Virginia Journal of Science / Volume 72, Issue 1 & 2 / Spring & Summer 2021
doi: 10.25778/184m-mg12

The Effect of Storm Events on Diet of Adult Mummichogs (*Fundulus heteroclitus*)

Jessica S. Thompson[1], Cade P. Cobbs, Emma S. Dryden, and Heather D. Harwell

Department of Organismal and Environmental Biology
Christopher Newport University, Newport News, Virginia, USA

ABSTRACT

More frequent storms due to climate change may impact estuarine species such as the mummichog (*Fundulus hetereoclitus*), an ecologically important salt marsh fish. This study investigated the effect of storm events and month on consumption of terrestrial insects by mummichogs in Hoffler Creek, Portsmouth, VA, as well as the effect of storms on consumption of major categories of benthic prey. Samples were taken monthly in the summers of 2017 and 2019. Additional paired samples were taken in June and July 2019, with the first collection during dry weather and the second during a subsequent storm. Month had a significant effect on the proportion of terrestrial insect prey in the diet in both years; consumption was highest in August, particularly in 2017 when the sample coincided with a storm event. However, storms increased consumption of terrestrial insects in only one of four paired dry weather-storm samples in 2019, indicating that temporal variation in insect abundance has a larger effect than increased availability that might occur when storms knock insects into the water. Storms had a significant effect on the proportion of different benthic prey in the diet in paired samples from 2019, but these effects were not consistent across months, sites, or in whether storms increased or decreased consumption. These patterns may be driven by mummichogs taking advantage of small-scale temporal or spatial variation in benthic prey. The ability to utilize locally abundant resources, including terrestrial insects, may help minimize the negative impacts of climate change on mummichogs.

[1] Corresponding author: CNU, 1 Avenue of the Arts, Newport News, VA 23606, jessica.thompson@cnu.edu

INTRODUCTION

Rising global temperatures are expected to cause an increase in intensity and frequency of storm events (Bender et al., 2010) that can have notable effects on the water chemistry and physical structure of aquatic habitats. Estuaries, in particular, can be impacted by drastic, but temporary, fluctuations in temperature (Wenner et al., 2004), salinity (Richmond and Woodin, 1996), and dissolved oxygen (Stevens et al., 2006) as a result of storms. Such changes in physical conditions affect species distribution, survival, and recruitment rates and may be especially pronounced in shallow estuarine habitats (Godley and Brodie, 2007; Rountree and Able, 2007; Muhling et al., 2018).

Salt marshes, in particular, are strongly influenced by both atmospheric conditions and overland flow (Hackney et al., 1976; Rountree and Able, 2007), leading to large changes in physical conditions during storms. Changes in temperature and salinity can have direct consequences on the survival and performance of resident salt marsh fish species (e.g., Collar et al., 2020), as well as affecting the abundance and availability of their prey. The mummichog (*Fundulus heteroclitus)* is an abundant resident of salt marshes along the east coast of the USA (Kneib, 1986). Although young individuals can remain in shallow pools on the marsh surface throughout the tidal cycle (Galleher et al., 2009), adult mummichogs in most systems move into the intertidal marsh with the flooding tide before returning to the subtidal creek at low tide (Teo and Able, 2003). Occupying the intertidal marsh provides mummichogs with refuge from predation (Banikas and Thompson, 2012) and an abundance of prey due to high levels of primary production (Kreeger and Newell, 2000) that support marsh invertebrate populations (Deegan et al., 2000). Mummichogs are opportunistic feeders that consume different prey items depending on body size and location within each subhabitat of the salt marsh (Thompson, 2015). Main prey items include terrestrial insects and small benthic invertebrates such as polychaetes, ostracods, and copepods (Kneib and Stiven, 1978; Allen et al., 1994; James-Pirri et al., 2001; Thompson, 2015).

Storm events could impact prey availability for mummichogs and other salt marsh fish species by causing immediate mortality of aquatic prey or by influencing the distribution of prey as they seek to avoid unfavorable water quality conditions. Studies on a variety of nearshore benthic communities find that those habitats become more homogenous with reductions in the abundance of invertebrate species as storms pass through (Blockley et al., 2007; Roberts et al., 2007; Corte et al., 2017). The availability of terrestrial insect prey, however, may be increased by storm events due to the higher likelihood of collisions between rain and insects, causing the insects to fall in the water and become more readily accessible for consumption by mummichogs. A previous study on mummichog diet in a Virginia tidal creek found that the level of terrestrial insect consumption was highest during a storm event in August (Thompson, 2015), and this pattern was even more pronounced in data collected in 2017 as part of an ongoing study on benthic prey selectivity of mummichogs (J. S. Thompson, unpublished data). Although these results suggest that storm events may increase consumption of terrestrial insects, samples in both studies were collected only once each month so the effects of rain, as opposed to monthly variation in insect abundance, could not be distinguished.

Little research has been done on how shifts in the abundance or availability of prey species during storm events directly impact resident salt marsh fish like the mummichog. The objective of our study was to observe the effects of storm events on the prey consumed by mummichogs found in intertidal salt marshes of a Virginia tidal creek, with a focus on the portion of the diet composed of terrestrial insect prey. We present monthly data on insect consumption collected in the summer of 2017 as part of a mummichog diet selectivity study, as well as data on insect and non-insect prey from paired dry weather-storm event samples collected in 2019 to better distinguish between the effects of storm events and seasonality. Mummichogs serve as an important prey species to many predatory estuarine fishes (Kneib, 1986; Nemerson and Able, 2003; Able et al., 2007), so understanding how storm events affect consumption of aquatic and terrestrial prey will help predict how this ecologically important fish may respond to climate change.

MATERIALS AND METHODS

Study Site

Mummichogs were collected from intertidal marshes at two sites along Hoffler Creek, a tributary of the James River, located in Portsmouth, VA, approximately 11 km from where the James River flows into the Chesapeake Bay. Hoffler Creek is brackish (12-28 ppt salinity) and has a mean tidal range of 0.84 m (Thompson, 2015). The intertidal habitat is composed of vegetated marsh (primarily *Spartina alterniflora*) and unvegetated mudflats. Mummichogs are abundant in the intertidal habitat at high tide but return to the subtidal creek at low tide (Thompson 2015). Hoffler Creek was selected for this study because it contains areas of fringing marsh with connection to the upland habitat that are typical of low to moderately impacted tidal creeks along the lower Chesapeake Bay, and the diet of mummichogs in Hoffler Creek (Thompson 2015) is comparable to other systems along the Atlantic coast (e.g., Kneib and Stiven, 1978; Allen et al., 1994; James-Pirri et al., 2001). This system also provided easy access to sampling sites both downstream, close to the mouth of the creek, and upstream, close to the creek's origin.

The downstream sampling site was approximately 485 m from the creek mouth and had an extensive marsh area along a wide and deep subtidal creek. Mummichogs were collected from the eastern edge of a large contiguous intertidal habitat with an area of 33,480 m^2 composed of approximately 73% vegetation and 27% intertidal mud flat or channel. The average intertidal width (measured from the subtidal creek to the upland habitat) was 106 m. The upstream site was located 1,790 m from the creek mouth. It had intermittent patches of fringing marsh along a narrow and shallow subtidal creek. Mummichogs were collected from the middle of a patch of marsh with an average intertidal width of 29 m and an area of 2,400 m^2, composed of approximately 82% vegetation and 18% intertidal mud flat.

Mummichog Collection

Mummichogs ≥40 mm total length were collected in unbaited, cylindrical minnow traps (22.9 cm diameter, 44.5 cm long, 6.4-mm mesh) following the protocol of Thompson (2015). In brief, traps were set in areas of intertidal marsh vegetation within two hours of a daytime high tide to ensure diet items included in the study were consumed while fish occupied intertidal habitats. To minimize digestion of prey item, fish were removed from traps set for no more than 15 minutes. A maximum of 30 fish from each site on each sampling date was retained for inclusion in the study. After fish were euthanized in an MS-222 solution, a slit was made in the body cavity to allow for perfusion of the gut, and fish were placed in 10% buffered formalin for preservation. When more than 30 fish were captured, fish of different sizes were chosen in approximate proportion to their occurrence in the sample to account for size-specific differences in the diet (Thompson 2015), and the surplus fish were released at their site of collection. Mean total length of fish retained for diet analysis was similar across samples (Table 1).

TABLE 1. Sample size (number of fish and number of diet items identified) and total length (mm; mean ± s.d.) of mummichogs collected from downstream and upstream sites along Hoffler Creek, Portsmouth, VA, and included in analysis of the effects of month and storm events on diet. Single monthly samples were taken in May-August, 2017, and in August, 2019; paired dry weather and storm samples were taken in June and July, 2019.

	Downstream site			Upstream site		
	Number of fish	Number of diet items	Total length	Number of fish	Number of diet items	Total length
May, 2017 (dry weather)	22	397	64 ± 12	25	445	65 ± 13
June, 2017 (dry weather)	25	282	65 ± 13	25	834	60 ± 12
July, 2017 (dry weather)	25	236	65 ± 14	25	318	63 ± 13
August, 2017 (storm)	25	234	58 ± 12	25	311	54 ± 10
June, 2019 (dry weather)	25	78	65 ± 10	25	385	56 ± 5
June, 2019 (storm)	25	555	59 ± 12	19	184	57 ± 6
July, 2019 (dry weather)	25	177	63 ± 8	25	316	59 ± 7
July, 2019 (storm)	25	122	67 ± 12	25	438	60 ± 7
August, 2019 (dry weather)	25	126	60 ± 8	24	206	55 ± 7

To determine the effect of storm events on mummichog diet, prey items consumed during periods of dry weather were compared with those items consumed during storms. Dry weather samples were collected in periods without precipitation and at least 48 hours after any previous rainfall. The original study objective was to determine whether storm events make terrestrial insects more available to mummichogs by washing insects into the marsh from the upland habitat or knocking insects into the water from marsh grasses. In the absence of any established protocol for this type of study, 48 hours (four full tidal cycles) were assumed to be sufficient for any terrestrial insects washed into the marsh in a previous storm to be carried out of the habitat by tidal action and no longer be available for mummichog consumption. Storm samples were collected during precipitation events with at least 30 minutes of steady rain prior to minnow traps being set in the marsh. Thirty minutes of rain were assumed to be sufficient to increase mummichog access to terrestrial insects washed into the marsh.

In 2017, both upstream and downstream samples were taken on the same day in monthly collections from May through August. Samples from the first three months met the criteria for a dry sample, whereas the sample collected in August met the criteria for a storm sample.

In 2019, pairs of dry and storm samples were taken at both the upstream and downstream sites in June and again in July. Dry samples were taken no more than 3-5 days before the paired storm sample to ensure that temporal differences in prey availability independent of the occurrence of storms would be minimized. An additional dry sample was taken in August for comparison with dry samples from earlier months; no storms occurred during daytime high tides in this month, preventing collection of a corresponding storm sample.

<u>Diet Analysis</u>

In the lab, prey items were removed from the anterior portion of the gut (Sections I and II; Babkin and Bowie, 1928) to ensure that only the most recently consumed items were analyzed (Thompson, 2015). Identifiable food items were tallied for each fish using broad prey categories to allow for comparisons between dry and storm samples and across months. These categories included terrestrial insects, aquatic larval insects, polychaetes, copepods, ostracods, tanaids, and nematodes. Empty stomachs were excluded from the analysis. Twenty-five individuals were processed from each site and date (randomly selected from the 30 fish collected), except in cases where the number of fish collected was too low or the number of empty stomachs was too great to attain this sample size (Table 1).

<u>Statistical Analysis</u>

Mummichog diet was analyzed based on (1) the frequency of occurrence of terrestrial insect prey, defined as the proportion of fish in a sample with at least one terrestrial insect in the gut, and (2) the numerical proportion of terrestrial insect prey relative to non-insect prey for all fish in a given sample. The effect of month (May-August) on each metric was assessed in 2017 using 2×4 Chi-square tests for each sampling site. In 2019, 2×3 Chi-square tests were used to assess the effect of month (June-August) on the numerical proportion of terrestrial insect prey in dry samples. A small number of mummichogs consumed insects in 2019 so the Freeman-Halton extension of the Fisher's exact test for a 2×3 contingency table (Freeman and Halton, 1951) was used to assess the effect of month on frequency of occurrence in dry samples.

The effect of storm events on frequency of occurrence and numerical proportion of terrestrial insect prey was assessed for paired dry weather-storm samples (collected at each sampling site in June and July of 2019, as described above) using one-tailed Fisher's exact tests (Fisher, 1925). This test was chosen to accommodate the small number of terrestrial insects in the diet in 2019, and a one-tailed test was chosen based on the hypothesis that storms would increase insect consumption due to insects being knocked into the water by the rain.

Substantial variation was observed between paired dry weather and storm samples collected in June and July, 2019, for some categories of benthic prey. Therefore, post hoc analyses were conducted to test for significant effects of storms on the proportion of major benthic prey items, defined as accounting for ≥5% of total identifiable prey items on at least one sample date at one site. A two-tailed Fisher's exact test was used to compare the number of items in the given prey category versus items in the other major categories in paired dry weather and storm samples for each sampling site. The Bonferroni correction was used to determine the significance of each individual comparison in order to hold $\alpha=0.05$ across all 24 of the resulting post hoc tests.

RESULTS

Consumption of terrestrial insects was low to moderate in May through July of 2017 but increased in August at both sites, with the most substantial increase observed at the upstream site (Table 2). Month had a significant effect on the numerical proportion of terrestrial insect prey in the diet at both the downstream ($X^2=34.02$ with $df=3$, $p<0.001$) and upstream ($X^2=967.97$ with $df=3$, $p<0.001$) sites. At least 40% of fish in each sample from 2017 had at least one terrestrial insect in the gut, but this value increased to 96% in August at the upstream site (Table 2). Month had a significant effect on the frequency of occurrence of terrestrial insects in the diet at the upstream site ($X^2=17.98$ with $df=3$, $p<0.001$).

TABLE 2. Consumption of terrestrial insects by mummichogs at downstream and upstream sites along Hoffler Creek, Portsmouth, VA, in May through August of 2017. Samples from May through July were collected during dry weather, whereas the August sample was taken during a storm event. Values are the numerical percentage of total diet items that were terrestrial insects and, in brackets, the frequency of occurrence (the percentage of fish with at least one terrestrial insect in the gut). Sample sizes and mean fish lengths are provided in Table 1.

	May	June	July	August
Downstream site	4.5 [50]	8.2 [40]	5.5 [40]	17.1 [64]
Upstream site	6.1 [60]	3.1 [56]	10.3 [40]	77.8 [96]

Consumption of terrestrial insects by mummichogs was low throughout 2019 (Table 3). Although storm events generally increased the proportion of terrestrial insect prey in the diet (Table 3), this increase was only significant at the upstream site in June (one-tailed Fisher's exact test p=0.04). The frequency of occurrence of terrestrial insects in the diet was two to three times higher during storm events than in dry weather samples (Table 3), but this increase was not significant in paired samples from June or July at either site.

Comparison of dry weather samples from 2019 showed an increase in the numerical proportion of terrestrial insect prey in the diet in August at both sites (Table 3), but month had a significant effect on these proportions only at the upstream site (X^2=16.46 with df=2, p<0.001). The frequency of occurrence of terrestrial insects in the diet was also highest in August (Table 3), and again, monthly differences were significant only at the upstream site (Fisher-Freeman-Halton 2x3 exact test p=0.018).

TABLE 3. Consumption of terrestrial insects by mummichogs at downstream and upstream sites along Hoffler Creek, Portsmouth, VA, for paired dry weather and storm samples in June and July, as well as a dry weather sample in August, of 2019. Values are the numerical percentage of total diet items that were terrestrial insects and, in brackets, the frequency of occurrence (the percentage of fish with at least one terrestrial insect in the gut). Sample sizes and mean fish lengths are provided in Table 1.

	June		July		August
	Dry	Storm	Dry	Storm	Dry
Downstream site	5.1 [16]	2.3 [36]	3.4 [12]	6.6 [28]	8.7 [32]
Upstream site	0.5 [8]	2.7 [21]	1.3 [12]	1.8 [24]	5.3 [38]

Significant differences in the proportion of non-insect diet items consumed by mummichogs in paired dry weather and storm samples from June and July, 2019, were detected for all major prey categories except nematodes (Table 4). However, these differences were not consistent between sites or months, and for some prey categories, including copepods and ostracods at the upstream site, storm events caused a significant decrease in consumption of that item in one month and a significant increase in consumption in the other month (Table 4).

TABLE 4. Consumption of benthic prey by mummichogs at downstream and upstream sites along Hoffler Creek, Portsmouth, VA, for paired dry weather and storm samples in June and July of 2019. Values are the percentage of total diet items in that prey category and are shown only for major prey categories that accounted for ≥5% of diet items in at least one sample. Paired samples in bold are significantly different between dry weather and storm samples for that site in that month based on two-tailed Fisher's exact tests with a Bonferroni correction to ensure α=0.05 across all tests. Sample sizes and mean fish lengths are provided in Table 1.

	Downstream site				Upstream site			
	June		July		June		July	
	Dry	Storm	Dry	Storm	Dry	Storm	Dry	Storm
Polychaetes	**48.7**	**6.8**	48.6	33.6	9.6	17.4	15.8	10.3
Aquatic larval insects	2.6	9.5	9.6	10.7	**13.0**	**36.4**	9.2	6.4
Copepods	10.3	10.3	8.5	20.5	**6.8**	**35.9**	**43.0**	**3.0**
Ostracods	**25.6**	**3.4**	29.4	22.1	**68.1**	**5.4**	**29.4**	**78.3**
Tanaids	**1.3**	**66.1**	0.6	0.8	0.5	1.6	1.3	0
Nematodes	6.4	1.4	0	5.7	1.6	0.5	0	0.2

DISCUSSION

This study found consistent seasonal variation in the consumption of terrestrial insect prey by mummichogs (Tables 2 and 3), with the highest consumption observed in August, particularly in 2017. However, only one of the four paired samples collected in 2019 showed a significant increase in insect during storm events (Table 3), revealing that storms had a minor effect on the consumption of terrestrial insects by mummichogs. The main groups of terrestrial insects consumed in 2017 and 2019 were *Prokelisia* spp. (marsh-dependent planthoppers) and a variety of Diptera (flies and midges) that would be present in the marsh and at the marsh edge. Planthopper abundance can increase rapidly as a result of increasing host plant biomass and quality (Denno and Roderick, 1990; Gratton and Denno, 2003). In *Spartina alterniflora*-dominated marshes, this increase in plant biomass would be expected over the summer growing season (Dame and Kenny, 1986), potentially leading to increased planthopper abundance by August. Dipteran populations tend to increase with higher temperatures and precipitation rates (Alto and Juliano, 2001), which may contribute to the observed higher rates of consumption by mummichogs in August of both years.

The effect of precipitation on insect populations may also help explain the overall increase in insect consumption in 2017 compared to 2019, given that higher rainfall was recorded in Portsmouth, VA, over the summer in 2017 (68.7 cm from May to August) versus 2019 (51.1 cm over the same time period) (NOAA's National Centers for Environmental Information

Climate Data Online, https://www.ncdc.noaa.gov/cdo-web/). The highest levels of terrestrial insect consumption by mummichogs may, therefore, occur with a combination of high seasonal abundance, as in August in both years of this study, and high availability, as might occur during some storm events or after prolonged seasonal precipitation. This pattern is most evident in the very high insect consumption observed during the storm event in August 2017.

Both our upstream and downstream sampling sites had areas of dense marsh vegetation that would support populations of marsh-dependent insects, along with an unimpeded connection between marsh and upland habitats that may increase access to terrestrial insects at this ecotone. Except for August 2017, the consumption of terrestrial insects in a given month was similar at both sites, which was expected since each site has similar compositions of mud flat and vegetation. In addition to the *Prokelisia* spp. and Diptera mentioned above, storm samples collected in 2019 had a notable increase in the quantity of Formicidae (ants) consumed, particularly at the upstream site, and the increase in ant consumption led to the significant difference in the proportion of terrestrial insects consumed between dry weather and storm samples in June at that site. Ants can be abundant along the upland edge of marshes (Brandt et al., 2010), and storm events may lead to higher water levels that allow mummichogs to more easily access this edge habitat and may also increase the rate at which ants are washed into the marsh itself. This suggests that insect consumption overall depends on having both sufficient areas of marsh vegetation and access to marsh-upland edge and that increases in terrestrial insect availability with storms may be particularly dependent on upland access.

Substantial and significant differences in the consumption of most major non-insect prey categories were seen in at least one paired dry weather-storm sample in 2019 (Table 4). However, these differences were not consistent across sites, months, or the direction of change between dry weather and storm samples. Two possible explanations for this variation are that (1) the abundance of benthic invertebrate prey species varies over small spatial and temporal scales, independent of the influence of storms, and mummichogs then consume those locally abundant resources at higher rates, or (2) prey species respond to storms but variation in the most abundant species or life stage across spatial and temporal scales results in inconsistent patterns when comparing dry weather and storm samples. Substantial spatial variation in the abundance of major benthic invertebrate taxa has been reported over the scale of meters in a variety of soft-bottom nearshore and intertidal habitats (Morrisey et al., 1992; Paiva, 2001; Whaley and Minello, 2002; Ysebaert and Herman, 2002), and temporal variation is seen in many benthic invertebrate populations at time scales ranging from days to weeks (Morrisey et al., 1992; Whaley and Minello, 2002). Morrisey et al. (1992) also identified substantial interaction between patterns of temporal and spatial variation, such that most sampled taxa exhibited different temporal patterns even across plots at the same location; in the context of this study, that would suggest that prey species at the upstream and downstream sites may display different temporal patterns of abundance and lead to inconsistent patterns in consumption by mummichogs across even the short number of days between dry weather and storm samples.

Although the effect of storm events on benthic communities is not well studied, reductions in the immediate abundance of some taxa, most notably crustaceans, have been detected (Blockley et al., 2007; Roberts et al., 2007; Corte et al., 2017). Of the crustaceans found in the mummichog diet in this study, consumption of ostracods declined significantly during storms in two paired samples and consumption of copepods declined in one paired sample. However, consumption of ostracods and copepods each increased significantly during storms in one additional paired sample, as did consumption of tanaids. These inconsistencies may reflect the fact that the effects of storms on abundance of some species would be layered over small-scale temporal and spatial variation in the composition of the benthic community (Morrisey et al., 1992), and different species even within the same taxonomic category may respond differently to storms, as observed for polychaetes by Corte et al. (2017). In addition, it is important to note that the means by which abundances of invertebrates in the benthos are reduced can impact their susceptibility to predators. If storms physically disrupt the substrate and scour invertebrates into the water column (Corte et al., 2017) or lead to increased movement by mobile individuals seeking to avoid adverse water quality conditions (Blockley et al., 2007), these individuals may become more available to mummichogs feeding in the habitat even as their abundance in the substrate declines.

The criteria used to designate dry weather and storm samples in this study were based on the primary objective of assessing the effect of storms on mummichogs' consumption of terrestrial insects. Specifically, it was expected that the availability of terrestrial insects responded fairly rapidly to changing precipitation patterns if the dominant mode of increased availability was insects being washed into the marsh or being knocked off of marsh grasses or overhanging vegetation during rain events. The time scale over which soft sediment benthic communities may be impacted by storms, however, is unknown, which raises the possibility that 48 hours without rain (the definition of dry weather used here) may be insufficient to negate latent effects of earlier storms. Similarly, a minimum of 30 minutes of steady rain (the definition of a storm event used here) may be insufficient for changes in the benthic community to occur. The fact that there were observed differences in mummichog diet in some paired dry weather-storm samples suggests that this sampling design captured differences in benthic prey availability based on precipitation patterns, but further research on the rate of recovery of intertidal, soft sediment benthic communities after storms will be important to fully predict how the diet of salt marsh fishes will respond to storm events.

The small number of storm events sampled in this study also limits the ability to discern how specific characteristics of storms may affect benthic invertebrates and terrestrial insects, as well as resulting patterns in fish diet. The amount of rainfall in each storm event included in this study was comparable (1.2-1.6 cm in 24 hours), but the amount of rainfall in the 48 hours prior to sampling was higher in August 2017 (4.6 cm) and June 2019 (3.6 cm) than in July 2019 (no rainfall; NOAA's National Centers for Environmental Information Climate Data Online, https://www.ncdc.noaa.gov/cdo-web/). Rainfall over the days leading up to storm samples would result in higher water levels in the marsh, increasing access to upland habitat and insects such as ants, which were observed in high numbers in the upstream June 2019 sample. Storm sampling is necessarily opportunistic, and unfortunately, there were a limited number of opportunities to collect paired samples in 2019. Future sampling across storms with a broader range of characteristics may help to determine which components of these storms are most important for increasing fish access to terrestrial insects and for modifying benthic communities in ways that affect fish diet.

Overall, these findings suggest that the consumption of terrestrial insects by mummichogs depends mainly on seasonal abundance and, to a lesser degree, increased availability due to storms. Virginia is in the middle latitudes expected to experience more pulsed precipitation events due to climate change (Trenberth, 2011), and average precipitation in the Tidewater region, particularly in autumn months, has increased in the last two decades compared to historical values (Hoffman et al., 2019). Climate change is further predicted to increase insect population growth in species living in middle to high latitudes due to higher fitness brought on by warmer temperatures closer to the species' optimum range (Deutsch et al., 2008). The stronger storms created by these warmer temperatures can have varying effects on insect species based on location (Gandhi et al., 2007), although more research is necessary. The ability of mummichogs to take advantage of terrestrial insect prey, in addition to locally and temporally available benthic prey, may allow mummichogs to maintain a more robust diet and help to buffer negative impacts of climate change on this ecologically important species. However, the utilization of terrestrial insect prey by mummichogs is dependent upon preservation of sufficient marsh area, which can be destroyed or severely impacted by strong storms (Scavia et al., 2002), and unimpeded marsh-upland connections, which can be disrupted by shoreline hardening put in place to protect upland development from sea level rise (Gittman et al., 2015). Shoreline hardening and coastal development can also negatively impact the benthic macroinvertebrates (Bilkovic et al., 2006) that mummichogs depend on for the majority of their diet. Thus, preserving salt marsh habitat will be essential to support stable mummichog populations that serve as an important link in the estuarine food webs of Virginia and the broader Atlantic coast (Kneib, 1986).

ACKNOWLEDGEMENTS

This study was funded by Christopher Newport University through the Office of Undergraduate Research and Creative Activity, the Department of Organismal and Environmental Biology, and the Office of the Provost. This work was conducted under Christopher Newport University's Institutional Animal Care and Use Committee (IACUC) Protocol #2017-8. Katherine Hodges, Megan Moran, and Michelle Bridgeman assisted with collection of field samples in 2017, and Katherine Hodges identified diet items from mummichogs collected in that year. This manuscript was improved by comments from Sujan Henkanaththegedara, Bob Rose, and one anonymous reviewer. Statement of Author Responsibility: JST and HDH designed the 2017 and 2019 studies and collected field samples in 2017; JST, CPC, and ESD collected field samples in 2019 and identified diet items from that year; JST conducted data analyses; and JST, CPC, and ESD collaborated in writing the manuscript.

LITERATURE CITED

Able, K. W., J. H. Balleto, S. M. Hagan, P. R. Jivoff, and K. Strait. 2007. Linkages between salt marshes and other nekton habitat in Delaware Bay, USA. Reviews in Fisheries Science 15: 1-61. https://doi.org/10.1080/10641260600960995

Allen, E. A., P. E. Fell, M. A. Peck, J. A. Gieg, C. R. Guthke, and M. D. Newkirk. 1994. Gut contents of common mummichogs, *Fundulus heteroclitus* L., in a restored impounded marsh and in natural reference marshes. Estuaries 17: 462–471. https://doi.org/10.2307/1352676

Alto, B. W. and S. A. Juliano. 2001. Precipitation and temperature effects on populations of *Aedes albopictus* (Diptera: Culicidae): implications for range expansion. Journal of Medical Entomology 38:646-656. https://doi.org/10.1603/0022-2585-38.5.646

Babkin, B. P. and D. J. Bowie. 1928. The digestive system and its function in *Fundulus heteroclitus*. The Biological Bulletin 54: 254-277. https://doi.org/10.2307/1536857

Banikas, E. M. and J. S. Thompson. 2012. Predation risk experienced by mummichog, *Fundulus heteroclitus*, in intertidal and subtidal salt marsh habitats. Estuaries and Coasts 35: 1346-1352. https://doi.org/10.1007/s12237-012-9517-8

Bender, M. A., T. R. Knutson, R. E. Tuleya, J. J. Sirutis, G. A. Vecchi, S. T. Garner, and I. M. Held. 2010. Modeled impact of anthropogenic warming on the frequency of intense Atlantic hurricanes. Science 327: 454-458. https://doi.org/10.1126/science.1180568

Bilkovic, D. M., M. Roggero, C. H. Hershner, and K. H. Havens. 2006. Influence of land use on microbenthic communities in nearshore estuarine habitats. Estuaries and Coasts 29: 1185-1195. https://doi.org/10.1007/BF02781819

Blockley, D. J., V. J. Cole, J. People, and M. G. Palomo. 2007. Effects of short-term rain events on mobile macrofauna living on seawalls. Journal of the Marine Biological Association of the United Kingdom 87: 1069-1074. https://doi.org/10.1017/S0025315407055117

Brandt, M., K. Bromberg Gedan, and E. A. Garcia. 2010. Disturbance type affects the distribution of mobile invertebrates in a high salt marsh community. Northeastern Naturalist 17: 103-114. https://doi.org/10.1656/045.017.0108

Collar, D. C., J. S. Thompson, T. C. Ralston, and T. J. Hobbs. 2020. Fast-start escape performance across temperature and salinity gradients in mummichog *Fundulus heteroclitus*. Journal of Fish Biology 96: 755-767. https://doi.org/10.1111/jfb.14273

Corte, G. N., T. A. Schalcher, H. H. Checon, C. A. M. Barboza, E. Siegle, R. A. Coleman, and A. C. Z. Amaral. 2017. Storm effects on intertidal invertebrates: increased beta diversity of few individuals and species. PeerJ 5: e3360. https://doi.org/10.7717/peerj.3360

Dame, R. F. and P. D. Kenny. 1986. Variability of *Spartina alterniflora* primary production in the euhaline North Inlet estuary. Marine Ecology Progress Series 32: 71-80. https://doi.org/10.3354/meps032071

Deegan, L, A., J, E. Hughes, and R, A. Rountree. 2000. Salt marsh ecosystems support of marine transient species. In: Weinstein, M. P. and D. A. Kreeger (Eds.), Concepts and Controversies in Tidal Marsh Ecology. Kluwer Academic Publishers, Dordrecht. pp. 333-365. https://doi.org/10.1007/0-306-47534-0_16

Denno, R. F. and G. K. Roderick. 1990. Population biology of planthoppers. Annual Review of Entomology 35:489-520. http://doi.org/10.1146/annurev.en.35.010190.002421

Deutsch, C. A., J. J. Tewksbury, R. B. Huey, K. S. Sheldon, C. K. Ghalambor, D. C. Haak, and P. R. Martin. 2008. Impacts of climate warming on terrestrial ectotherms across latitude. Proceedings of the National Academy of Sciences of the United States of America 105: 6668-6672. https://doi.org/10.1073/pnas.0709472105

Fisher, Ronald A. 1925. Statistical methods for research workers. Oliver & Boyd, Edinburgh. 336p. https://doi.org/10.1007/978-1-4612-4380-9_6

Freeman, G. H. and J. H. Halton. 1951. Note on an exact treatment of contingency, goodness of fit and other problems of significance. Biometrika 40: 74-86. https://doi.org/10.2307/2332323

Galleher, S. N., I. Gonzalez, M. R. Gilg, and K. J. Smith. 2009. Abundance and distribution of larval and juvenile *Fundulus heteroclitus* in northeast Florida marshes. Southeastern Naturalist 8: 495-502. https://doi.org/10.1656/058.008.0310

Gandhi, K. J. K., D. W. Gilmore, S. A. Katovich, W. J. Mattson, J. R. Spence, and S. J. Seybold. 2007. Physical effects of weather events on the abundance and diversity of insects in North American forests. Environmental Reviews 15: 113-152. https://doi.org/10.1139/A07-003

Gittman, R. K., F. J. Fodrie, A. M. Popowich, D. A. Keller, J. F. Bruno, C. A. Currin, C. H. Peterson, and M. F. Piehler. 2015. Engineering away our natural defenses: An analysis of shoreline hardening in the US. Frontiers in Ecology and the Environment 13: 301-307. https://doi.org/10.1890/150065

Godley, J. and R. Brodie. 2007. Effect of summer storms on early life stages of *Uca minax*, *U. pugnax*, and *U. pugilator* in North Inlet Estuary, South Carolina, USA. Marine Ecology Progress Series 342: 197-204. https://doi.org/10.3354/meps342197

Gratton, C. and R. F. Denno. 2003. Seasonal shift from bottom-up to top-down impact in phytophagous insect populations. Oecologia 134: 487-495. https://doi.org/10.1007.s00442-002-1137-8

Hackney, C. T., W. D. Burbanck, and O. P. Hackney. 1976. Biological and physical dynamics of a Georgia tidal creek. Chesapeake Science 17: 271-280. https://doi.org/10.2307/1350514

Hoffman, J. S., M. J. Allen, and C. F. Labosier. 2019. Detecting change: Observations of temperature and precipitation across Virginia's climate divisions. Virginia Journal of Science 70. https://doi.org/10.25778/eq3r-pv57

James-Pirri, M. J., K. B. Raposa, and J. G. Catena. 2001. Diet composition of mummichogs, *Fundulus heteroclitus*, from restoring and unrestricted regions of a New England (U.S.A.) salt marsh. Estuarine, Coastal and Shelf Science 53: 205-213. https://doi.org/10.1006/ecss.2001.0807

Kneib, R. T. 1986. The role of *Fundulus heteroclitus* in salt marsh trophic dynamics. American Zoologist 26: 259–269. https://doi.org/10.1093/icb/26.1.259

Kneib, R. T. and A. E. Stiven. 1978. Growth, reproduction, and fecundity of *Fundulus heteroclitus* (L.) on a North Carolina salt marsh. Journal of Experimental Marine Biology and Ecology 31: 121-140. https://doi.org/10.1016/0022-0981(78)90125-9

Kreeger, D. A. and R. I. E. Newell. 2000. Trophic complexity between producers and invertebrate consumers in salt marshes. In: Weinstein, M. P. and D. A. Kreeger (Eds.), Concepts and Controversies in Tidal Marsh Ecology. Kluwer Academic Publishers, Dordrecht. pp. 187-220. https://doi.org/10.1007/0-306-47534-0_10

Morrisey, D. J., A. J. Underwood, L. Howitt, and J. S. Stark. 1992. Temporal variation in soft-sediment benthos. Journal of Experimental Marine Biology and Ecology 164: 233-245. https://doi.org/10.1016/0022-0981(92)90177-C

Muhling, B. A., C. F. Gaitan, C. A. Stock, V. S. Saba, D. Tommasi, and K. W. Dixon. 2018. Potential salinity and temperature futures for the Chesapeake Bay using a statistical downscaling spatial disaggregation framework. Estuaries and Coasts 41: 349-372. https://doi.org/10.1007/s12237-017-0280-8

Nemerson, D. M. and K. W. Able. 2003. Spatial and temporal patterns in the distribution and feeding habits of *Morone saxatilis* in marsh creeks of Delaware Bay, USA. Fisheries Management and Ecology 20: 337-348. https://doi.org/10.1046/j.1365-2400.2003.00371.x

Paiva, P. C. 2001. Spatial and temporal variation of a nearshore benthic community in southern Brazil: Implications for the design of monitoring programs. Estuarine, Coastal and Shelf Science 52: 423-433. https://doi.org/10.1006/ecss.2001.0763

Richmond, C. E. and S. A. Woodin. 1996. Short term fluctuations in salinity: Effects on planktonic invertebrate larvae. Marine Ecology Progress Series 133: 167-177. https://doi.org/10.3354/meps133167

Roberts, D. A., A. G. B. Poore, and E. L. Johnston. 2007. MBACI sampling of an episodic disturbance: Stormwater effects on algal epifauna. Marine Environmental Research 64: 514-523. https://doi.org/10.1016/j.marenvres.2007.04.005

Rountree, R. A. and K. W. Able. 2007. Spatial and temporal habitat use patterns for salt marsh nekton: implications for ecological functions. Aquatic Ecology 41: 25-45. https://doi.org/10.1007/s10452-006-9052-4

Scavia, D., J. C. Field, D. F. Boesch, R. W. Buddemeier, V. Burkett, D. R. Cayan, M. Fogarty, M. A. Harwell, R. W. Howarth, C. Mason, et al. 2002. Climate change impacts on U.S. coastal and marine ecosystems. Estuaries 25: 149-164. https://doi.org/10.1007/BF02691304

Stevens, P. W., D. A. Blewett, and J. P. Casey. 2006. Short-term effects of a low dissolved oxygen event on estuarine fish assemblages following the passage of Hurricane Charley. Estuaries and Coasts 29: 997-1003. https://doi.org/10.1007/BF02798661

Teo, S. L. H. and K. W. Able. 2003. Habitat use and movement of the mummichog (*Fundulus heteroclitus*) in a restored salt marsh. Estuaries 26: 720–730. https://doi.org/10.1007/BF02711983

Thompson, J. S. 2015. Size-selective foraging of adult mummichogs, *Fundulus heteroclitus*, in intertidal and subtidal habitats. Estuaries and Coasts 38: 1535-1544. https://doi.org/10.1007/s12237-014-9913-3

Trenberth, K. E. 2011. Changes in precipitation with climate change. Climate Research 47: 123–138. https://doi.org/10.3354/cr00953

Wenner, E., D. Sanger, M. Arendt, A. F. Holland, and Y. Chen. 2009. Variability in dissolved oxygen and other water-quality variables within the National Estuarine Research Reserve System. Journal of Coastal Research 45: 17-38. https://doi.org/10.2112/SI45-017.1

Whaley, S. D. and T. J. Minello. 2002. The distribution of benthic infauna of a Texas salt marsh in relation to the marsh edge. Wetlands 22: 753-766. https://doi.org/10.1672/0277-5212(2002)022[0753:TDOBIO]2.0.CO;2

Ysebaert, T. and P. M. J. Herman. 2002. Spatial and temporal variation in benthic macrofauna and relationships with environmental variables in an estuarine, intertidal soft-sediment environment. Marine Ecology Progress Series 244: 105-124. https://doi.org/10.3354/meps244105