The percentage of the total volume of the gut contents made up by each prey category was estimated by spreading the gut contents evenly across a graduated slide (Hyslop 1980). Only prey categories making up at least 10 % of gut content volume were assigned to the individual fish; this cutoff was used in order to exclude items that were consumed incidentally during feeding on other resources or items consumed in very small quantities that are, therefore, unlikely to be of great nutritional importance (Bowen 1996).

Frequency of occurrence of each prey category in each habitat was then calculated as the proportion of fish consuming that prey type out of all fish collected from that habitat (Hyslop 1980; Bowen 1996). Frequency of occurrence was calculated for all fish collected over the summer as well as separately for each month of the study to examine the consistency with which diet items were included in the diet across the growing season. I chose to describe the diet using frequency of occurrence, rather than measures based on counting the number of prey items, because detrital-algal complex was a common component of the diet and could not be counted in discrete units and because small invertebrates (particularly insects and ostracods) were disarticulated, making counting individual specimens difficult. Frequency of occurrence can overestimate the importance of small diet items that are commonly ingested (Bowen 1996). This issue was addressed, in part, by only considering diet items that composed at least 10 % of gut volume for an individual fish (as noted above). In addition, frequency of occurrence was recalculated for each prey category based on the proportion of fish for which a diet item accounted for ≥50 % of gut volume, in order to give an indication of the frequency with which a prey category composed the majority of the diet, by volume, for individual fish. Hereafter, FO_{10} is used to denote frequency of occurrence for a prey category based on the number of fish for which that diet item composed ≥10 % of gut volume, and FO_{50} is used to denote frequency of occurrence for a prey category based on the number of fish for which that diet item composing ≥50 % of gut volume.

Statistical Analysis

Analysis of variance (ANOVA) and generalized linear models (GLM) described below were initially tested with a term indicating whether fish were collected from site A or site B. This term was not significant in any model, so data from both sites were pooled for all analyses.

Gut fullness indices were arcsine-square root transformed to achieve normality (tested with the Kolmogorov-Smirnov test). Two-way ANOVA was used to test for the effect of fish size on GFI for all fish collected from the intertidal zone, controlling for the effect of month. The effect of fish size on GFI for all fish collected from the subtidal zone was tested similarly in a separate two-way ANOVA. *t* tests (experimentwise alpha of 0.05 using the Bonferroni adjustment) were used to test for differences in mean GFI between fish collected in intertidal versus subtidal habitats in each length category (40–49, 50–59, 60–69, 70–79, and 80–89 mm TL). *F* tests (alpha=0.05) were used to test for equal variance between intertidal and subtidal groups within each length category, and heteroscedastic *t* tests were used in cases where variances were not equal (Quinn and Keough 2002).

Frequency of occurrence was analyzed for major diet components, defined as those prey categories for which FO_{10} was greater than 0.1 in at least one habitat type when considering all fish collected over the summer. For each major diet component, FO_{10} for intertidal and subtidal fish were compared in each month of the study, as well as for data pooled over the entire summer, using chi-square tests with an experimentwise

Table 2 Percentage of mummichogs ($FO_{10} \times 100$) collected from subtidal and intertidal habitats along Hoffler Creek, Portmouth, VA, USA, for which selected diet items composed ≥10 % of gut volume, number of fish guts examined (*n*), and mean gut fullness index (GFI±SE)

	May		June		July		August		Total	
	Subtidal *n*=67	Intertidal *n*=61	Subtidal *n*=63	Intertidal *n*=63	Subtidal *n*=62	Intertidal *n*=68	Subtidal *n*=62	Intertidal *n*=62	Subtidal *n*=254	Intertidal *n*=254
GFI	5.0±0.3	4.7±0.3	*3.4*±0.4	*4.4*±0.3	*4.1*±0.6	*4.8*±0.2	*3.9*±0.2	*4.5*±0.1	*4.2*±0.1	*4.6*±0.1
Major diet components										
Detritus-algae	35.8	50.8	47.6	46.0	67.7	64.7	58.1	48.4	54.7	54.3
Insects	*0*	*36.1*	*0*	*38.1*	*6.5*	*27.9*	*3.2*	*56.5*	*2.8*	*40.0*
Shrimp	*91.0*	*9.8*	*60.3*	*1.6*	*38.7*	*1.5*	*38.7*	*3.2*	*52.4*	*3.1*
Crabs	*0*	*13.1*	7.9	7.9	1.6	8.8	4.8	14.5	*3.5*	*10.6*
Copepods	*0*	*23.0*	*0*	*30.2*	6.5	4.4	6.5	12.9	*4.3*	*15.4*
Ostracods	0	9.8	*0*	*52.4*	9.7	23.5	*0*	*19.4*	*2.4*	*27.6*
Minor diet components										
Amphipods	0	9.8	0	6.3	0	13.2	1.6	9.7	0.8	9.8
Spiders	3.0	3.3	0	0	0	1.5	0	1.6	0.4	1.6
Snails	0	0	0	0	8.1	11.8	0	0	2.0	4.3
Polychaetes	3.0	3.3	0	11.1	1.6	5.9	1.6	12.9	1.2	9.1
Nematodes	0	6.6	0	1.6	6.5	2.9	1.6	1.6	2.4	2.8
Foraminifera	0	6.6	0	30.2	0	0	0	6.5	0	9.8
Fish	0	0	0	0	1.6	1.5	0	1.6	0.4	0.8

Italicized pairs of percentages for a diet item in a given month are significantly different between subtidal and intertidal habitats (2×2 chi-square on count data with experimentwise alpha of 0.05 using the Bonferroni adjustment); statistical analyses were conducted only on major diet components. Italicized pairs of GFI in a given month are significantly different between subtidal and intertidal habitats (*t* tests with experimentwise alpha of 0.05 using the Bonferroni adjustment). Italicized pairs of percentages for diet items or GFI in the total column are significantly different between subtidal and intertidal habitats for all fish pooled over the summer

alpha of 0.05 using the Bonferroni adjustment. Differences in FO_{50} between intertidal and subtidal fish were assessed using the same approach. Statistical tests on GFI, FO_{10}, and FO_{50} were conducted in Sigma Plot 12.0 (Systat Software, San Jose, CA, USA).

The effect of mummichog length on the probability of consumption of major diet items in intertidal and subtidal habitats was assessed with a GLM with a binomial link function that considered the outcome for each individual fish to be a success (consumption of the diet item) or failure (no consumption of the diet item). Factors of length were tested in the model in cases where the relationship between fish length and the proportion of fish consuming a given prey item did not appear to be linear. Model fit was assessed by testing the difference in deviance between the parameterized model and a null model with only the intercept against a chi-square

Table 3 Percentage of mummichogs ($FO_{50} \times 100$) collected from subtidal and intertidal habitats along Hoffler Creek, Portmouth, VA, USA, for which major diet items composed ≥50 % of gut volume and number of fish guts examined (*n*)

	May		June		July		August		Total	
	Subtidal *n*=67	Intertidal *n*=61	Subtidal *n*=63	Intertidal *n*=63	Subtidal *n*=62	Intertidal *n*=68	Subtidal *n*=62	Intertidal *n*=62	Subtidal *n*=254	Intertidal *n*=254
Detritus-algae	9.0	19.7	*42.9*	*17.5*	33.9	23.5	*50.0*	*11.3*	*37.0*	*18.1*
Insects	*0*	*23.0*	*0*	*27.0*	1.6	16.2	*1.6*	*35.5*	*0.8*	*24.8*
Shrimp	*86.6*	*6.6*	*47.6*	*1.6*	*38.7*	*1.5*	*33.9*	*3.2*	*47.6*	*2.8*
Crabs	0	9.8	4.8	6.3	1.6	7.4	0	9.7	*0.8*	*7.9*
Copepods	0	6.6	0	3.2	0	0	1.6	1.6	0.4	2.4
Ostracods	0	3.3	0	7.9	0	11.8	0	0	*0*	*6.7*

Italicized pairs of percentages for a diet item are significantly different between subtidal and intertidal habitats for the given month or for data pooled over the summer (“Total”), as in Table 2 distribution for significance; analysis of deviance in GLM is analogous to analysis of variance in ordinary least squares linear regression (Quinn and Keough 2002). GLM models were fit in R (www.r-project.org).

Results

A total of 512 mummichogs were collected from Hoffler Creek, 255 from the intertidal zone, and 257 from the subtidal zone. Three subtidal fish and one intertidal fish were collected with no discernable food items in their gut; these fish were excluded from the analysis. Common food items among fish foraging in the intertidal zone (in order of decreasing FO_{10} among all fish collected over the summer) included detrital-algal complex, insects (Hemiptera adults, Orthoptera adults, Diptera adults and larvae), ostracods, copepods, crabs (*Uca* spp.), amphipods, foraminifera, and polychaete worms (Table 2). In the subtidal zone, only detrital-algal complex and shrimp (*Palaemonetes* spp.) were common diet components over the entire summer, although ostracods and crabs were moderately common in some months (Table 2).

Significant differences between intertidal and subtidal FO_{10} were seen for all major diet items except detrital-algal complex. When considering pooled data on all fish collected over the summer, FO_{10} of insects, crabs, copepods, and ostracods were all significantly greater in the intertidal zone, whereas FO_{10} of shrimp was greater in the subtidal zone (Table 2). When considering only fish captured in a given month, this pattern was consistent for intertidal consumption of insects and subtidal consumption of shrimp in all months of the study (Table 2). Intertidal FO_{10} was significantly greater for copepods in May and June, for ostracods in June and August, and for crabs in May (Table 2).

Diet items most commonly composing greater than 50 % of gut volume included detrital-algal complex in both habitats, insects in the intertidal zone, and shrimp in the subtidal zone (Table 3). Although FO_{10} of detrital-algal complex was fairly even between habitats, FO_{50} was significantly greater in the subtidal zone when considering pooled data for all fish collected over the summer as well as for only those fish collected in June and again in August (Table 3). FO_{50} of shrimp was significantly greater in the subtidal zone for data pooled over the summer as well as when considering only fish collected in a given month for all months of the study. FO_{50} of insects was significantly greater in the intertidal zone for data pooled over the summer as well as for only fish collected in a given month for each month except July (Table 3). When considering pooled data for all fish collected over the summer, FO_{50} was also significantly greater in the intertidal zone for crabs and ostracods (Table 3).

Mean GFI was significantly greater for mummichogs foraging in the intertidal zone than for fish foraging in the subtidal zone when considering all fish collected over the summer (*t* test *p* value <0.01) as well as for fish collected in each individual month of the study with the exception of May (Table 2). Fish length did not have a significant impact on GFI in the intertidal zone (ANOVA *p* value 0.48), but in the subtidal zone, mean GFI increased significantly (ANOVA *p* value <0.01) with increasing fish length (Fig. 2).

The increase in subtidal GFI among larger fish followed a pattern in which an increasing percentage of fish consumed grass shrimp at larger fish sizes (Fig. 3), and fish length had a significant effect (*p* value <0.01) on the probability of a fish consuming shrimp in the subtidal zone. Fish length also had a significant effect (*p* value <0.01) on the probability of fish consuming detrital-algal complex in the subtidal zone, with smaller mummichogs being more likely to consume this diet item (Fig. 3).

Fish length had a significant effect on the probability of mummichogs consuming several major intertidal diet items. Smaller fish were significantly more likely (*p* value <0.01) to consume copepods, whereas moderately sized fish (50–69 mm TL) were significantly more likely (*p* value <0.01) to consume ostracods (Fig. 3). Although the data suggest that consumption of insects may decline among larger mummichogs (Fig. 3), the effect of fish length on consumption of insects was not significant (*p* value 0.09). Crabs were the only intertidal diet item consumed significantly more often (*p* value 0.02) by large mummichogs (Fig. 3). In contrast to the results for subtidal diet, fish length did not have a significant effect (*p* value 0.27) on the probability of mummichogs consuming detrital-algal complex in the intertidal zone (Fig. 3).

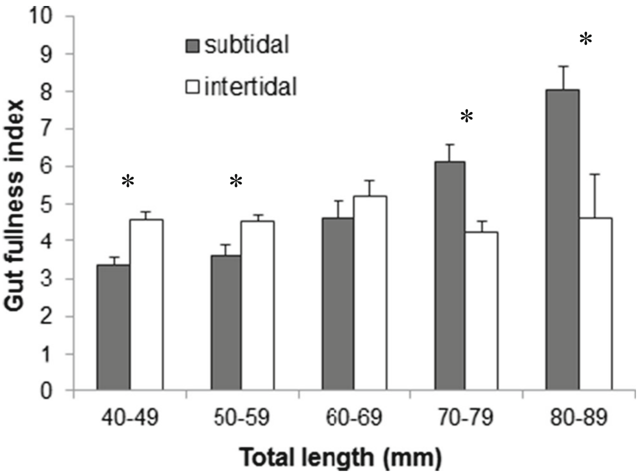

Fig. 2 Mean gut fullness index (GFI) of mummichogs foraging in subtidal (*gray bars*) and intertidal (*white bars*) habitats along Hoffler Creek, Portsmouth, VA, USA, by 10-mm categories of total fish length. *Error bars* indicate one standard error. *Asterisks* indicate significant differences (*t* test, alpha=0.05) between subtidal and intertidal GFI for that length category

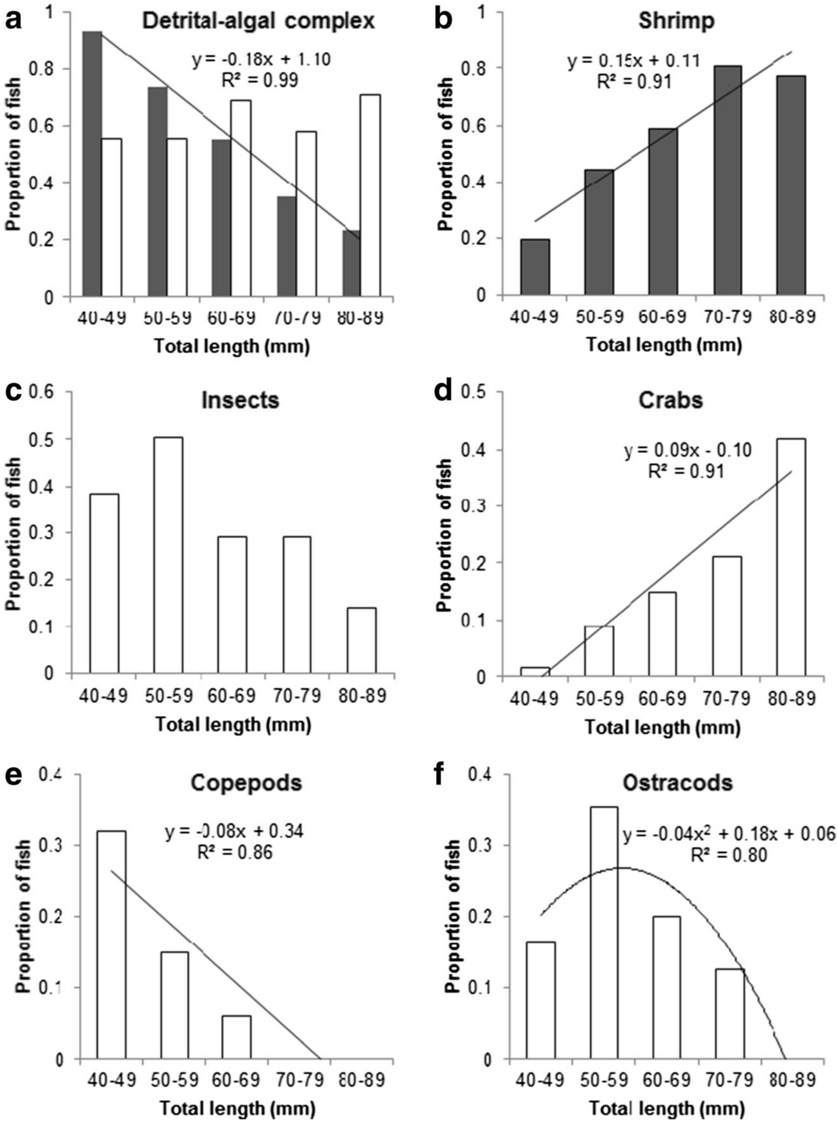

Fig. 3 Proportion of mummichogs in each 10-mm total length category consuming major diet items in subtidal habitats (*gray bars*, panels **a** and **b**) and intertidal habitats (*white bars*, panels **a** and **c**–**f**). Trendlines, regression equations, and R^2 values given for diet items with a significant effect of fish length on the probability of fish consuming that item; trendline in panel **a** is for subtidal values. *Missing bars* indicate no fish in that length category having consumed that diet item, rather than no fish collected in that length category

Discussion

This study found significant differences in the diet of mummichogs known to be foraging in subtidal and intertidal habitats. Furthermore, fish length had significant effects on the probability of an individual mummichog consuming major diet items in both subtidal and intertidal environments. Although previous studies have shown effects of size on mummichog foraging in intertidal environments (Kneib and Stiven 1978; Allen et al. 1994; Goto and Wallace 2011), this study demonstrated important size effects on subtidal diet as well. Mummichogs larger than 70 mm TL in Hoffler Creek consumed significantly more food in the subtidal creek than in the intertidal marsh, with the largest contribution to the subtidal diet coming from grass shrimp. It is important to note that while GFI in the subtidal zone was higher than in the intertidal marsh for larger fish, intertidal GFI of larger mummichogs was still comparable to that attained by smaller fish while in the marsh. Therefore, the consumption of shrimp in the subtidal creek did not occur at the expense of intertidal foraging, but rather represents a potentially important supplement to the energy obtained from diet items consumed in the marsh. This foraging pattern may have population-level implications considering that fecundity increases greatly with increasing length of female mummichogs (Kneib and Stiven 1978), and increasing consumption can lead to higher energy investment in reproductive activities (Jobling 1994).

Grass shrimp were much less commonly consumed by larger mummichogs in the intertidal marsh or small mummichogs in either intertidal or subtidal habitats. Although grass shrimp were abundant in intertidal seine net hauls, vegetation in the intertidal marsh may make predation by mummichogs less effective (Heck and Thoman 1981; Minello and Zimmerman 1983). Kneib and Stiven (1978) also found grass shrimp to be rare in guts of mummichogs collected in intertidal salt marshes, although Goto and Wallace (2011) found grass shrimp to be an abundant component of the diet of mummichogs in chronically polluted intertidal habitats. In the subtidal creek, mummichogs and grass shrimp were observed at high densities in shallow water along the creek bank. Although putting them at greater risk of avian predation, this distribution may offer both grass shrimp and mummichogs some protection from larger aquatic predators (Ruiz et al. 1993). Selection of shallow water concentrates grass shrimp and may make attacks by mummichogs more effective in the creek. Although small mummichogs would likely also have access to grass shrimp in the creek, they rarely utilized this prey resource. Other field studies have found shrimp to be more common in the diet of larger mummichogs (Kneib and Stiven 1982; Goto and Wallace 2011), and smaller mummichogs in the lab prefer smaller size classes of shrimp (Smith and Weis 1997). These patterns suggest that capture success of mummichogs on grass shrimp may decline with decreasing fish size. In this study, mummichogs smaller than 60 mm TL predominantly consumed grass shrimp in May and June, suggesting that as the summer progressed, grass shrimp grew too large to be available to smaller fish.

Small arthropod prey (including insects, copepods, and ostracods) were major components of the intertidal diet of mummichogs and were all significantly more likely to be consumed by smaller fish. Mummichogs <60 mm TL also had significantly higher GFI when collected from the intertidal zone as compared to the subtidal zone, a pattern that may be related to a greater abundance of these small arthropod prey in the intertidal marsh. The predation refuge offered by the vegetated marsh (Banikas and Thompson 2012) may also be especially important for smaller mummichogs, allowing them to focus more time and energy on foraging and less on predator avoidance. Insects constituted the most common intertidal diet item overall, other than detrital-algal complex, and was the most common diet item composing ≥50 % of the gut volume for individual fish in the intertidal zone. These insects were most commonly adult marsh-dependent planthoppers (*Prokelisia* spp.; Denno et al. 1987) rather than aquatic insect larvae. Other studies have also found insects to be a major component of the intertidal diet of mummichogs (Kneib and Stiven 1978; Allen et al. 1994; Fell et al. 1998; James-Pirri et al. 2001), and consumption of these insects in the marsh represents a supplement to the estuarine food web that would not likely occur along nonvegetated shorelines, confirming the importance of vegetated marshes to the feeding ecology of mummichogs.

When considering all mummichogs collected over the course of this study, gut fullness was significantly greater among fish collected in the intertidal zone, similar to the results obtained by other researchers (Kleypas and Dean 1983; Rozas and LaSalle 1990; Rountree and Able 1992; Allen et al. 1994; Fell et al. 1998; Laffaille et al. 2001; Hampel and Cattrijsse 2004). However, this result masked differences among size classes of mummichogs that would not have been apparent if the influence of fish length on diet was not considered explicitly. Mummichogs larger than 70 mm were generally rare in this study (accounting for only 22 % of fish collected over the summer), a pattern that has been noted in other studies of mummichogs (Kneib and Stiven 1978; Allen et al. 1994; Fell et al. 1998). Therefore, results pooled across all sizes of fish will predominantly reflect the foraging patterns of small individuals. While this study confirmed that small mummichogs forage mainly in the intertidal marsh, it also demonstrated that the subtidal creek may potentially be an important feeding area for larger individuals. Although large individuals are relatively rare, they may contribute disproportionately to population growth (Kneib and Stiven 1978).

Therefore, the impact of activities that modify the marsh-creek landscape should be considered holistically when attempting to predict the responses of resident marsh fishes. Access to intertidal marsh is clearly important for mummichog foraging, but maintenance of shallow, subtidal habitat that provides mummichogs with some refuge from aquatic predators and may offer valuable foraging environments for larger individuals should also be considered an important goal. Similarly, attempts to use changes in mummichog diet to evaluate anthropogenic impacts on marsh systems (e.g., Fell et al. 1998; Laffaille et al. 2005; Goto and Wallace 2011; Schein et al. 2013) or to determine the success of restoration activities (e.g., Moy and Levin 1991; Allen et al. 1994; James-Pirri et al. 2001) should explicitly consider changes in the diet of different size classes of fish in both intertidal and subtidal habitats.

Acknowledgments Randi Strutton, executive director of the Hoffler Creek Wildlife Foundation, generously provided access to the Hoffler Creek system. Field assistance was provided by John Agee, Kassi Avent, Erica Banikas, Isaac No, Abigail Thomas, and Nicole Voyles. Funding was provided by Christopher Newport University. This manuscript was greatly improved by comments from Richard Osman and three anonymous reviewers.

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