

Feedbacks Between Nutrient Enrichment and Geomorphology Alter Bottom-Up Control on Food Webs

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ABSTRACT

Classic bottom-up theory predicts that increased resource availability (for example, nutrients) at the base of the food web will stimulate primary production and, in turn, secondary production. Recent studies, however, indicate that bottom-up controls on food web production can be modified by other factors, such as landscape configuration and continuity. As part of a 10-year ecosystem-scale experiment in a New England salt marsh, we investigated the response of secondary consumers, specifically a fish, the mummichog (*Fundulus heteroclitus*), to nutrient enrichment. In the first 6 years, we observed a classic bottom-up response of increased production of algae, invertebrate prey, and mummichogs. After the sixth year, however, mummichog biomass declined to below reference levels by

the eighth year. This decline in mummichog biomass coincided with nutrient-induced collapse of the low-marsh habitat. Based on stable isotope analyses, field surveys, and small-scale experiments, we suggest that the geomorphic changes induced a trophic decoupling between creek and marsh habitats, thereby reducing mummichog access to prey in the intermittently flooded marsh. Thus, despite continued stimulation of algal and invertebrate prey production, fish abundances declined to below pre-enrichment levels. Our results demonstrate how geomorphic controls can override classic bottom-up control and emphasize the importance of long-term studies in detecting the response of slow-turnover phenomena (for example, changing landscapes).

Key words: food web theory; nutrient enrichment; landscape control; saltmarsh; estuary; trophic subsidy; spatially coupled; geomorphology.

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Author contributions: JN, DJ, and LD conceived the study, performed research, and analyzed data. JN, AS, and NS conceived the mesocosm and tank experiments and analyzed the data. All authors contributed to writing the paper.

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INTRODUCTION

Bottom-up nutrient driven-controls can have powerful effects on food web structure and complexity, species distributions and interactions, and

the magnitude and rates of biogeochemical processes (Menge and others 2003; Ware and Thomson 2005; Spivak and others 2007). In coastal systems, for example, increasing nutrient loads can stimulate primary production and, in turn, increase the density and biomass of benthic macroinvertebrates, particularly epibenthic algal grazers (Heck and others 2006; Spivak and others 2009; Johnson and Short 2013). Small-scale plot-level and mesocosm experiments have been important for understanding how top-down and bottom-up controls interactively shape community and ecosystem structure (McQueen and others 1989; Menge and others 2003; Sanders and Platner 2007); however, these experiments can miss dynamics that occur over longer time periods and at the landscape scale (Carpenter and others 2005). It is widely accepted that the landscape complexity, diversity, and arrangement of habitats are important controls on the distribution of organisms in ecosystems (McIvor and Odum 1988; Hansen 2000), but the implications of this on food webs are not fully understood. At the ecosystem scale, both bottom-up and top-down controls on food webs could be modified by habitat access or configuration, with consequences for species distribution and ecosystem function.

Landscape theory predicts that local geomorphology may influence species distributions and interactions, production, and energy flow (Hershey and others 1999; Ward and others 1999; Baker and others 2013). Interactions across geomorphic boundaries can often be unidirectional, with energy primarily flowing from habitats with greater productivity to those with lesser productivity (Power and others 1996; Ward and others 1999; Sheaves 2009). This unequal energy distribution can result in food web configurations or linkages that would not occur in either habitat in isolation (Pringle and Fox-Dobbs 2008; Christian and Allen 2014). Because of this, changes in habitat structure or configuration have the potential to disrupt ecosystem-level energy flows by altering the ability of mobile consumers to access critical resources (Sabo and Power 2002; Baxter and others 2004; Sheaves 2009).

Saltmarshes offer a unique setting to understand the role of geomorphology in shaping energy flow in food webs because geomorphology is a primary control on the spatial distribution of habitats as well as the time that those habitats are available to consumers. In this context, geomorphology can control food web dynamics by altering predator access to specific habitats and, as a result, change the magnitude of top-down control on local prey

communities (Power and others 1996; McCann and others 2005). In turn, if the geomorphic configuration limits predator access, then the magnitudes of top-down and bottom-up forcing will be a function of the duration of access and the intensity of predation (Power and others 1996; Fleeger and others 2008; Johnson and Fleeger 2009).

In New England saltmarshes, a small fish (the mummichog—*Fundulus heteroclitus*, adults typically 30–40 mm in length) is a key species in the food web because it is the dominant mobile nekton species (> 80% by biomass; (Deegan and others 2007)) and an important link in the trophic relay that connects marshes and open bay areas (Kneib 1997; Baker and others 2016). Mummichogs are important omnivorous consumers that can move across habitat boundaries as the flooding tide inundates low- and high-marsh habitats. They consume a variety of food items from detritus and algae and macroinfaunal annelids in the creeks (Johnson and others 2007) to arthropods on the high marsh (Kneib 1986; Lockfield and others 2013). Access to high-marsh areas increases mummichog trophic level (Nelson and others 2015) and growth rate (Javonillo and others 1997), suggesting that high-marsh habitats are an important energy source for mummichogs. Mummichog movement also serves to couple the food webs on the intermittently flooded high marsh with the aquatic food webs in the creek, increasing energy flow across the landscape.

We examined the relative strength of bottom-up nutrient control versus landscape geomorphic configuration on food webs in a decade-long ecosystem-level nutrient enrichment experiment (Deegan and others 2007, 2012). In our experimental system, long-term nutrient enrichment has caused shifts in primary production as well as changes in the plant and microbial community (Johnson and others 2016; Kearns and others 2016; Spivak and Ossolinski 2016). Nutrient enrichment has also induced changes to the marsh creek edge structure and geomorphic characteristics (Deegan and others 2012), including disrupting the natural ramp form of the creek bank through the development of large cracks between the creek and the marsh platform, in addition to low-marsh slumping and loss. Prior to the observed changes in geomorphic structure, mummichog diets shifted to a greater dependence on algal production and, in the nutrient-enriched systems, fish abundance increased (Lockfield and others 2013). The observed changes in diet, growth, and geomorphology provide an extraordinary opportunity to examine the relative effects on the food web of bottom-up

(nutrient driven) versus top-down (habitat configuration) processes.

We used a combination of approaches to evaluate how nutrient enrichment and changes in marsh geomorphology may have affected food web structure and mummichog production. Within paired nutrient-enriched and reference marsh systems, we looked for evidence of a causal relationship between the observed changes in creek bank geomorphology, food web structure, and mummichog production. To understand the mechanisms driving the underlying patterns in mummichog diet and production, we conducted a diet and growth mesocosm experiment. This experiment was designed to determine if mummichogs (an omnivore) could grow to typical field sizes by consuming predominantly algal-based diets (as under nutrient enrichment), or if they are required to consume prey to grow optimally.

METHODS

Site Description

This study was conducted in the Plum Island estuary (PIE), Massachusetts (42°44'N, 70°52'W), a temperate, bar-built, macrotidal (2.8 m mean tidal range) estuary with extensive areas of productive tidal marshes interlaced with small marsh creek channels that connect marshes to the larger open bay area (<http://pie-liter.ecosystems.mbl.edu/>). The marshes are typical New England marshes (Warren and Niering 1993), with creeks bordered by a 2–5 m band of tall-form *Spartina alterniflora* (occupying elevations from ~2 to 2.5 m relative to mean lower low water) and the high-marsh platform (starting at elevation ~2.5 m relative to mean lower low water) dominated by *Spartina patens* mixed with *Distichlis spicata* (Johnson and others 2016) (Figure 1).

In terms of the prey available to mummichog, polychaete worms are the dominant prey item in the creek (Johnson and others 2007). Epibenthic and semi-infaunal mollusks such as the ribbed mussel (*Geukensia demissa*) or mudsnails (*Nassarius obsoletus*) are present but are too large to be consumed by mummichogs. In the high-marsh macroinfaunal prey biomass is only around 20% of that in the creek habitats (Johnson and others 2007), whereas biomass of epibenthic prey such as amphipods and insects is higher than in the creeks (Johnson and Jessen 2008; Johnson and Short 2013).

10 y Nutrient Enrichment Experiment

Three primary creek watersheds were artificially enriched with inorganic nutrients, and two creeks

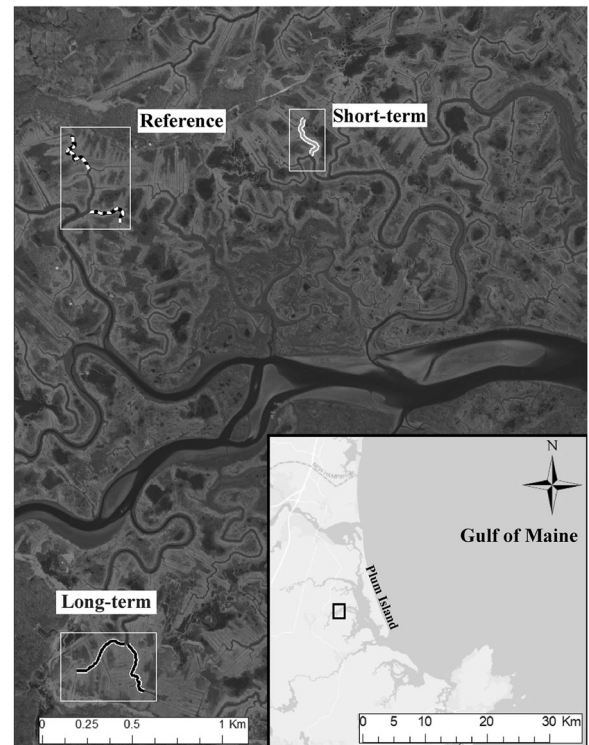


Figure 1. Map of Plum Island experimental tidal creeks. The nutrient-enriched creeks are outlined in solid white and the reference creeks in dashed black and white.

remained as ambient nutrient reference watersheds. Each system consisted of a total area of about 60,000 m², with a single primary tidal creek 300–500 m in length, similar tidal volumes ($4.1\text{--}7.5 \times 10^6$ L), and physicochemical characteristics (Deegan and others 2007). The muddy creek bottoms are 1–4.5 m wide with 60–80% of the mud-flat exposed at low tide. Two treatment creeks were initiated in 2004 and a third in 2009. The third creek was added because the creek edge geomorphic change results of the initial long-term enrichment experiment were unexpected (Deegan and others 2012) and thus not measured in the first few years of nutrient enrichment. The third enrichment creek serves as a space-for-time comparison to track geomorphic changes from the beginning of nutrient enrichment. In each treatment creek, nutrient-enriched seawater was added in proportion to the incoming tide to achieve moderately-to-severely eutrophic conditions, as designated by the Environmental Protection Agency (target 70–150 μM NO_3^-) (Deegan and others 2007, 2012). Nutrients were added during the temperate growing season (mid-May to mid-September) each year (2004–2012), with the pump rate adjusting every 10 min to the flux of incoming

flooding water, as a function of average predicted tide height for the day and measured water level, and stopped when the high marsh was flooded by approximately 20 cm of enriched water (Deegan and others 2007; Johnson and others 2016). Reference creek water had low, ambient nutrient concentrations ($< 5 \mu\text{M NO}_3^-$, $\sim 1 \mu\text{M PO}_4^{3-}$) (Spivak and Ossolinski 2016).

Creek Bank Edge Geomorphology

We used a combination of metrics to examine the response of mummichog production to changes in creek edge geomorphology and to select the sites for the landscape survey. These methods were the same as in Deegan and others (2012). The first metric was the number and length of fractures at the *S. alterniflora*/*S. patens* border per 50 m of primary creek length. Fractures, defined as a visible break in the marsh surface of 10 cm width or more that paralleled the creek channel within 3 m of the high marsh from the *S. alterniflora*/*S. patens* border. We calculated the fracture proportion by dividing the sum of measured fracture lengths by the 50 m of edge measured. Fracture proportion was estimated for 5–6 sections per creek, depending on the length of the primary creek. The second metric was the proportion of creek edge with *S. alterniflora*. This metric was based on a point intercept survey of the entire length of the primary creek, with points at 1-m intervals along a line 1 m from the high-marsh border toward the creek. Points were scored as either no vegetation (score of 0 representing mud bank or no bank present) or vegetated with *S. alterniflora* (score of 1). Sections where no bank was present, due to precipitous slumping, were excluded. The number of points with vegetation divided by the total number of points measured along the entire 250–300 m creek was used as an estimate of the percentage of vegetated creek bank. A creek bank edge Geomorphic Index was estimated as the mean of the proportion of fractured creek edge and the proportion of vegetated habitat. All creek bank edge geomorphic measurements were taken early in the growing season (April–May) so that vegetation did not obscure creek bank characteristics.

Nekton and Invertebrate Production

To quantify food web responses to nutrient enrichment, we compared the biomass and production of invertebrates and mummichogs between nutrient-enriched and reference creek areas over time. To measure invertebrate biomass, animals were collected from three habitats: the regularly

flooded mudflats, low marsh, and the infrequently flooded high marsh.

Macroinfaunal biomass was assessed in all three habitats using cores (6.6 cm diameter to a depth of 5 cm; $n = 3$ per habitat per creek) in late summer (July or August) in 2003–2006, 2009, and 2012. Animals retained on a 500- μm sieve were identified and counted. High-marsh epibenthic invertebrates (e.g., amphipods, isopods, spiders, crickets) were estimated using quadrats (0.0625 m²; $n = 10$ per creek) in the high-marsh habitat of each creek in 2009–2010, 2012. Samples were taken at least 5 m from the creek-side *S. alterniflora*/*S. patens* border, the short form *S. alterniflora*/*S. patens* border, and the upland terrestrial border. All vegetation was removed to the sediment surface and all invertebrates observed were recorded and collected. Some fast-moving species (for example, spiders) were counted but escaped collection. Macroinvertebrate production was calculated using an empirical production model (Tumbiolo and Downing 1994).

$$\log P = 0.24 + 0.96 \log B - 0.21 \log W + 0.3T - 0.16 \log (Z + 1) \quad (1)$$

where P is production in dry biomass, B is the mean annual biomass m⁻², W is the maximum individual body mass of the species, T is the mean annual surface water temperature, and Z is the mean depth of the water. We used a mean water temperature of 12 °C determined from the PIE LTER long-term water quality data (<http://ecosystems.mbl.edu/PIE/data>) and a mean depth of 0 m because our sites were intertidal.

To quantify mobile consumer biomass, flume nets (3–4 per primary creek treatment; (Rozas and Minello 1997)) were installed perpendicular to the creek channel and separated by at least 30 m. The flume nets extend 10 m back from the creek band and contain both high- and low-marsh habitats, providing a measure of the number of fish accessing these areas. From June to September, during a night-time slack high tide (within 48 h of the monthly spring tide), the walls were quickly pulled up, and the back and front panels attached to enclose all the nekton in the approximately 30 m² area. As the tide dropped, the fish moved into the low water refuge provided by the front conical panel that stretched into the creek channel. Capture efficiency was approximately 80% as estimated by adding tagged mummichogs when the nets were closed. The nets varied slightly among years; in 2003–2006, 2011–2012 nets dimensions were 10 m $\times$ 3 m $\times$ 1.5 m ($l \times w \times d$) and the mouth was placed at the creek edge in the low-

marsh tall *S. alterniflora* and extended into the *S. patens*-dominated high marsh; in 2009–2010 nets were 5 m $\times$ 2 m $\times$ 1.5 m and the opening was at the high-marsh/low-marsh boundary. Individual nekton were identified and measured (total length $\pm$ 1 mm; weight $\pm$ 0.01 g). Annual production (gC m⁻²) was estimated from the average of the 2 months with the greatest wet biomass m⁻² (typically August and September) converted to dry mass (20% of wet mass), and dry mass to C 50% of dry mass, and production estimated using a production to biomass (*P/B*) ratio based on body size-specific production rates (Banse and Mosher 1980).

To determine a maximum potential contribution of measured invertebrate production to mummichog, we applied a 10% trophic transfer efficiency and scaled the available production to the amount of time each habitat was inundated (50% for mudflat, 40% for low-marsh habitat, and 5% for high marsh; Johnson and others 2016), and then subtracted the annual mummichog production. A positive number indicates invertebrate production in excess of mummichog food demand, while a negative number indicates insufficient production to meet mummichog food demand. Typical trophic transfer efficiencies in aquatic systems range between about 3–12%, with ten percent the most common estimate in aquatic systems (Pauly and Christensen 1995; Jennings and others 2002).

Fish Growth Experiment

We conducted a mesocosm experiment testing fish responses to diets representing food availability in different habitat types in an outdoor, flow-through seawater system at Woods Hole Oceanographic Institution in May–July of 2015. We compared four diet treatments: (1) micro- and macroalgae, (2) detritus (dead marsh grass and associated microbes), (3) an arthropod (crickets (*Acheta domestica*)) representing terrestrial arthropods that mummichog are known to consume (Haas and others 2009; Nelson and others 2015) in high marshes, and (4) a mixed treatment which included algae, detritus, and crickets representing high-marsh arthropod prey. For 6 weeks, beginning in May 2015, mummichogs (total length 15 $\pm$ 2 mm; each treatment contained 20 fish at a density of 8 fish m⁻²) were held in 270-l translucent fiberglass tanks (n = 4 per diet treatment), with plastic vertical substrate to provide structure, that were situated in larger fiberglass tanks (2.7 m $\times$ 1.2 m $\times$ 0.8 m, 1 $\times$ w $\times$ d) serving as water baths to minimize day–night temperature fluctuations. The mesocosm system was exposed to

ambient light and weather conditions, and experimental tanks were continuously supplied with seawater from Vineyard Sound that was sequentially filtered through 500- and 150- μ m mesh bags to remove large particles and organisms (Spivak 2015; Spivak and Reeve 2015). Tanks were cleaned weekly. Fish were fed ad libitum during daylight hours, with food replenished as soon as it was consumed, in each of the diet treatments. At the end of 6 weeks, every individual fish from each treatment was measured (weight $\pm$ 0.01 g; total length $\pm$ 1 mm) and a random subset of 3–5 individuals from each treatment was immediately frozen (-40 °C) for lipid measurements. Lipids were extracted from fish muscles using a modified Folch method (Folch and others 1957) by placing tissues in a 2:1 chloroform: methanol (v/v) mixture, sonication for 20 min, and extracting overnight. Samples were then partitioned and the organic phase was removed. The total lipid extract (TLE) was concentrated under N₂ and determined gravimetrically.

Stable Isotope Analysis

To determine if a shift in resource use occurred as a result of the change in geomorphology, we analyzed the stable isotope composition of mummichogs and potential primary producer sources. Subsamples of mummichog from flume net samples were collected from each creek in August of 2014 and 2015. The fish were divided into three groups of 15 fish of similar size, total 45 fish per creek. Approximately 20 mg of flank muscle tissue was extracted from each fish, dried at 50 °C for 48 h, and homogenized using a ball-mill grinder. We collected samples of four primary producers (n = 5) from each creek in August of 2014 and 2015. Green filamentous algae were collected from the creek walls by hand. Mudflat detritus was collected using a 2 cm diameter core to a depth of 1 cm. Low-marsh *Spartina alterniflora* and high-marsh *Spartina patens* leaves were collected at five locations approximately 25 m apart running the length of each creek. The leaves were washed with deionized water to remove salts and encrusting material, dried at 50 °C, and ground using a ball-mill grinder.

Stable isotope analysis was performed using a Europa ANCA-SL elemental analyzer attached to a continuous flow Europa 20–20 gas source stable isotope ratio mass spectrometer at the Marine Biological Laboratory in Woods Hole, MA. For each sample, approximately 500 μ g of tissue was wrapped in a tin capsule and analyzed for $\delta^{13}\text{C}$, $\delta^{15}\text{N}$, $\delta^{34}\text{S}$, %C, %N, and %S. Isotope values are

expressed in δ notation according to the following equation:

$$\delta X = \left[\left(R_{\text{sample}} / R_{\text{standard}} \right) - 1 \right] \times 1000 \quad (2)$$

where X represents ^{13}C , ^{15}N , or ^{34}S and R represents the ratio of heavy to light isotopes. Standards used for $\delta^{13}\text{C}$, $\delta^{15}\text{N}$, and $\delta^{34}\text{S}$ values were Pee Dee Belemnite (PDB), ambient air (AIR), and Canyon Diablo Troilite (CDT), respectively. Duplicate values were obtained for about 20% of samples for quality assurance purposes.

The relative contribution of algae, mudflat detritus, low marsh, and high marsh organic matter sources to mummichogs was determined with a Bayesian mixing model. All stable isotope data were analyzed in R (v 3.4.3, R Development Core Team) using the package *MixSIAR* (v 3.1.7, (Semmens and others 2014)). Models were run in three chains with 1,000,000 iterations and a burn-in of 500,000 to allow for adequate model convergence. Concentration-dependent percent contributions of each source were calculated. From these source contributions, the trophic level of fish in each creek system was calculated according to the following formula:

$$\text{TL} = \frac{\delta^{15}\text{N}_{\text{ind}} - \sum(\delta^{15}\text{N}_{\text{source}} * \% \text{cont}_{\text{source}})}{\Delta\delta^{15}\text{N}} + 1 \quad (3)$$

where $\Delta\delta^{15}\text{N} = 3.2$ (Hussey and others 2014), $\delta^{15}\text{N}_{\text{ind}}$ is the nitrogen value of mummichogs, $\delta^{15}\text{N}_{\text{source}}$ is the nitrogen value of each particular source of primary production, and $\% \text{cont}_{\text{source}}$ is the percent contribution of each source to the consumer diet (Wilson and others 2009; Hussey and others 2014; Nelson and others 2015).

Statistical Methods

All statistical analysis was done in R (R Development Core Team) v3.4.3 (<http://www.R-project.org/>). We analyzed biomass and fish density by year using a linear mixed effects analysis in the *lme4* package (De Boeck and others 2011). Fish biomass and density were the dependent (y) variables and year of treatment the independent (x) variable. Control and treatment flume nets were paired 1–3 or 1–4 depending the number of nets used and treated as random effects. To control for changes in capture methods, we used a response ratio (Eq. 3) (Hedges and others 1999). For the long-term enriched creek, we first determined the break point in the response using a restricted maximum likelihood approach and then compared the model with the estimated break point to a null model with no

break point. For the short-term enriched, we used a Type III analysis of variance with Satterwaite approximation of degrees of freedom in the *lmerTest* package (Kuznetsova and others 2017). We generated p values for both creeks using a likelihood ratio test in the *lmerTest* package (Kuznetsova and others 2017).

$$\text{Response} = \log \frac{\text{Treatment}}{\text{Reference}} \quad (4)$$

The growth experiment was analyzed using one-way analysis of variance (ANOVA) and post hoc pairwise t tests to determine the effect of diet on mummichog growth.

RESULTS

Creek Bank Edge Geomorphology

There were 4–5 times as many vertical fractures in creek banks of the long-term nutrient-enriched creeks than in the reference creeks (Figure 2). As a result, blocks of low marsh had separated from the high marsh by deep crevices and slumped into the creek bottom, which created vertical scarps of high marsh directly adjacent to the creek edge. Long-term enrichment creeks had a higher percentage of cracked edge (mean 27%) than the reference creeks (mean 5%) over the same time period (2009–2012; t test, $p = 0.0005$, $df = 11$). There was no trend in the proportion of fractured creek bank

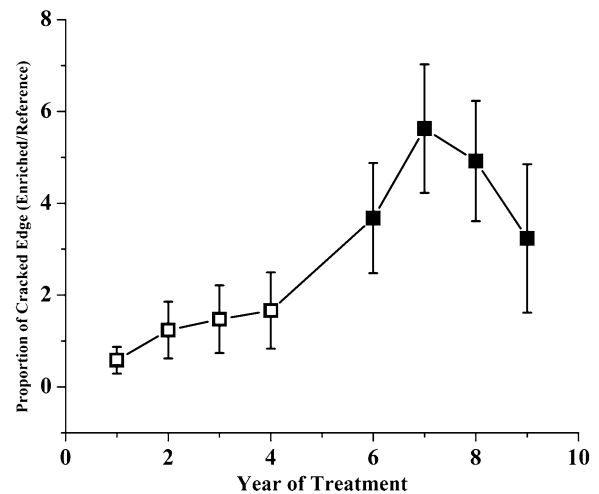


Figure 2. Changes to marsh creek edge in nutrient-enriched creeks relative to reference creeks. Open squares (short-term fertilization) and black squares (long-term fertilization) show the proportion of cracked creek edge relative to the control. We used the short-term creek as a space-for-time replacement since these measurements began in year six of the long-term enrichment. Error bars are standard error.

in the reference creeks (mean 5%). However, the rate of fracture development in the long-term enrichment creeks slowed in the last 3 years (Figure 2). The decline in fracture development was likely due to the high elevation of the *S. patens* edge, which was now adjacent to the creek and is not as frequently inundated with nutrient-enriched water (Johnson and others 2016). Creek edge geomorphic change was also evident in the short-term enrichment creek, in which the proportion of fractured edge progressively increased (linear regression, $p = 0.05$) from 5 to 13% over the four years of nutrient enrichment.

Nekton and Invertebrate Production

The ratio of fish biomass and density between the treatment and reference creeks varied significantly during the course of the experiment (Supplemental Table 1, Figure 3). In the long-term enriched, fish biomass and density increased during the first five years of the experiment and then declined after the change in creek geomorphic structure. The estimated break point was 5.31 years with a 95% confidence interval of 4.1–6.6. The model including the break point at year 5 explained significantly more of the data than the model by year with no break point (biomass $p < 0.0001$, density $p < 0.0001$). Both biomass and fish density increased in the short-term enriched creek until year six, although it appears the increase may have leveled off (LMER, biomass $p = 0.004$, density $p = 0.0002$). In the year prior to nutrient enrichment, fish biomass was lower in the short- and long-term enriched creeks compared to the reference creeks. In the long-term enriched creek, fish biomass increased by approximately 400% in the first 6 years of nutrient enrichment. However, in years 7–12 fish biomass production declined to levels at or below initial conditions. In the short-term enrichment creek, fish biomass increased $1.43\times$ reference in the first six years of enrichment. This is similar to pattern observed in the first 6 years of the long-term enrichment.

Invertebrate production increased in mudflat and both low- and high-marsh habitats following nutrient enrichment. However, infaunal invertebrate production within the regularly flooded *S. alterniflora* low-marsh and mudflat habitats was not sufficient to support the observed mummichog production, the annual deficits being 0.28 ± 0.11 and $0.12 \pm 0.13 \text{ gC m}^{-2}$, respectively (Table 1, Figure 4). It appears that mummichog energetic demand could only be met by adding high-marsh prey to the total invertebrate production. High-

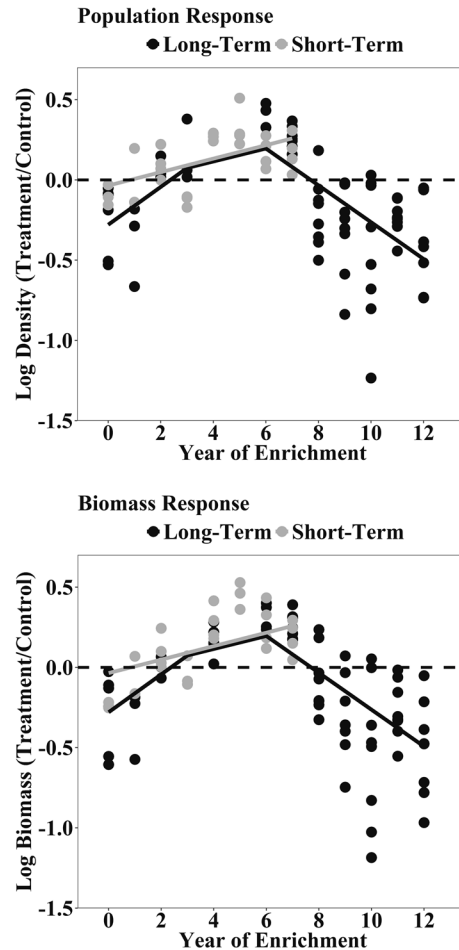


Figure 3. Top panel: The log ratio of mummichog peak biomass (measured as gC m^{-2}) in the long-term nutrient-enriched creek (black) and the short-term enriched creek (gray) relative to the reference against years of nutrient enrichment in that creek system. A ratio greater than zero indicates more production in the nutrient-enriched compared to the reference treatment areas. Year 0 is a pre-nutrient enrichment year (2003 long term, 2006 short term). Lines fitted using linear mixed effects regression.

marsh invertebrate production increased the available production by 55% relative to in-creek production in the reference creek. In the nutrient-enriched systems, high-marsh invertebrate production increased available production by 139%, which was $0.05 \pm 0.08 \text{ gC m}^{-2}$ greater than the production required to support mummichogs in the enriched system (Figure 4).

Fish Growth Experiment

Fish-fed insects or a mixed diet of insects, detritus, and algae grew nearly twice as large (insects $16 \pm 1.5 \text{ mm}$, mixed $12 \pm 1.1 \text{ mm}$) as fish

Table 1. Mean Annual Biomass in Creek Habitats of Macroinfauna, Macroinvertebrates, and Mummichog from the Control and Enriched Systems

Year	Years enrichment	Benthic macroinfauna production g y^{-1}						Macroinvertebrates production g y^{-1}		Mummichog production g y^{-1}	
		Mudflat		<i>S. alterniflora</i>		<i>S. patens</i>		High marsh		Creek mean	
		Control	Enriched	Control	Enriched	Control	Enriched	Control	Enriched	Control	Enriched
		Control	Enriched	Control	Enriched	Control	Enriched	Control	Enriched	Control	Enriched
2003	0	3.9 $\pm$ 0.8	2.4 $\pm$ 0.4	4.3 $\pm$ 1.0	0.7 $\pm$ 0.4	0.4 $\pm$ 0.2	0.4 $\pm$ 0.2	NA	NA	0.57 $\pm$ 0.43	0.38 $\pm$ 0.13
2004	1	0.9 $\pm$ 0.3	1.6 $\pm$ 0.6	4.4 $\pm$ 0.9	1.4 $\pm$ 0.8	0.9 $\pm$ 0.3	0.4 $\pm$ 0.1	NA	NA	0.54 $\pm$ 0.09	0.42 $\pm$ 0.05
2005	2	0.6 $\pm$ 0.3	2.9 $\pm$ 0.6	2.4 $\pm$ 0.6	2.5 $\pm$ 1.3	0.8 $\pm$ 0.2	0.4 $\pm$ 0.2	NA	NA	1.46 $\pm$ 0.21	1.42 $\pm$ 0.20
2006	3	6.3 $\pm$ 1.0	7.6 $\pm$ 1.3	2.2 $\pm$ 0.6	1.9 $\pm$ 0.6	0.1 $\pm$ 0.1	0.1 $\pm$ 0.1	NA	NA	0.92 $\pm$ 0.07	1.17 $\pm$ 0.07
2009	6	3.3 $\pm$ 0.9	6.3 $\pm$ 1.1	6.1 $\pm$ 1.3	0.2 $\pm$ 0.2	0.2 $\pm$ 0.1	0.2 $\pm$ 0.1	12.1 $\pm$ 2.8	33.9 $\pm$ 6.2	0.12 $\pm$ 0.05	0.27 $\pm$ 0.06
2010	7	NA	NA	NA	NA	NA	NA	26.7 $\pm$ 9.6	49.9 $\pm$ 16.0	NA	NA
2012	9	6.5 $\pm$ 0.8	12.4 $\pm$ 2.6	8.2 $\pm$ 1.6	9.3 $\pm$ 1.8	0.1 $\pm$ 0.1	0.4 $\pm$ 0.2	23.4 $\pm$ 1.0	24.4 $\pm$ 2.7	0.95 $\pm$ 0.14	0.39 $\pm$ 0.07

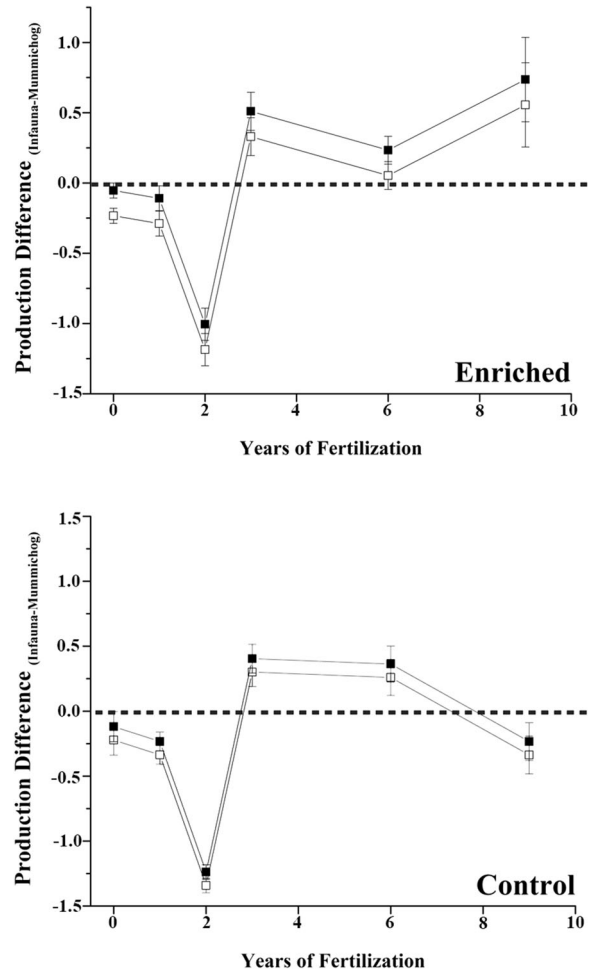
All values in $\text{g dry biomass m}^{-2} \text{ y}^{-1}$.

Figure 4. Macroinvertebrate production scaled to mummichog production. Open squares indicate combined production of macroinfaunal invertebrates (that is, annelids) from the mudflat, *Spartina alterniflora*, and *Spartina patens* habitats. Black squares represent combined macroinfaunal production with the addition of macroinvertebrates that occur only in *Spartina patens* habitat ($\text{g dry biomass m}^{-2}$). Production difference is the amount of invertebrate production minus the mummichog production. Values less than zero indicate production below levels that could sustain the observed production of fish. Error bars are standard error.

consuming algae-only ($4 \pm 0.7 \text{ mm}$) or detritus-only diets ($2 \pm 0.7 \text{ mm}$) (ANOVA, $p < 0.0001$) (Figure 5). Fish total lipid extract (TLE $\text{mg}^{-1} \text{ C fish}$), a proxy for lipid content, was significantly greater when they were fed more carnivorous diets (insects: $0.76 \pm .08$ or mixed diet: $0.68 \pm 0.02 \text{ mg}^{-1} \text{ C fish}$) compared to algal ($0.41 \pm .04 \text{ mg}^{-1} \text{ C fish}$) or detrital diets ($0.36 \pm 0.1 \text{ mg}^{-1} \text{ C fish}$) (ANOVA, $p < 0.0001$; Figure 5). Fish mortality was low and similar be-

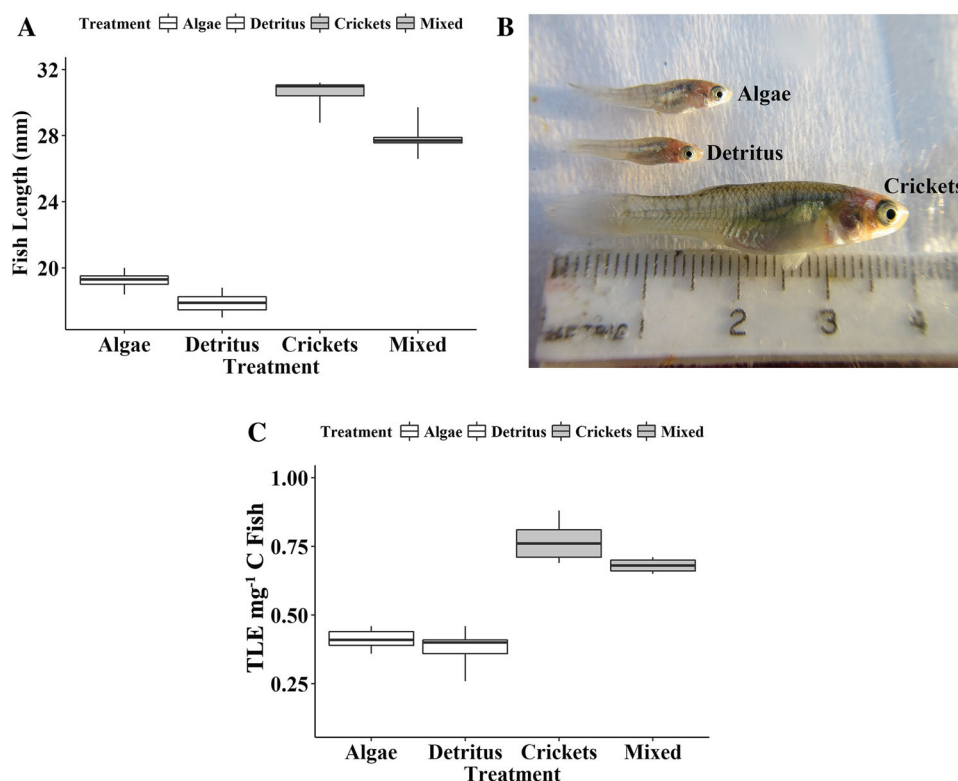


Figure 5. Mean fish size (upper panel). **A** Boxplot of fish length (boxes = standard deviation, whiskers = 95th and 5th percentiles) fed different diets, **B** image of average mummichog from each diet [algae only (top), detritus only (middle), arthropod protein only (bottom)], **C** boxplot of total lipid extract (TLE) per mg C of fish.

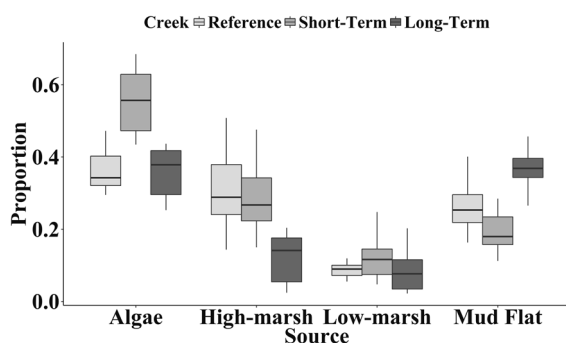


Figure 6. Boxplots of the source contributions to mummichog determined by MixSIAR (bars = mean, boxes = standard deviation, whiskers = 95th and 5th percentiles).

tween treatments, ranging from 7 to 11% (ANOVA, $p < 0.0001$).

Stable Isotope Analysis

The stable isotope values of carbon, nitrogen, and sulfur for mummichogs varied between the enriched and reference creeks, but the stable isotope values of the primary producers were fairly consistent between creeks, indicating differences in mummichog resource

use between systems (Supplemental Table 2). The stable isotope mixing model (MixSIAR) results indicated that mummichog in the reference creek had the highest contribution from high-marsh habitats ($27.8 \pm 16.2\%$), whereas fish in the long-term enriched creeks had the least contribution from high-marsh producers ($18.8 \pm 17.7\%$) (Supplemental Table 3, Figure 6). Mummichog in the long-term enriched creeks had the highest contribution from mudflat producers ($34.2 \pm 10.2\%$) compared to the reference creeks ($29.6 \pm 8.3\%$) and the short-term enriched creek ($19.8 \pm 6.0\%$) (Supplemental Table 3, Figure 6). In addition, fish in the short-term enriched creeks had the highest mean trophic level (3.0 ± 0.18) followed by the reference creek mummichog (2.7 ± 0.23) and the long-term enriched creek exhibited the lowest mean trophic level (2.2 ± 0.26) (Supplemental Table 3), suggesting fish in the long-term enrichment creeks had decreased access to prey items.

DISCUSSION

Our results demonstrate a feedback between bottom-up nutrient forcing and landscape control on the production of a key species that links salt marsh

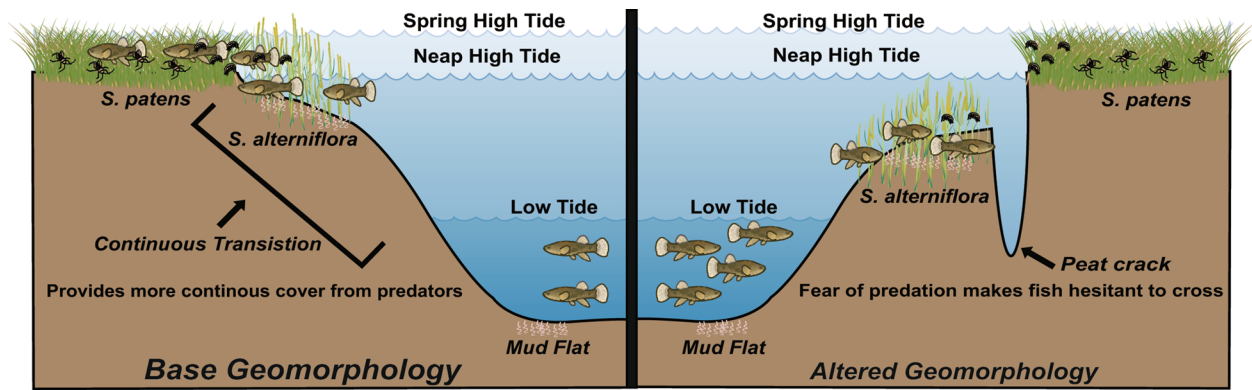


Figure 7. Long-term nutrient enrichment causes *S. alterniflora* habitat to collapse into the creek, limiting access to high-marsh invertebrates. Fish use more energy to access the high marsh which reduces trophic efficiency. In addition, these cracks also create crevasses where fish predators, such as American eel, can hide and feed on mummichog. Courtesy of the Integration and Application Network, University of Maryland Center for Environmental Science (ian.umces.edu/symbols/).

and estuarine food webs. The bottom-up stimulation of the food web initially increased mummichog production in both the long- and short-term nutrient-enriched systems (Deegan and others 2007) (Figure 3). Counter to our initial hypothesis, however, fish biomass declined over the long-term. We suggest that the decline in fish production was caused by a decoupling of the high-marsh food web from the creek food web due to the changes in creek geomorphology induced by nutrient enrichment (Figs. 2, 7).

Under bottom-up control, the initial increase in fish biomass was consistent with greater production of benthic algae, epibenthic invertebrates, and high-marsh invertebrates (Deegan and others 2007; Johnson 2011; Johnson and Short 2013). These observations correspond to those of plot-level and mesocosm studies that have demonstrated increased algal production and increased grazing (Neckles and others 1993; McGlathery 1995; Hillebrand and Kahlert 2001). Based on these initial results and the observations in other studies, we expected that rates of fish production would level off and persist at the new higher level of production as long as other components of the food web remained stimulated from the bottom-up press. We did not expect the sudden and sustained decline in fish production observed in the long-term enriched creeks (Figure 3). However, this same pattern has been observed in one other long-term nutrient enrichment experiment in headwater streams (Davis and others 2010). Although these results and other theoretical work suggest that nutrient enrichment can elicit unexpected responses to increased primary production via changes in food web efficiency (Rosenzweig 1971;

Bohannon and Lenski 2000; Stevens and Steiner 2006), we did not observe any change in the number or size of prey produced in the long-term enrichment (Table 1) (Johnson and Fleeger 2009).

We hypothesize that the loss of low marsh in the long-term enrichment that occurred after 5–6 years (Deegan and others 2012) overrode the bottom-up stimulation of mummichog production. Creek bank slumping and scarping disconnected the high-marsh habitat from the open water creek habitat, thereby reducing the availability of high-marsh invertebrates (that is, energy) to mummichogs. The loss of low-marsh habitat decreased the availability of invertebrate prey items to mummichogs, while the edge cracks and loss of a ramp of low-marsh habitat transformed the creek bank edge from a vegetated transitional area providing cover from potential predators, into an exposed cracked vertical edge with little protective cover (McIvor and Odum 1988; Deegan 2002).

Studies on mummichog diet and growth in this system prior to the extensive geomorphic change showed a 115% increase in herbivory and 43% decline in growth rate indicating greater reliance on the algal food web pathway in the enriched creeks (Lockfield and others 2013). Our stable isotope analysis of the current food web showed a decline in high-marsh resource use by approximately 20% in the long-term enriched creeks, whereas high-marsh resource use was similar between the reference and short-term enriched systems (Figure 6). Mummichog in the long-term enriched creeks relied more heavily on mudflat detrital sources, supporting our hypothesis of the lack of access to high-marsh resources. Further, fish in the long-term enriched creeks fed at a lower

trophic level (2.2) compared with the fish in the reference (2.7) and short-term enriched system (3.0) suggesting less access to invertebrate prey (Supplemental Table 3). Previously, a long-term (9y) isotope survey of Plum Island Sound showed a significant positive linear relationship between the number of days the tide floods the high marsh and mummichog trophic level (Nelson and others 2015). In that study, mummichog trophic level increased from approximately 2.25 with 20 days of high-marsh flooding to 3.25 with 36 days of high-marsh flooding during the growing season (Nelson and others 2015). The trophic levels observed here for mummichog fall within the ranges observed previously in the long-term isotope study. The lower trophic level of mummichog in the long-term enriched creek suggests they receive approximately 10–14 days less access to high-marsh habitats than fish in the reference or short-term enriched creeks. In a typical year, this would equate to approximately one-third to a half of the growing season flooding high tides.

Our growth experiment supports these results and demonstrated that mummichog must have adequate access to invertebrate prey to reach sizes similar to fish observed in the creeks (Figure 5). Mummichogs are seasonally abundant with the majority of fish hatching on the same full moon in the spring and remaining within the primary tidal channel (300 m home range) in which they hatched (Taylor and others 1979; Able and others 2006). Therefore, size differences between marshes are due to local conditions within the areas where the mummichog hatch. Our results are consistent with other ecosystems that show that access to prey items in intermittently available habitats is important for growth (Clavero and others 2009; Howe and others 2014).

Rapid growth is important for young-of-year fishes to escape predation, survive winter, and reach reproductive maturity (Halpin 2000). In our experiment, mummichogs that consumed insects had higher lipid/carbon ratios which suggest they were better able to store lipids (Figure 5C). This is important because adequate lipid reserves are needed for winter survivorship and recruitment to older age classes. Slower growth rates in the algae- and detritus-only treatments indicate that it is unlikely that a diet shift to algae in the nutrient-enriched creek could account for the bottom-up stimulation of mummichog production in the landscape-scale experiment.

At both the control and long-term enriched sites, macroinfaunal invertebrate production in the mudflat and *S. alterniflora* habitat was generally not

sufficient to support mummichog production (Figure 4). Despite being flooded only 5% of the time, inclusion of the macroinvertebrates that occur only in *S. patens* high-marsh habitat increased the available insect prey resources by 55% in the reference creeks and 139% in the long-term enriched creeks (Figure 4). This observation combined with the results from the mummichog growth experiment suggests that access to marsh habitats is critical to mummichog production.

Mummichog access to marsh habitats is intermittent and controlled by local marsh geomorphic characteristics, such as bank characteristics, marsh elevation, and tidal height (Able and others 2003; Currin and others 2003). The magnitude of high-marsh productivity supporting creek channel food webs, as well as mummichog trophic level, is directly correlated with flooding frequency and duration (Nelson and others 2015; Baker and others 2016). In macrotidal New England marshes (tide range 2.8 m), creek mudflats and the low marsh are inundated by 100% of the tides, whereas the high marsh is inundated by 35% of the tides but for only 5% of the time (Drake and others 2009; Johnson and others 2016). Mummichogs follow the leading edge of the flooding tidal water up into the marsh habitat, using the low marsh both as a foraging area and as a ramp to the high marsh. Increased access to high-marsh areas provides greater foraging opportunities for terrestrial insects (Haas and others 2009; Nelson and others 2015) and decreases competitive interactions between conspecifics by increasing effective ecosystem size and forage space by several orders of magnitude over the confines of the tidal creeks.

Although top-down control by predators could have decreased mummichog abundance, we found no evidence to support this. First, we did not observe an increase in potential predators, such as juvenile American eel (*Anguilla rostrata*), that can remain in the creek through low tide. Plum Island estuary is in the Acadian biogeographic province, north of Cape Cod; thus, the classic crab predators of more southern estuaries are not present. During the years of this study, there were no blue crabs and no burrowing crabs of any kind found in PIE. The presence of blue crab and fiddler crab was documented after 2012 (Johnson 2014, 2015), but they are scarce. The only potential crab predator of mummichog is the green crab (*Carcinus maenas*), but they were very sparse (1–2 caught in our flume nets) and we did not observe any change in green crab density during the course of the experiment. Second, larger predators like striped bass (*Morone saxatilis*) do not usually move into, or remain at low

tide, in these relatively shallow primary creeks and do not forage on the marsh surface (Pautzke and others 2010; Kennedy 2013). Additionally, mummichog represent less than 15% of the gut contents by weight of striped bass in the spring and summer months in Plum Island (Ferry and Mather 2012).

Perceived predation risk may have changed mummichog foraging behavior and their use of different marsh habitats. Predation risk can alter species distribution across a landscape, with risk-averse prey avoiding areas of high predation risk (Lima 2002; Thomson and others 2006; Laundré and others 2010). In salt marshes, juvenile American eel hide in crevices to ambush their prey, which includes mummichog (Wenner and Musick 1975). The mummichog may perceive the cracks and crevices as potential hiding places for predators and avoid them in favor of continuous bottom.

CONCLUSION

Our ecosystem-scale experiment demonstrated that a nutrient-induced spatial change in habitat structure altered the energy flow across landscape elements in the food web, and this effect was greater than the bottom-up stimulation in the habitats that were still accessible (for example, the creek and mudflats). The functional loss of access to essential production sources via the change in creek habitat structure overrode the initial bottom-up stimulation of the food web and caused a decline in mummichog production. Loss of habitat area and quality of creek edge marsh have ecosystem-scale impacts that are disproportionate to the areal extent of this habitat (~ 4% of the vegetated marsh) because of its critical role in providing the access to the much larger in extent high marsh. Our results suggest that nutrient enrichment and landscape configuration are competing controls on secondary production and that identifying which mechanism is operating in a system is important to understand how a system may respond to change.

These results provide insight into the function of spatially coupled food webs. Higher trophic level organisms utilize and connect multiple food web channels via their movement (Neutel and others 2007; Rooney and others 2008). Others have observed, and we provide further evidence here, that food webs become increasingly coupled at higher trophic levels (Rooney and others 2008; Rooney and McCann 2012). In our system, the more compartmentalized saltmarsh creek and marsh platform food webs are coupled in space by mummichog (Figure 7). In turn mummichogs are a critical food web node that couples terrestrial

(wading birds) and aquatic (fish) predator food webs (Figure 7). Loss of saltmarsh productivity to these predators could result in increased top-down pressure on other energy channels as these highly mobile and longer-lived consumers switch to alternative prey sources. Thus, our observations support the landscape food web theory proposed by Rooney and others (2008) that changes in the flow of energy at smaller spatial scales could elicit food web change at the ecosystem scale by disrupting spatially coupled food webs.

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