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Cross-habitat access modifies the ‘trophic relay’ in New England saltmarsh ecosystems

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ABSTRACT

In New England saltmarshes, mummichogs (*Fundulus heteroclitus*) connect the vegetated marsh and creek food webs by opportunistically foraging on the invertebrate communities of the marsh surface when access is permitted by tidal flooding and marsh-edge geomorphology. Via their movements, mummichog represent a critical food web node, as they can potentially transport energy from the marsh surface food web to creek food web and exert top-down control on the communities of the vegetated marsh surface. Here, we demonstrate that access to the marsh surface (afforded by marsh-edge geomorphology) did not impact mummichog distribution across the marsh platform and exhibited no evidence of top-down control on their invertebrate prey. Thus, mummichogs function as initial nodes in the trophic relay, unidirectionally moving energy from the vegetated marsh to the creek food web. Reduced marsh surface access via altered marsh-edge geomorphology results in a 50% to 66% reduction in total energy available to aquatic predators via this route. Estuarine systems are intimately connected to coastal and offshore systems via consumer mediated flows of energy; thus, disruptions to the trophic relay from the marsh surface at the tidal creek scale can have far reaching impacts on secondary productivity in multiple disparate systems and must be accounted for in considerations of impacts to future food-web function.

1. Introduction

The Landscape Theory of Food Web Ecology predicts that the asynchrony of production in space and time at lower trophic levels produces large variation in the concentration of resources that support food webs (Rooney et al., 2008). Higher trophic level mobile consumers are capable of responding to changes in the distribution of resources by coupling food webs to facilitate the transfer of energy across spatial gradients (Abrantes et al., 2015; Nelson et al., 2012; Rooney et al., 2008). In saltmarsh ecosystems this concept was first described as a “trophic relay”, where small mobile consumers access intermittently available habitats (e.g. high marsh habitats periodically flooded at high tides), transferring energy and nutrients from these habitats and making it available to consumers in the larger, spatially-coupled estuarine food web (Bergamino et al., 2014; Kneib, 2002; Nelson et al., 2013). This production is then transported across the ecotone to the coastal ocean via a series of trophic interactions between increasingly mobile consumers (Jones et al., 2020; Nelson et al., 2013).

The first leg of the aquatic portion of the saltmarsh trophic relay begins at the land/water interface where the highest astronomical tides infrequently inundate the marsh habitats higher in elevation, establishing the zonation of habitats and allowing small but mobile aquatic consumers to forage on semi-terrestrial prey (Lesser et al., 2020; Nelson et al., 2019; Rozas, 1995). When these consumers return to deeper water as the tides fall, they transfer the energy and nutrients produced in these habitats to the food webs in the tidal creeks as they are consumed by larger predators (Kneib, 2002). Therefore, movements by the consumers that couple energy channels across these boundaries are critical to the

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flow of energy in the entire ecosystem. It has been well documented that the configuration of the marsh landscape can influence this flow of energy by facilitating or preventing consumer movement via bank characteristics, marsh elevation, and tidal height (Able et al., 2003; Currin et al., 2003; Kneib, 2002; Lesser et al., 2020; Nelson et al., 2019). Changes to the marsh creek edge structure and geomorphic characteristics are well documented in marshes of the northeastern U.S. These changes include the disruption of the continuous transitional habitats from the tidal creek edge to the high marsh through the development of large cracks (>10 cm) between the creek and the marsh, in addition to slumping and loss of this habitat (Able et al., 2018; Deegan et al., 2012; Nelson et al., 2019). These changes can regulate food web dynamics by altering aquatic predator access to specific marsh habitat zones and, as a result, the magnitudes of top-down and bottom-up forcing in these systems can be considered a function of the duration of access and the intensity of predation (Fleeger et al., 2008; Johnson and Fleeger, 2009; Minello and Rozas, 2002; Power et al., 1996).

Mummichogs (*Fundulus heteroclitus*) are the most abundant mobile consumer in the saltmarshes of coastal New England (Deegan et al., 2007) and act as a critical coupler of marsh and creek systems. Mummichogs are omnivorous, consuming detritus, algae, and benthic invertebrates (Kneib, 1997; Kneib, 1986). As the monthly spring tides flood the high-marsh (area above mean high water dominated by *Spartina patens* and *Distichlis spicata*), these fish leave the creek and move across the low marsh transition onto the high marsh and feed on terrestrial and semi-terrestrial invertebrates (Kneib, 1997; Lockfield et al., 2013). Increased access to this semi-terrestrial zone is correlated with elevated trophic level (Nelson et al., 2015) and increased terrestrial invertebrate consumption (Lesser et al., 2020). Nelson et al. (2019) demonstrated that the geomorphology of the low to high marsh transition is a more important control on mummichog production than bottom-up stimulation of the creek food web via nutrient addition.

Mummichogs link the aquatic and terrestrial food webs by moving between them; altered geomorphology disrupts their function within the aquatic portion of the food web by reducing their movement of energy from terrestrial area to the creek (Lesser et al., 2020). However, it is unknown how reduced access impacts the function of mummichogs within the marsh platform food web from which they remove energy. Mobile consumers can locally depress prey in the habitats from which they consume energy (Polis et al., 1997; Randall, 1965; Schindler et al., 1996); in this way, mummichogs have the potential to influence energy flow patterns in the terrestrial areas of the marsh through top-down control of the invertebrate communities. Less mummichog access would release these communities from mummichog predation and increase the flow of energy to other connected systems (i.e. upland forests, or other marsh systems via migratory birds). However, the extreme disparity in area of the marsh vs. creek habitat, as well as the uniquely short time window in which natural access to the marsh is afforded to mummichogs in this system would make it difficult to apply these case studies to this system. Moving between two systems has the potential to make mummichogs the preeminent node in the functioning of both the marsh platform and aquatic food web. Understanding their role in the flow of energy within and between both systems, as well as how these connections are impacted by their ability to move from one to the other, is essential to predict how systems of energy flow and consumer production will shift with continued marsh change.

The objective of this study was to assess the impact of mummichogs within the food web of the marsh platform and its relationship to access regimes afforded by the geomorphic features of the marsh landscape. We focus on the connection between high marsh invertebrate prey and mummichog because previous work has shown that access to intermittently flooded habitats increases fish growth and biomass (Haas et al., 2009; Nelson et al., 2019). Although, other studies have shown that mummichogs frequently feed on detritus and algae (Allen et al., 1994; McMahon et al., 2005), we have demonstrated that mummichog growth rate is nearly double when fed diets that contain insect prey compared to algae or detritus alone (Nelson et al., 2019). Further, long-term food web analysis in Plum Island shows that mummichog trophic level increases significantly with greater access to high marsh habitats during the growing season (Nelson et al., 2015). Given this line of evidence demonstrating the importance of access to the prey items on the high marsh to mummichog we have two primary hypotheses. First, we hypothesized that altered geomorphology would limit high marsh area accessed by individual mummichog. Decreased high marsh access would then impact the trophic relay by decreasing the amount of high marsh area from which energy is exported to the creek food web and impact the function of mummichogs on the marsh platform by lessening the area over which they exert predation pressure. Second, we hypothesized that decreased access to the high marsh by mummichog populations would not alter invertebrate populations, because mummichogs do not exert any top-down control on the vegetated marsh given the limited time of high marsh access and large area of the high marsh platform. Finally, after testing these two hypotheses, we combine these results with previous work assessing marsh energy relay via mummichog production to outline the energetic connections between marsh, creek, and coastal/offshore food webs, and the potential impacts of altered mummichog high marsh access to the vegetated marsh on mobile predator behavior, production, and movement. This study provides insight into the mechanisms by which landscape configuration impacts the relay of energy in marsh food webs, and in turn, the broader connections between the estuarine and coastal system.

2. Methods

2.1. Site description

This study took place in Plum Island Estuary (PIE), a temperate, macrotidal estuary with extensive areas of productive tidal saltmarshes connected to tidal rivers and the open bay by small tidal creek channels (Fig. 1). The saltmarshes of PIE are typical New England marshes (Niering and Warren, 1980; Warren and Niering, 1993). Creek mudflat areas are exposed only at low tide. A 2–5 m wide band of low-marsh along the creek edge, dominated by tall-form *Spartina alternaflora*, is regularly inundated at high tide, and a high-marsh, dominated by *Spartina patens* and *Distichlis spicata* and inundated only during spring cycle high tides, accounting for 35% of the tides but for only 5% of the total time during the summer growing season (Drake et al., 2009; Johnson et al., 2016).

Sampling for this study occurred at 3 tidal creeks (Fig. 1, Lat 42.731430, Long −70.839473); Sweeney Creek and Club Head Creek, which have altered low marsh geomorphology, and West Creek, which is an established reference creekshed in this system (Deegan et al., 2012; Lesser et al., 2020; Nelson et al., 2019). These three creek systems are sites of the TIDE Project (Deegan et al., 2012; Deegan et al., 2007), a long term ecological study on the ecosystem effects of nutrient enrichment on saltmarsh ecosystems. Sweeney and Club Head Creeks were the subject of 13 and 8 years (respectively) of nutrient enrichment via the addition of nitrate fertilizer. One of the major findings of the TIDE Project was the long-term, enrichment-induced degradation of the creek edge at these two sites relative to reference systems (Deegan et al., 2012). Sweeney and Club Head Creeks have low marsh zones that contain large cracks and areas that have completely separated from the high marsh platform (See Fig. S1A–B and Deegan et al., 2012 for examples of this degradation). While these features also occur naturally and can be found in the low marshes of most creeks in this system, these two creeks have low marshes that are significantly more degraded than would be found naturally (Deegan et al., 2012; Lesser et al., 2020; Nelson et al., 2019). Nutrient addition ceased in 2016; however, a legacy of this manipulation remains in the form of this altered creek edge regime (Deegan et al., 2012; Lesser et al., 2020; Nelson et al., 2019).

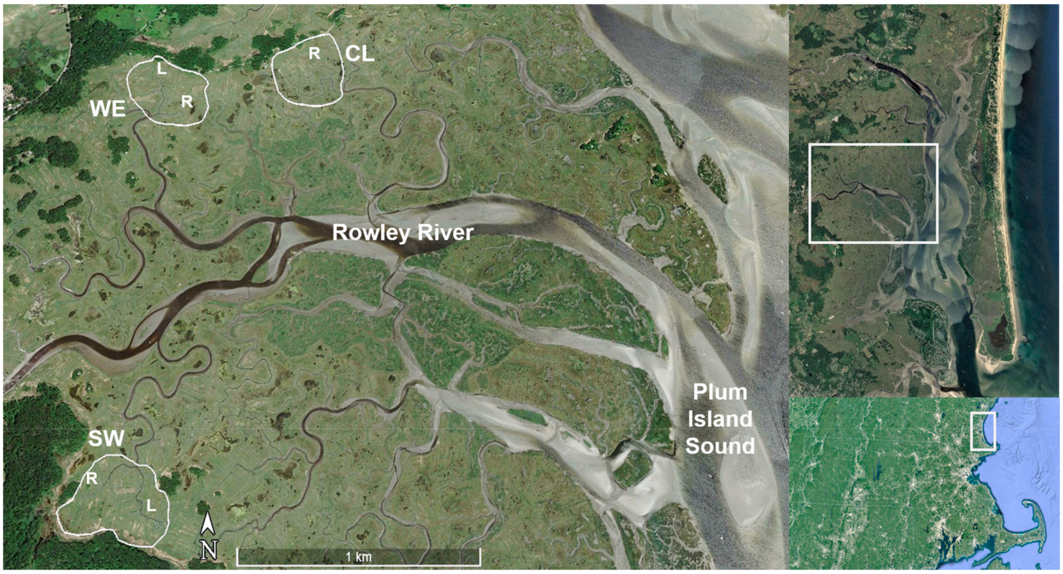

Fig. 1. Map depicting creeksheds used in this study. Creeks are located in the tidal marshes near Rowley, Massachusetts (Lat 42.731430, Long −70.839473). WE = West Creek (reference geomorphology creekshed), SW = Sweeney Creek, CL = Club Head Creek (altered geomorphology creeksheds). "L" and "R" refer to the reaches of each creekshed used in this study; two reaches were surveyed at WE and SW and one was surveyed at CL. Top-right inset depicts Plum Island Estuary, MA with a box that outlines the bounds of the larger map in relation to the rest of the estuary. Bottom-right inset depicts MA with a box that outlines the location of Plum Island Estuary within the coastline.

2.2. *Mummichog field surveys*

In order to understand the impact access (i.e. creek edge geomorphologies, Deegan et al., 2012), Fig. S1A–B) has on the extent of the foraging area used by mummichogs, biomass and abundance on the high marsh were assessed using lift traps and flume nets (McIvor and Odum, 1986; Rozas, 1992). Flume nets have been continuously used to sample marsh nekton entering the high marsh in this system throughout the duration of the TIDE Project (Nelson et al., 2019). These nets are permanently installed perpendicular to the creek channel. Each net consists of 5 mm (bar size) polyethylene mesh enclosing an area 3 m wide and 10 m back from the creek edge, capturing animals using the first 10 m of the high marsh (Nelson et al., 2019). The mesh sides of the nets were rolled down flush with the marsh surface; during a nighttime flooding high tide during the spring tidal cycle, the walls and front were quickly pulled up, enclosing all nekton within. As the tide dropped, nekton moved into the low water refuge provided by the front conical panel that stretches into the creek channel and was collected the following morning (McIvor and Odum, 1986; Nelson et al., 2019). Lift traps were made of the same polyethylene mesh material, but instead enclosed a 2 × 2 m area and were installed 15 m, 30 m, and 45 m from the creek edge. These traps were used to capture consumers in the same manner as flume nets; lift traps sample nekton across the marsh platform (>10 m from the creek edge) and were used to assess the distribution of mummichog individuals that successfully cross the low marsh boundary into the high marsh. Four flume nets and 2 transects of 3 lift traps (at 15 m, 30 m, and 45 m) were deployed per study creek reach (2 reaches for Sweeney and West creeks, one reach for Club Head creek). Flume net and lift trap sampling occurred over two nights in July and again in August 2019. Catches from the 30 m and 45 m traps were combined into one bin for analyses; all bins are standardized as the biomass or abundance per m2 sampled within each bin. All fish were euthanized using MS-222 in accordance with University of Louisiana Lafayette IACUC #2019–8717-003.

2.3. *Bomb calorimetry*

In order to calculate the amount of energy made available to consumers via mummichog populations, we include mummichog calorimetric analysis. Previous work has shown mummichog have similar caloric densities across systems (Lesser et al., 2020, Table 1). In addition to calorimetric data from mummichogs in Club Head and West Creeks previously reported in Lesser et al., 2020, we include previously unreported data from Sweeney to calculate the energy produced per m2 and per creek reach (Table 1). As reported in Lesser et al., 2020, 16 additional mummichogs were collected in each creek for calorimetric analysis, during the last 1–2 h of the falling tide via beach seine. In the lab, each individual was weighed, measured, and dried for 48 h at 60 °C before being ground into a powder. Each dried individual sample then was split into two 0.10 g - 0.15 g subsamples, which were pressurized to 30 PSI in a stainless-steel bomb and run in a Parr 6725 calorimeter attached to a Parr 6772 calorimetric thermometer. The calories/g of each mummichog was determined by taking the average of the two subsamples (Lesser et al., 2020).

2.4. *Terrestrial invertebrate sampling*

We surveyed invertebrate communities before and after periods of mummichog predation to determine whether mummichogs exert control on invertebrate populations in this system, and whether creek edge geomorphology modulates this control. Terrestrial invertebrates were sampled in conjunction with mummichog sampling. The invertebrate sampling took place on the day prior to the first tide to flood the high marsh and the post spring tide sampling on the first day after the last tide to flood the high marsh. Two 45 m transects, starting at the low/high marsh boundary and ending towards the upland border of the marsh, were sampled per creek reach (2 reaches for Sweeney and West creeks, one reach for Club Head creek). A 0.0625 m2 quadrat was randomly tossed in the high marsh at 4 sites along each transect, once each at 0 m (the high marsh side of the low/high marsh boundary), 15 m, 30 m, and 45 m from the low/high marsh boundary towards the upland. Invertebrates within each quadrat were sampled in two steps. First, invertebrates in the high marsh canopy were captured via suction sampling. This was accomplished using a modified Stihl BG55 leaf blower with a small flowerpot with the bottom removed attached to the end of the blower tube, and a 0.0625 m2 piece of wedding tulle clipped

Table 1
Total mummichog abundance, biomass, mummichog biomass per m^2 per creek, as well as average caloric content of mummichog individuals, at each creek and reach surveyed. Biomass data is from all flume nets and lift traps at each creek reach surveyed. "Calories Produced" refers the mummichog calories per m^2 of high marsh surveyed, and "Total Calories" refers to the total calories of captured mummichog populations. Caloric data from West and Club Head Creeks was reported in Lesser et al., 2020; caloric data from Sweeney Creek was collected at the same time but was previously unreported.

Creek	Reach	Total abundance	Total biomass (g)	Biomass (g/m^2)	Average caloric content (cal/g)	Calories produced (/m^2)	Total calories (cal)
West Creek	*L*	285	465.65	3.23	4283.68	13,836.29	19,94,695.60
	R	298	405.1	2.81		12,037.14	17,35,318.77
Sweeney Creek	*L*	144	220.88	1.53	4116.64	6298.46	9,09,283.44
	R	141	161.95	1.12		4610.64	6,66,689.85
Club Head Creek	*R*	118	175.52	1.22	4218.69	5146.80	7,40,464.47

inside the flower plot. The blower was run over the quadrat in the vacuum setting, pulling in invertebrates and capturing them on the tulle. Next, invertebrates were sampled from the marsh surface by removing the vegetation within the quadrat down to the sediment and picking invertebrates off the bare quadrat for 10 min. A second observer was present during this entire process, recording information about any invertebrates seen escaping from each quadrat before they could be sampled; these were included in analysis of invertebrate abundance but not in analysis of invertebrate biomass. Sampling was conducted once right before the spring tidal cycle began and once right after the spring tidal cycle had completed (1.5 to 2 weeks later, ~20 flooding tides per spring tidal cycle), capturing the invertebrate communities before and after periods of mummichog access and predation. Sampling was repeated for 3 consecutive spring tidal cycles (3 pre-spring tide sampling events, 3 post-spring tide sampling events, 6 events in total).

Suction and clip plot samples were placed on ice and taken to the lab for analysis. Organisms were identified to the lowest taxon possible, usually to level of order, unless they could be further identified to the family level. Invertebrate taxa were classified as "terrestrial" (based on the same criteria used in Lesser et al., 2020, primarily spiders, mites, and other insects), "semi-terrestrial", which included amphipods (*Orchestia grillus*) and isopods (*Littorophiloscia vittata*), or "snails" (coffee bean snails *Melampus bidentatus* and Hydrobiidae spp.). The total biomass and number of individuals of each terrestrial and semi-terrestrial taxon was recorded; for snails, the number of individuals and individual shell length was recorded and used to determine the shell-free weight (Johnson, 2011).

2.5. Data analysis

Mummichog biomass and abundance was assessed by distance from creek edge (0-10 m, 15 m, 30-45 m) using non-parametric Kruskal-Wallis tests followed by post-hoc Wilcoxon tests to determine statistically significant comparisons between creeks at each distance from the creek edge, where appropriate. Spatially paired biomass and abundance response ratios were calculated as

$$Response\ \ Ratio = log\frac{Altered_{dist}}{Reference_{dist}}$$

where *Altered* and *Reference* refer to the invertebrate biomass or abundance at geomorphically altered (Sweeney and Club Head) or reference (West) creeks, and *dist* refers to the quadrat at each distance from the creek edge, transect, and creek reach (Hedges et al., 1999; Nelson et al., 2019). Two-sample Wilcoxon tests were used to determine statistical difference between total and taxa category-specific invertebrate biomass and abundance response ratios before and after the spring tide, and one-sample Wilcoxon tests were used to determine if spatially-paired biomass and abundance response ratios were statistically different from zero. Two-sample *t*-tests were used to assess invertebrate community diversity (Simpson's Diversity, D) before and after the spring tide (Fig. S3). All data were analyzed in R (v4.0.0).

3. Results

Total mummichog biomass, abundance, biomass per m2 of high marsh, calories per m2 of high marsh were higher in the reference systems with more high marsh access (Table 1). Total calories available to predators via mummichogs was 50–66% greater in the reference system than in the altered systems (Table 1).

Mummichog biomass (Fig. 2A, $\chi^2_{df=2} = 13.048$, $P < 0.05$) and abundance (Fig. 2B, $\chi^2_{df=2} = 14.363$, $P < 0.05$) per m2 was significantly higher in West Creek than in Sweeney Creek and Club Head Creek at 0 m–10 m from the creek edge (Wilcoxon, $P < 0.05$). There were no differences in mummichog biomass (Fig. 2A, $\chi^2_{df=2} = 2$ (15 m), $\chi^2_{df=2} = 3.665$ (30–45 m), both $P > 0.05$) or abundance (Fig. 2B, $\chi^2_{df=2} = 0.324$ (15 m), $\chi^2_{df=2} = 0.527$ (30–45 m), both $P > 0.05$) per m2 at any creekshed at 15 m or 30 m–45 m from the creek edge.

There were no differences in the total biomass (Fig. 3A) or

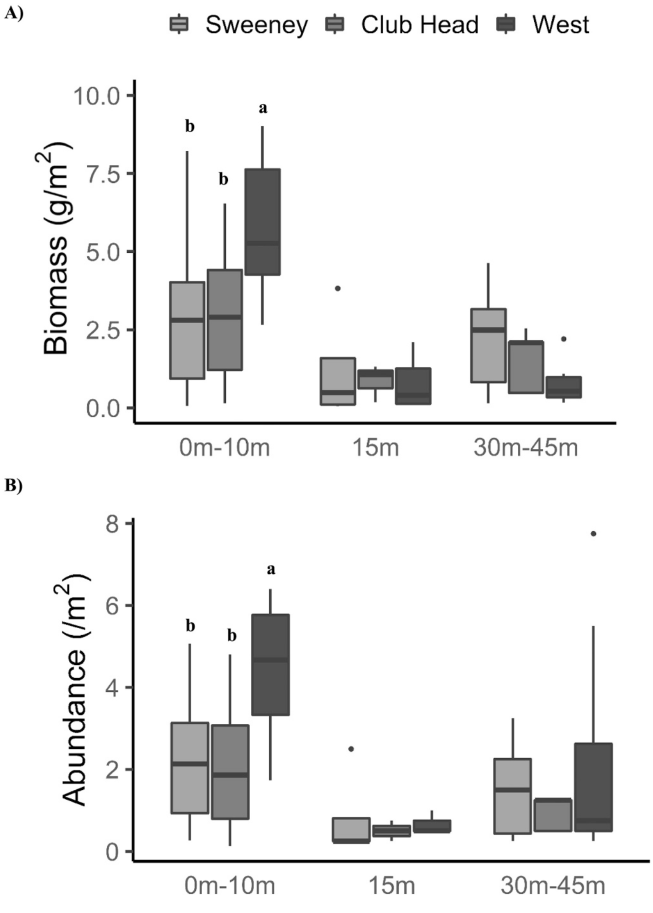

Fig. 2. Mummichog biomass (A) and abundance (B) per m^2 of sampled area across the high marsh platform at 0-10 m, 15 m, and 30–45 m from the creek edge. Letters refer to significant differences between creeksheds at a given distance (Wilcoxon test, $P < 0.05$).

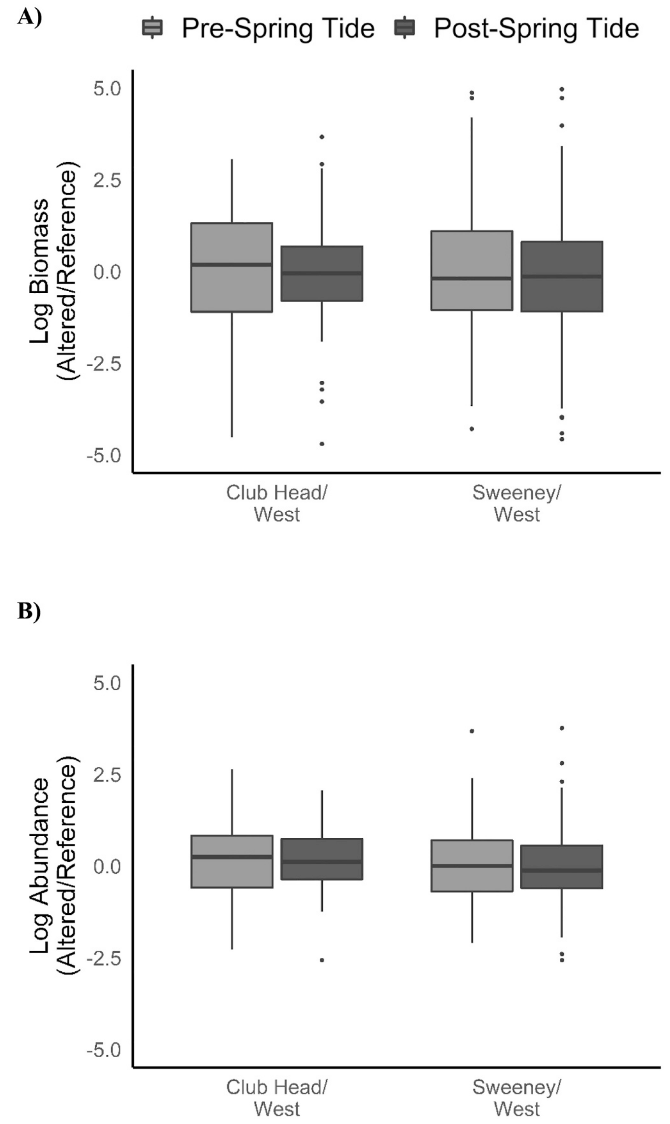

Fig. 3. Total invertebrate biomass (A) and abundance (B) response ratios. No ratio was found to be significantly different from zero (One sample Wilcoxon test, $P > 0.05$) and response ratios were not statistically different before and after the spring tidal cycle at all creeks (Two sample Wilcoxon, $P > 0.05$).

abundance (Fig. 3B) response ratios of invertebrate communities before and after the spring tidal cycle at all creeks (Two sample Wilcoxon test, all $P > 0.05$), and response ratios were not different from zero (One sample Wilcoxon test, all $P > 0.05$). Taxa category-specific invertebrate biomass (Fig. S2 A–C) and abundance (Fig. S2 D–F) response ratios were not significantly different before and after the spring tidal cycle (Two sample Wilcoxon, $P > 0.05$) or from zero (One sample Wilcoxon, $P > 0.05$) for all categories. There were no differences in the diversity (Simpson's Diversity Index, D) of invertebrate communities on the high marsh platform at Club Head Creek, Sweeney Creek, and West Creek before and after the spring tidal cycle (Fig. S3, Two sample t-test, $p > 0.05$).

4. Discussion

Here, we demonstrate that within these spatially-coupled food webs, mummichogs function solely as the first node in the trophic relay of energy from the marsh food web to the creek food web and exhibit no reciprocal impact on energy flow within the marsh platform. Creek systems with altered marsh geomorphology presented reduced overall mummichog population sizes and biomass (Lesser et al., 2020; Nelson et al., 2019). However, fish that successfully reached the marsh platform despite reduced access in these altered systems were able to access the same extent of high marsh habitat as in reference systems (Fig. 2). Mummichog foraging also had no effect on invertebrate communities at any creek, suggesting that mummichogs do not exert top-down control on terrestrial invertebrate populations in this system (Fig. 3, S2, S3). This demonstrates that creek geomorphology impacts energy flow unidirectionally from the high marsh to the aquatic food web by functioning as a gate that limits mummichog access on the flooding tides. This reduces the number of mummichog individuals altered creeks can support, reducing the total amount of energy that is moved from the marsh platform to the creek, and is therefore available to predator populations. The dampening of the relay from the marsh impacts the degree to which the system can support secondary production, as well as elicits altered patterns of movement and predation pressure across the estuary as a response to this reduction in energy.

The geomorphology of the marsh edge influences the total number of fish that access the marsh, but not how they are distributed across the marsh once they get there (Fig. 2). The amount of high marsh energy that individual mummichog can gather and move from the high marsh to the creek food web is limited by how efficiently they can access the high marsh within the short window of tidal inundation that affords them the ability to be there. Our data indicate mummichogs that successfully enter the high marsh in altered creeks cover a similar marsh area as in the reference creek system (Fig. 2). This suggests that even though creeks with altered creek edge geomorphology limit the ability of mummichog to access the high marsh, those that are still able to make it through the low marsh into the high marsh are not limited in foraging area. Low marsh geomorphology likely acts like a filter, preventing most fish from accessing the marsh; however, if a fish does successfully navigate the marsh edge, they forage throughout the entire high marsh habitat. Thus, geomorphologic change potentially disrupts the link between the high marsh and creek by altering number of individuals supported by high marsh derived materials and not by changing the amount of high marsh area over which energy that gets incorporated into the creek food web.

Mummichog foraging removes invertebrate biomass from the high marsh (Lesser et al., 2020; Nelson et al., 2019). Despite this, we found no evidence that foraging by aquatic predators during spring tides was enough to limit invertebrate populations on the high marsh (i.e., no top-down control, Fig. 3, S2, S3). Previous studies in this ecosystem have come to similar conclusions, with mummichog removal experiments showing little effect on the abundance and biomass of annelids in the tidal creeks (Fleeger et al., 2008; Johnson and Fleeger, 2009). Creek edge geomorphology asymmetrically dampens energy movement in this system, decreasing the flow of energy from the marsh platform to the creek food web, but not changing the way that energy flows through the food web of the marsh platform itself through any cascading feedback due to predation release (for example, via the release of shredders (e.g. isopods, amphipods) from predation by mummichogs increasing litter decomposition).

A feature of saltmarsh food webs is their reliance on energy relayed from disparate food webs within the marsh landscape mosaic by consumers moving between habitats (Kneib, 2002). The results presented here demonstrate the importance of marsh landscape features in the unidirectional relay of energy from the high marsh to aquatic food webs, mediated by mummichogs (Fig. 4). Poor linkage with high marsh in altered creeks reduces the total number of individual mummichogs that acquire the resources they need to survive, and in that way reduces the total amount of energy that is conveyed from the high marsh into subtidal aquatic food webs. Using our biomass and caloric measurements we determined that the total amount of energy available via mummichogs in altered creeks is approximately 50% to 66% lower than in unaltered creek systems (Table 1). This energy deficit that arises from the loss of the trophic subsidy from the marsh must be dealt with by the

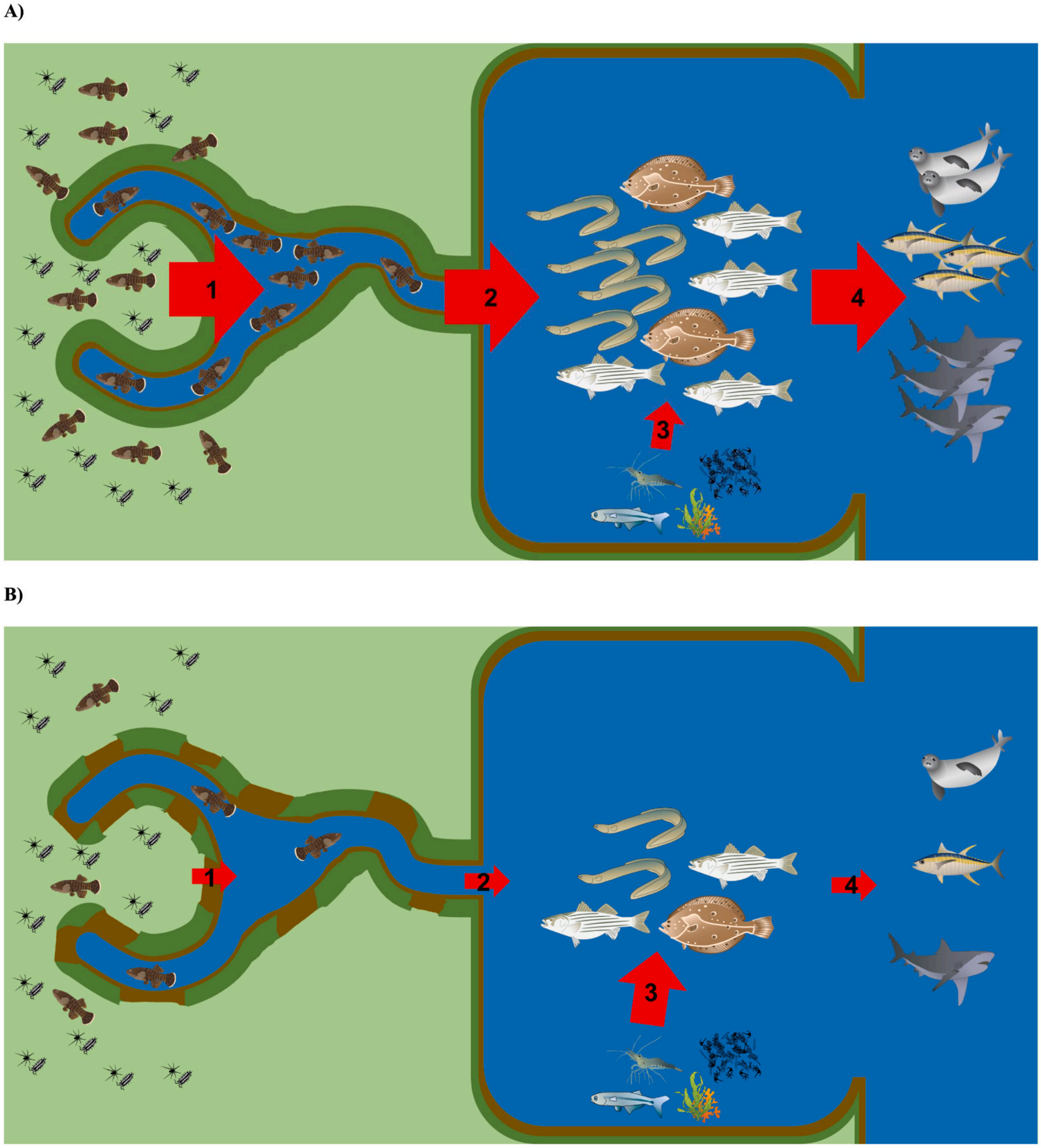

Fig. 4. Conceptual diagram of the “trophic relay” from reference (A) and altered (B) PIE marsh creeks. A) 1: Energy is transferred from the semi-terrestrial high marsh to the aquatic areas of the creek via mummichog consumption of invertebrates in the high marsh zone on the flooding spring tides. 2: Mummichogs are consumed by larger predators and, in this way, the terrestrial zone supports the populations of these predators via trophic relay by mummichogs (Baker et al., 2016). 3: consumers in PIE rely on prey produced via multiple energy pathways (i.e. benthic, water column production). 4: Consumers migrate out of PIE, supporting populations of larger coastal predators. Thus, energy from the semi-terrestrial marsh zone supports offshore/coastal populations (including many fisheries-relevant species) via trophic relay from marsh creeks. B) 1: Altered geomorphology prevents mummichogs from accessing the marsh during the flooding spring tides; this means less total energy is relayed from the semi-terrestrial zone to the creek. 2: Fewer mummichogs are supported by the altered creek system, and therefore less terrestrial energy is relayed to predator populations via mummichog consumption. 3: In order to compensate for the reduced availability of energy from the high marsh relayed via mummichogs, predators may derive more energy from other channels of energy available to them in PIE. 4: The reduced energy provided by the altered system can support fewer predators, which in turn may reduce the ability of PIE to support offshore/coastal populations. Altered geomorphology on the scale of the creek impacts the ability of PIE to support coastal ecosystem by disrupting the trophic relay of production off the high marsh.

aquatic predator populations that rely on this channel of energy to support their biomass. On longer time scales, this may manifest as reduced secondary production in the system, as the predator population sizes adjust to the new pattern of energy available to support their biomass (Fig. 4). In a more immediate sense, predators may make up for the dearth of marsh-derived energy in the system by altering their movements, and therefore, patterns of predation, across the estuary (Furey et al., 2018; Kittle et al., 2017; Sims et al., 2006). For example, predators could focus their foraging efforts on more productive creeks with intact geomorphology (Figs. 5, 6) or, they could increase the amount of pressure they exert on other channels of energy that support the food web (for example in PIE, benthically-sourced *Paleomonetes pugio*, or pelagically-sourced *Menidia menidia*). Observed without considering the importance of the trophic relay in the food web, these potential responses to a change in the total amount of energy supporting the bottom of the food web may be instead interpreted as isolated increases in top-down control at the local scale. For example, in stream-riparian systems, the addition of marine-derived material (via anadromous salmon returning to freshwaters) to the system subsidizes stream fish production to levels beyond what is possible from internal sources alone. Larger-than-expected stream fish populations, then, are able to put additional pressure on emergent aquatic invertebrates within the

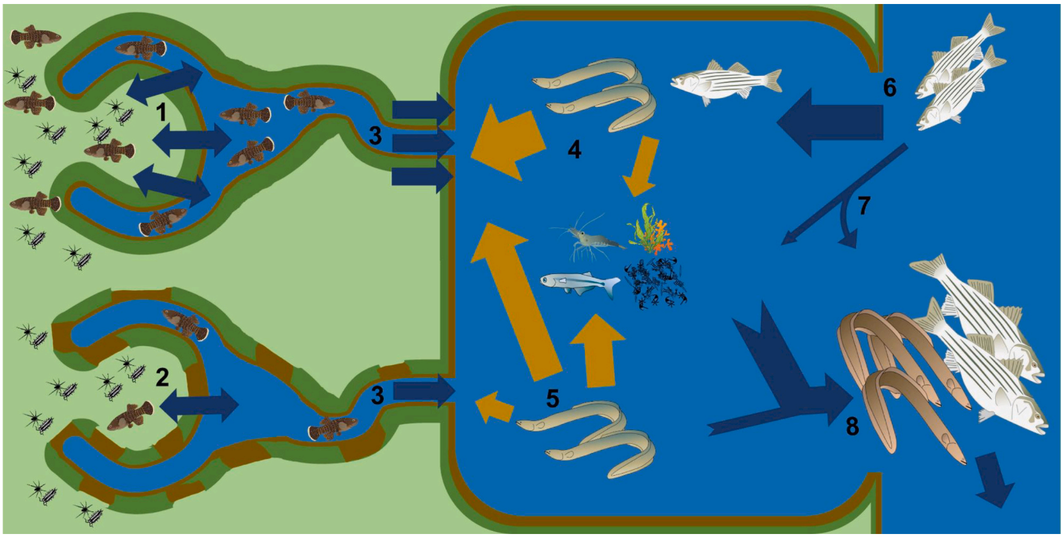

Fig. 5. Conceptual diagram of the patterns of movement (blue arrows) and predation pressure (yellow arrows) expected due to the "trophic relay" from reference and altered PIE marsh creeks. 1: Mummichogs move onto the high marsh during the flooding spring tides to consume semi-terrestrial invertebrates, then return to the creek as the tide recedes. 2: Altered geomorphology impacts this movement on the population scale; individual mummichogs are able to access and use the same extent of the marsh as the reference system (note the similar sized arrows at 1 and 2), but fewer of them cross the altered low marsh (reduced number of arrows at 2 compared to 1). 3: This leads to reduced mummichog populations in altered creeks that relay less energy from the high marsh to consumers. 4: Resident predators, such as yellow-stage American eels, prey on many species and therefore rely on multiple energy pathways. 5: In order to compensate for the reduced marsh energy available via mummichogs at altered systems, predators must exert increased predation pressure on these other energy pathways to support their biomass and/or abandon these less productive areas and consume prey from more productive creek systems. These impacts may illicit a response that appears top-down in these areas/on these other prey sources; however, they are the result of the reduction of the total energy available to support the base of the food web and are ultimately a bottom-up response. 6: Migratory predators, such as striped bass, arrive at PIE seasonally, and can consume prey across the entire estuary; reductions in energy may impact where and how they choose to forage across that extent, resulting in similar patterns that have the appearance of top-down effects but are, in reality, bottom-up responses. 7: Additionally, the migrating striped bass may choose not to enter or stay in PIE for the summer, as the altered system does not produce enough energy to support their populations. 8: ultimately, both eels and bass migrate out of PIE, acting as another step in the relay of marsh production to coastal/offshore food webs (i.e. adult eels) or influencing the trophic dynamics of other estuaries they choose to reside in (i.e. striped bass); the degree to which PIE marsh production supports their biomass and growth influences the effect they will have on these other systems. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

system, resulting in locally-depressed invertebrate populations and subsequent additional impacts on other connected systems (Collins et al., 2020). Observed without considering the influence of marine production on the food web of a particular stream-riparian area, one would mistakenly conclude that a feature of stream-riparian ecosystems is top-down control via stream fish on emergent aquatic invertebrates. In reality, this apparent "control" is merely stream fish responding to the total amount of energy available to them via all inputs of energy to the system (local and marine-derived). To truly understand the complete scope of energy flow within food webs, it is essential to consider all externally as well as internally-sourced connections, as interpreting responses without considering the entire scope of energy flow within and between systems may lead to misrepresentations of which factors alter food web function.

Disrupting the trophic relay of energy from the marsh surface to the estuary could ultimately reduce the amount of consumer productivity that can be supported by the system. This may have far reaching impacts, as estuarine systems are themselves intimately connected to offshore and coastal ecosystems via the movement of these consumer populations into and out of estuaries. For example, yellow-stage American eels (*A. rostrata*), important consumers when they reside in these estuaries, with mummichogs representing a large proportion of their diet (Eberhardt et al., 2015), migrate out of estuaries once reaching sexual maturity in order to join massive spawning aggressions in the Sargasso Sea. Migrating eel populations act as a conduit of estuarine productivity to coastal and offshore food webs, as they are preyed upon by large coastal consumers as they exit and migrate to these spawning grounds (Béguer-Pon et al., 2012). Thus, a reduction in high marsh energy relayed by mummichogs to eels at the scale of a marsh creek can ultimately influence the production of coastal consumers, as fewer eels can be supported by the degraded marsh system, and therefore less marsh productivity is further relayed to the coastal food web (Figs. 4, 5). Striped bass (*Morone saxatilis*), which derive as much as 44% of their biomass from marsh sources (Baker et al., 2016), are coastal migrants that can take up residence in PIE during the summer, or simply stop over for a shorter time period before leaving for other estuaries (Pautzke et al., 2010). Striped bass do not access the marsh platform directly; as high trophic-level predators, they rely on mummichogs as conduits of this productivity via consuming them from multiple creeks across the estuary (Baker et al., 2016). Reduced mummichog access to the high marsh due to altered geomorphology leads to reductions in the energy from the marsh platform that becomes available to these predators via this pathway and as a result the number and biomass of striped bass the system can support may be reduced (Figs. 4, 5). Additionally, altered mummichog relay may impact striped bass behavior in regards to entering and remaining in the estuary, altering trophic dynamics both within PIE and in other estuaries that they may decide to reside in instead (Fig. 5). The influence of geomorphology on the trophic relay of marsh energy via mummichogs in marsh creeks has the potential have an astonishingly vast impact on consumer production and behavior at large scales; quantifying the influence of this phenomenon on predator populations and the connection between linked systems is an area that requires further analysis. The connectedness of these food webs is vital to their function cannot be ignored when considering future impacts on these systems.

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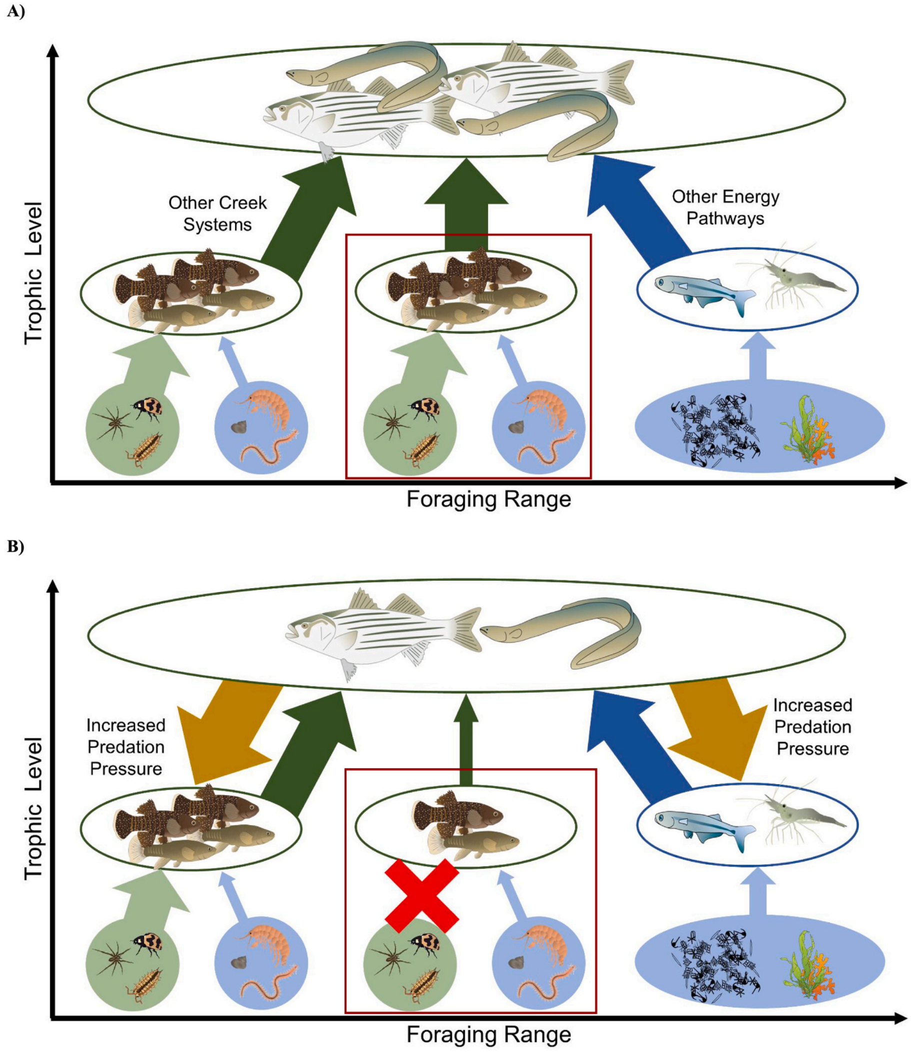

Fig. 6. Diagram depicting energy flow through PIE food webs as it relates to the size of an organism's foraging range. Red box refers to a creek system as focused on in this study; in A) the focal system has reference geomorphology (i.e. West Creek), and in B), the focal system is geomorphically altered (i.e. Sweeney and Club Head Creeks). As trophic level increases, foraging range tends to increase, and consumers couple more food webs/energy sources in space (Rooney et al., 2008). As geomorphology in some creeks becomes degraded (i.e., center in B), consumers that rely on energetic input from the marsh platform (via mummichogs) must respond to that loss of energy by increasing their pressure on other parts of the food web (yellow arrows) and/or by changing their population sizes to reflect the amount of energy available to them in the system. Thus, if space is not considered when assessing these food webs, these responses to a "bottom-up" change in the system may be misinterpreted as a "top-down" impact. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

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Author contributions

JL: Writing - original draft; Writing - review & editing; Conceptualization; Investigation; Data curation; Formal analysis; Investigation. OF, KF: Data curation; Formal analysis; Investigation. LD: Funding acquisition; Project administration; Resources; Supervision; Validation. DJ: Supervision; Validation; Methodology; Writing - review & editing. JN: Supervision; Validation; Methodology; Writing - review & editing.

Declaration of Competing Interest

There are no conflicts of interest concerning our article.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.fooweb.2021.e00206.

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