

Title:

Habitat decoupling via saltmarsh creek geomorphology alters connection between spatially-coupled food webs

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Lesser, J. S., Floyd O., Fedors K., Deegan L. A., Johnson, D. S., Nelson, J. A. 2021. Cross-habitat access modifies the ‘trophic relay’ in saltmarsh ecosystems. *Food Webs*, *in review*.

Abstract

Consumer-mediated movement can couple food webs in distinct habitats and facilitate energy flow between them. 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, I use gut content analysis, calorimetric analysis, and field surveys to demonstrate that access to the marsh surface (afforded by marsh-edge geomorphology) impacts the trophic relay of marsh production to creek food webs. Fish populations in creeks with greater connectivity had a higher total biomass of terrestrial invertebrates in their guts. However, bomb calorimetry showed no difference in the average caloric content of mummichog individuals from creeks with different creek edge geomorphology. Access also 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.

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 ensure the transfer of energy across spatial gradients (Rooney et al., 2008). The coupling of food webs in space enhances consumer biomass beyond the internal production of the system; thus, landscape features that control access to an external subsidy can alter the assembly of a food web and the trophic relationships between food web members (Polis et al., 1997). For example, aquatic insects can subsidize riparian predator populations, and therefore the geomorphologic properties that controls that ability of insects to thrive can indirectly influence the community of these adjacent riparian ecosystems, both by promoting predator growth (Sabo and Power, 2002) and altering the strength of trophic interactions between species (Graf et al., 2017). The distribution of external food web inputs across a landscape can alter local food web structures, as areas closer to high-quality fluxes may disproportionately rely on these external input sources, while areas further away may rely more on internally-sourced pathways (Marcarelli et al., 2011). Food webs in specific habitat types differ in their ability to incorporate and respond to subsidies, thus the distribution of habitats across a landscape alters the spatial organization of food webs and the

resource channel reliance of consumers (Marczak et al., 2007; Ziegler et al., 2019).

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), removing energy and nutrients from these habitats and making it available to consumers the larger, spatially-coupled estuarine food web (Kneib, 2002). This production is then transferred across the ecotone to the coastal ocean via a series of trophic interactions between increasingly mobile consumers. 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 flow of energy in the entire ecosystem. It has been well documented that the configuration of the marsh landscape can exert control on 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 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 control 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)

The mummichog (*Fundulus heteroclitus*), the dominant mobile consumer in the saltmarshes of coastal New England (Deegan et al., 2007), functions as an important link between different saltmarsh habitats due to its movement between marsh habitats. Mummichogs are omnivorous, consuming detritus and algae (and macroinfauna, once they grow large enough) in the creeks (Allen et al., 1994; James-Pirri et al., 2001; Kneib, 1997, 1986). Mummichog also use high tides during the monthly spring tidal cycle, which can flood the high-marsh platform, to leave their creek habitats and feed on invertebrates on the high marsh (Kneib, 1997; Lockfield et al., 2013). Access to the high marsh zone is correlated with elevated trophic level (Nelson et al., 2015), growth rate (Able et al., 2006; Javonillo et al., 1997), and increased protein consumption (Haas et al. 2009) in mummichog. Nelson et al. (2019) demonstrated that local creek geomorphology is a more important control on mummichog production than bottom-up stimulation of the food web via nutrient addition to saltmarsh creeks.

In this study, I sought to assess effect of high marsh access, via creek geomorphology, on mummichog diet, population energetic content, and role in the relay of energy between food webs of the marsh platform and the creek. I used gut content analysis to determine if mummichogs in creeks with varied geomorphological regimes alter the amount of high marsh prey they consume and paired this with bomb calorimetry and field surveys to examine the effects of geomorphology on fish energetic condition and movement of energy from high marsh food webs into aquatic food webs. I also used field surveys to determine how access impacts the

high marsh area accessed by individual mummichog and the ability of mummichogs to control prey populations on the high marsh. Decreased high marsh access could 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. Mobile consumers can locally depress prey in the habitats from which they consume energy from (Polis et al., 1997; i.e. 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. This study provides insight into the mechanisms by which landscape configuration impacts the relay of energy in marsh food webs, and in turn, its impact on the ability of estuarine ecosystems and coastal/offshore food webs to which they are connected.

Methods

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 creek channels (Figure 1). The saltmarshes of PIE are typical New England marshes (Niering and Warren, 1980; Warren and Niering, 1993), with creek mudflat areas exposed only at low tide, a 2-5 m wide band of low-marsh along the creek edge, dominated by tall-form *Spartina alterniflora* (TSA) and regularly inundated at high tide, and a high-marsh platform, dominated by *Spartina patens* (SP) and *Distichlis spicata*, and inundated only during spring cycle high tides.

Breder Trap Study

Creek bank measurements were taken early in growing season (May-June) so that geomorphologic features were not obscured by vegetation. First, cracks were counted and

measured along 200 m to 300 m transects (depending on creek length) laid along the TSA/SP boundary on both sides of each creek. “Cracks” are breaks in the low marsh 3 m from the TSA/SP boundary that were greater than 10 cm wide at any point and had intact marsh at their ends (Deegan et al., 2012; Lesser et al., 2020; Nelson et al., 2019). “Slumps” are large fractures that had progressed to point that they had completely broken off from the creek bank and left large peat blocks in the creek channel or had broken marsh at their ends. In addition, the proportion of vegetated creek edge was measured using a point-intercept survey along the transect. At 1m intervals, on a line 1m towards the creek from the TSA/SP boundary, the presence or absence of vegetation within a circle 30cm in diameter was assessed, with vegetated points scored as 1 and unvegetated points scored as 0. These metrics were used to create a creek bank Geomorphologic Index (Deegan et al., 2012; Lesser et al., 2020), defined as:

$$GI = \% \text{ vegetated creek edge} * \frac{\# \text{ of slumps}/50m}{\# \text{ of fractures}/50m} * \frac{\text{total length of fractures}}{50 m}$$

with lower values indicating a more intact low marsh, and high values signifying more disintegration of the low marsh habitat. Geomorphologic Index is a proxy for mummichog access to the high marsh; mummichogs using the high tide to access the high marsh prefer to cross the low marsh via uninterrupted stretches of vegetation, and do not cross large breaks in the benthic environment. In total, the geomorphology of 24 creek branches throughout PIE were surveyed; from these measured creeks, three were chosen along the *GI* gradient: Club Head (CL) had highly altered geomorphology, West (WE) had an intermediate amount of altered geomorphology, and Mud South (MS) creek was relatively intact (Figure 1A).

To assess the consumer use of the high marsh zones of the creeks of interest, eight stations per creek were established to capture mobile consumers moving in to and out of the high marsh during the nighttime spring high tide. Each station consisted of two Plexiglass Breder traps, each

of which was a 30 cm x 15 cm x 15 cm box made of two sections held together by size-84 rubber bands, and a funnel made from two 30 cm x 15 cm wings joined at a 45° angle with a 12 mm opening (Breder, 1960). One trap was placed in the low-marsh 1m from the TSA/SP boundary with its opening facing the creek, to capture consumers as they moved with the rising tide from the creek into the high marsh area, and one was placed in the high-marsh area 1 m from the TSA/SP boundary, to capture consumers exiting the high marsh as the tide receded. Breder traps were placed about 3 hours before the high tide by clipping the surrounding grass to the sediment and staking them to the ground to ensure they did not move. Stations were no less than 25 m apart to ensure independent samplings. Sampling spanned two nights in total; two creeks were sampled on the first night, and one creek was sampled on the second, due to the limited number of traps available. Traps were allowed to fish for 6 hours total, set 3 hours before the incoming tide and left for 3 hours on the outgoing tide, after which captured consumers were collected and frozen for analysis. The majority of the consumers captured were mummichogs, aligning with what is known about the structure of animal communities in these creeks (Deegan et al., 2007).

In the lab, mummichog guts were removed (stomach and intestines) and weighed, then the gut contents were removed and weighed. Contents were analyzed under a microscope and identified to the smallest recognizable taxa, as plant/algal material, or as unidentifiable digested material. The number of individuals of each identifiable taxa, and the estimated percent composition of gut content of identifiable taxa, plant/algal material, and unidentifiable digested material was recorded (Gibbons and Gee, 1972; Hyslop, 1980). Data was split into three separate categories for analysis: primary producers (plant/algal material), terrestrial prey, and aquatic prey. Terrestrial prey included invertebrate prey species found on the marsh platform that not found in the aquatic habitat (Lesser et al., 2020). Only individuals that had food material in their guts that

was recognizable as one the aforementioned categories were considered for analysis; loose prey fragments were not included in prey taxa counts but were included in estimations of percent compositions of gut content. In total, 346 mummichog individuals were analyzed for this study.

Marsh Platform Survey

Sampling for this study occurred in 2019 at 3 tidal creeks branching from the Rowley River (Figure 1B); Sweeney Creek and Club Head Creek, which have been well-established as systems with 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, 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 (Deegan et al., 2012). 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).

In order to understand the impact access (i.e. creek edge geomorphologies, Deegan and others 2012, Lesser et al., 2020) 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 ½ cm 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 x 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.

Terrestrial Invertebrate Sampling

Marsh platform invertebrate communities were surveyed before and after periods of mummichog predation to determine whether mummichogs exert control on invertebrate

213 populations in this system, and whether creek edge geomorphology modulates this control.

214 Terrestrial invertebrates were sampled in conjunction with mummichog sampling. Two 45 m

215 transects, starting at the low/high marsh boundary and ending towards the upland border of the

216 marsh, were sampled per creek reach. A 0.0625 m² quadrat was randomly tossed in the high

217 marsh at 4 sites along each transect, once each at 0 m (the high marsh side of the low/high marsh

218 boundary), 15 m, 30 m, and 45 m from the low/high marsh boundary towards the upland. Two

219 such transects were sampled per study creek reach (2 reaches for Sweeney and West creeks, one

220 reach for Club Head creek). Invertebrates within each quadrat were sampled in two steps. First,

221 invertebrates in the high marsh canopy were captured via suction sampling. This was

222 accomplished using a modified Stihl BG55 leaf blower with a small flowerpot with the bottom

223 removed attached to the end of the blower tube, and a 0.0625 m² piece of wedding tulle clipped

224 inside the flower plot. The blower was run over the quadrat in the vacuum setting, pulling in

225 invertebrates and capturing them on the tulle. Next, invertebrates were sampled from the marsh

226 surface by removing the vegetation within the quadrat down to the sediment and picking

227 invertebrates off the bare quadrat for 10 minutes. A second observer was present during this

228 entire process, recording information about any invertebrates seen escaping from each quadrat

229 before they could be sampled; these were included in analysis of invertebrate abundance but not

230 in analysis of invertebrate biomass. Sampling was conducted once right before the spring tidal

231 cycle began and once right after the spring tidal cycle had completed (1.5 to 2 weeks later, ~20

232 flooding tides per spring tidal cycle), capturing the invertebrate communities before and after

233 periods of mummichog access and predation. Sampling was repeated for 3 consecutive spring

234 tidal cycles (3 pre-spring tide sampling events, 3 post-spring tide sampling events, 6 events in

235 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. 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).

Calorimetric Analysis

Sixteen additional mummichog were collected in each creek for calorimetric analysis, during the last 1-2 hours of the falling tide via beach seine. In the lab, each individual was weighed, measured, and dried for 48 hours 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.

Methods Comparison: Breder Traps vs. Flume/Lift Nets

Breder traps, flume nets, and lift traps were compared to determine if their sampling capacities were comparable. The three nekton sampling methods were run in conjunction on one night in summer 2020. Breder traps were placed on the high marsh within 5m of every flume net and lift trap at 3 creek reaches, West Right, Sweeney Right, and Club Head. Breder traps were left to collect nekton on the nighttime high tide as described above; flume nets and lift traps were lifted on the same night and the same high tide in the mannered described above. In the morning after the tide receded, animals were collected and placed on ice to be identified and measured.

Data Analysis

Mummichog gut and caloric content was assessed statistically by using non-parametric

Kruskal-Wallis H -Tests along with Bonferroni- corrected Dunn's Tests to determine statistically significant comparisons between creeks, where appropriate. Mummichog biomass and abundance was assessed statistically by using Two-way Analyses of Variance (ANOVA) followed by post-hoc Tukey HSD 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

$$\text{Response Ratio} = \log \frac{\text{Altered}_{dist}}{\text{Reference}_{dist}}$$

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 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. Breder/ Flume/Lift comparison data was paired and analyzed for significant correlations. All data were analyzed in R (v4.0.0).

Results

Total mummichog biomass, biomass per m² of high marsh, calories per m² of high marsh was higher in systems with more high marsh access (Table 1). No measurable differences in individual mummichog caloric content (Kruskal-Wallis, $\chi^2 = 1.685$, $df = 3$, $p > 0.05$, Figure 3B) was found between mummichog captured in each creek. Total calories available to predators via mummichogs was 50-66% greater in the reference system than in the altered systems (Table 1).

Mummichog populations consumed more terrestrial invertebrates with increasing high marsh access (Kruskal-Wallis, $\chi^2 = 9.928$, $df = 2$, $p\text{-value} < 0.05$, Figure 3A). Mummichog consumed more prey from the high marsh in Mud South Creek than in Club Head Creek (Dunn's Test, $p < 0.01$, Figure 3A), and nearly more than in Mud South Creek in West Creek (Dunn's Test, $p = 0.05$, Figure 3A).

Mummichog abundance ($F_{2, 35} = 10.666$, $P < 0.05$, Figure 4A) and biomass ($F_{2, 35} = 10.165$, $P < 0.05$, Figure 4B) per m^2 was significantly higher in West Creek than in Sweeney Creek and Club Head Creek at 0 m-10 m from the creek edge (Tukey HSD, $P < 0.05$). There were no difference in mummichog abundance ($F_{2, 9} = 0.185$ (15 m), $F_{2, 20} = 0.543$ (30-45 m), both $P > 0.05$, Figure 4A) or biomass ($F_{2, 9} = 0.141$ (15 m), $F_{2, 20} = 0.155$ (30-45 m), both $P > 0.05$, Figure 4B) per m^2 at any creekshed at 15 m or 30 m-45 m from the creek edge.

There were no differences in the total abundance (Fig. 5A) or biomass (Fig. 5B) 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 $P > 0.05$). 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 (Two sample t -test, $p > 0.05$, Figure 5C).

No significant correlations were found between the abundance of animals in Breder trap and Flume/Lift trap catches. No significant correlations were found between the biomass of animals in Breder trap and Flume/Lift trap catches. (LM, all $p > 0.05$, Figure 2).

Discussion

The geomorphologic configuration of a habitat can have a large impact on how energy flows

within and between systems. This is particularly true of intertidal saltmarshes, where trophic relays mediated by aquatic consumer access to resource pools regulate the flow of organic matter between disparate systems connected via tides (Christian and Allen, 2014; Kneib, 1997). This study demonstrates how altered creek geomorphology can affect the magnitude of the connection between distinct saltmarsh food webs. Mummichog gut content analysis revealed that consumption of terrestrial invertebrate prey decreased in creeks with altered low marsh geomorphology (Figure 3A). Therefore, mummichog populations in less connected creeks move less terrestrial production from high marsh habitat to the aquatic food web, and in this way, altered creek edge geomorphology controls the connection between the distinct marsh platform and creek food webs. Additionally, fish that successfully reach 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 (Figure 4A-B). 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 (Figure 5A-C). 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. The role landscape features play in the transfer of energy between disparate saltmarsh food webs is important in considering how future climate scenarios may impact food web structure both within these systems as well the external systems to which they are connected (Baker et al., 2020; Colombano et al., 2021)

Mummichog populations in creeks with altered geomorphology consumed less terrestrial prey; no differences were found in caloric content between individuals in creeks with intact or altered low marsh edges. Fish in creeks with altered edge geomorphology are less likely to cross

the degraded low marsh and enter the high marsh, which is 55 % to 139 % more prey dense than the creeks (Nelson et al., 2019), and therefore should have less opportunity to grow. The high marsh platform in this system is flooded only 5 % of the time, so one would assume that any further reduction to this already small amount of access could result in mummichog in worse condition (less calorically rich) than ones with natural high marsh access, resulting in less growth and decreased mummichog energetic output at the level of the individual. Our results suggest that this is not the case; the fish that reside in the creek are the ones that were able to acquire enough of this high marsh energy to grow and survive, and any that are not able to reach this caloric threshold are no longer present. The mummichog that are left show no differences in individual length or mass between creeks (Lesser et al., 2020), evidence that the individual's growth is not affected by altered access. Thus, decreased mummichog energetic output of the altered creek occurs on the population level, not the individual level; since fewer mummichog occur in altered creeks, fewer total calories are exported to support higher trophic level consumers (Table 1).

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 (Figure 4A-B). 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 when it is flooded. An individual mummichog needs to be able to navigate a safe, continuous route through the low marsh, and spend time foraging on the flooded high marsh platform, all within the short window of tidal inundation. This finite window of tidal inundation means that any increase in the amount of time spent searching for continuous passage ultimately leaves less time for foraging once the high marsh is accessed. This could mean that mummichogs remain closer

to the marsh edge while foraging, thus limiting the total amount of high marsh energy effectively accessed by mummichogs, resulting in reduced population sizes (Lesser et al., 2020; Nelson et al., 2019) and limiting their influence on the communities of the marsh platform. However, this does not appear to be the case; our data indicate mummichogs that successfully enter the high marsh in altered creeks cover a similar marsh area as in the reference creek system (Figure 4A-B). This suggests that even though creeks with altered creek edge geomorphology limit the ability of mummichog to access to the high marsh, those that are still able to make it across the low marsh into the high marsh are not limited in the amount of space that they consume invertebrate prey over. Low marsh geomorphology acts like a filter rather than a maze; reduced mummichog populations on the high marsh of degraded creeks are the result of fewer individuals being able to make through the degraded low marsh barrier, rather than only a subset being able to “figure out” a safe path through the more complex degraded habitat. Thus, geomorphologic change 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 is produced.

Mummichog foraging removes substantial invertebrate biomass from the high marsh (Lesser et al., 2020). Despite this, found no evidence was found that foraging by aquatic predators during spring tides was enough to limit invertebrate populations on the high marsh (i.e., no top-down control) (Figure 5A-C). Previous studies in this ecosystem have come to similar conclusions, with mummichog removal experiments showing little effect on the abundance and biomass of polychaetes 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 in marsh food web through any cascading feedback due to predation release, for example, 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 (Figure 6). 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. Biomass and caloric measurements 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 aquatic predator populations that rely on this channel of energy to support their biomass (Figure 6, 7). 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 (Figure 6). 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 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*, Figure 7).

Observed without considering the importance of the trophic relay in the food web, these 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 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. 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 and may lead to misrepresentations of which factors alter food web function in future climate scenarios.

Disrupting the trophic relay of energy from the marsh surface to the estuary ultimately reduces the amount of consumer productivity that can be supported by the system as whole. This has 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 (*Anguilla rostrata*), resident consumers of mummichogs in PIE (Eberhardt et al., 2015), migrate out of estuaries once reaching sexual

maturity in order to join massive spawning aggregations 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 (Figure 6). 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. 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 therefore the number and biomass of striped bass the system can support (Figure 6, 7). This study demonstrates the role of the landscape structure in facilitating or hindering the flow of energy in spatially coupled food webs. These results highlight the potential consequences of habitat alteration beyond loss of the habitat itself. The influence of geomorphology on the trophic relay of marsh energy via mummichogs in marsh creeks can have an astonishingly vast impact on consumer production and behavior at large scales; 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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578 **Tables**

579 **Table 1:** Total mummichog biomass, mummichog biomass per m² per creek, as well as average caloric content of mummichog
 580 individuals, at each creek and reach surveyed. Biomass data is from all flume nets and lift traps at each creek reach surveyed.
 581 “Calories Produced” refers the mummichog calories per m² of high marsh surveyed, and “Total Available Calories” refers to the total
 582 calories of captured mummichog populations.

Creek	Reach	Total Biomass (g)	Biomass (g/m ²)	Average Caloric Content (cal/g)	Calories Produced (/m ²)	Total Available Calories (cal)
<i>West Creek</i>	<i>L</i>	465.65	3.23	4,283.68	13,836.29	1,994,695.60
	<i>R</i>	405.10	2.81		12,037.14	1,735,318.77
<i>Sweeney Creek</i>	<i>L</i>	220.88	1.53	4,116.64	6,298.46	909,283.44
	<i>R</i>	161.95	1.12		4,610.64	666,689.85
<i>Club Head Creek</i>	<i>R</i>	175.52	1.22	4,218.69	5,146.80	740,464.47

Figure Captions

Figure 1: Maps of study locations. Creeks are located in the tidal marshes of the Rowley River, MA (Lat 42.731430, Long -70.839473). A) Map depicting creeksheds used in the Breder trap portion of this study. MS = Mud South Creek (intact geomorphology), WE = West Creek (intermediate geomorphology), CL = Club Head Creek (altered geomorphology). Inset depicts Plum Island Estuary, Newbury, MA. Box outlines the bounds of the larger map in relation to the rest of the estuary. B) Map depicting creeksheds used in the Flume nets/Lift Trap/ Invertebrate portion of this study. WE = West Creek, SW = Sweeney Creek, CL = Club Head Creek. “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.

Figure 2: Comparison of A) number of animals captured and B) biomass captured in Breder traps and corresponding Flume/ Lift nets at Club Head, Sweeney Right, and West Right. Each Flume/Lift nets was paired with a corresponding Breder trap placed within 5m. No correlation was found between total catch or biomass in Breder and Flume/Lift traps. (LM, all $p > 0.05$)

Figure 3: A) Total mass of terrestrial prey consumed by mummichog populations in Club Head, West, and Mud South creeks. Brackets with stars refers significant differences between creeksheds (Dunn’s Test, $p < 0.01$). Brackets with a dot refers to nearly significant differences between creeksheds (Dunn’s Test, $p = 0.05$). B) Caloric content of mummichog captured in CL, WE, SW, and MS. No significant differences were found between any creekshed (Dunn’s test, all $p > 0.05$).

Figure 4: Mummichog abundance (A) and biomass (B) per m² across the high marsh platform at 0-10m, 15m, and 30-45m from the creek edge. Brackets with stars refers significant differences between creeksheds at a given distance (Tukey HSD, $P < 0.05$).

Figure 5: Total invertebrate abundance (A) and biomass (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, $P > 0.05$). C) Simpson's Diversity Index (D) of terrestrial invertebrate communities on the high marsh platform at Club Head, Sweeney, and West creeks before and after the spring tidal cycle. No significant differences were found in invertebrate communities before and after the spring tidal cycle at all creeks (Two sample t -test, $P > 0.05$).

Figure 6: 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. 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 supports fewer predators, which in turn reduces 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.

Figure 7: Diagram depicting energy flow through reference (A) and altered (B) PIE food webs as it relates to the size of an organism's foraging range. As increase trophic level increases, foraging range tends to increase, and consumers couple more food webs/energy sources in space (Rooney et al 2008). In altered creek systems (i.e., 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; these effects may be interpreted as "top-down" driven if space is not considered when assessing the food web.

643 **Figures**

644 **Figure 1**

645 A)

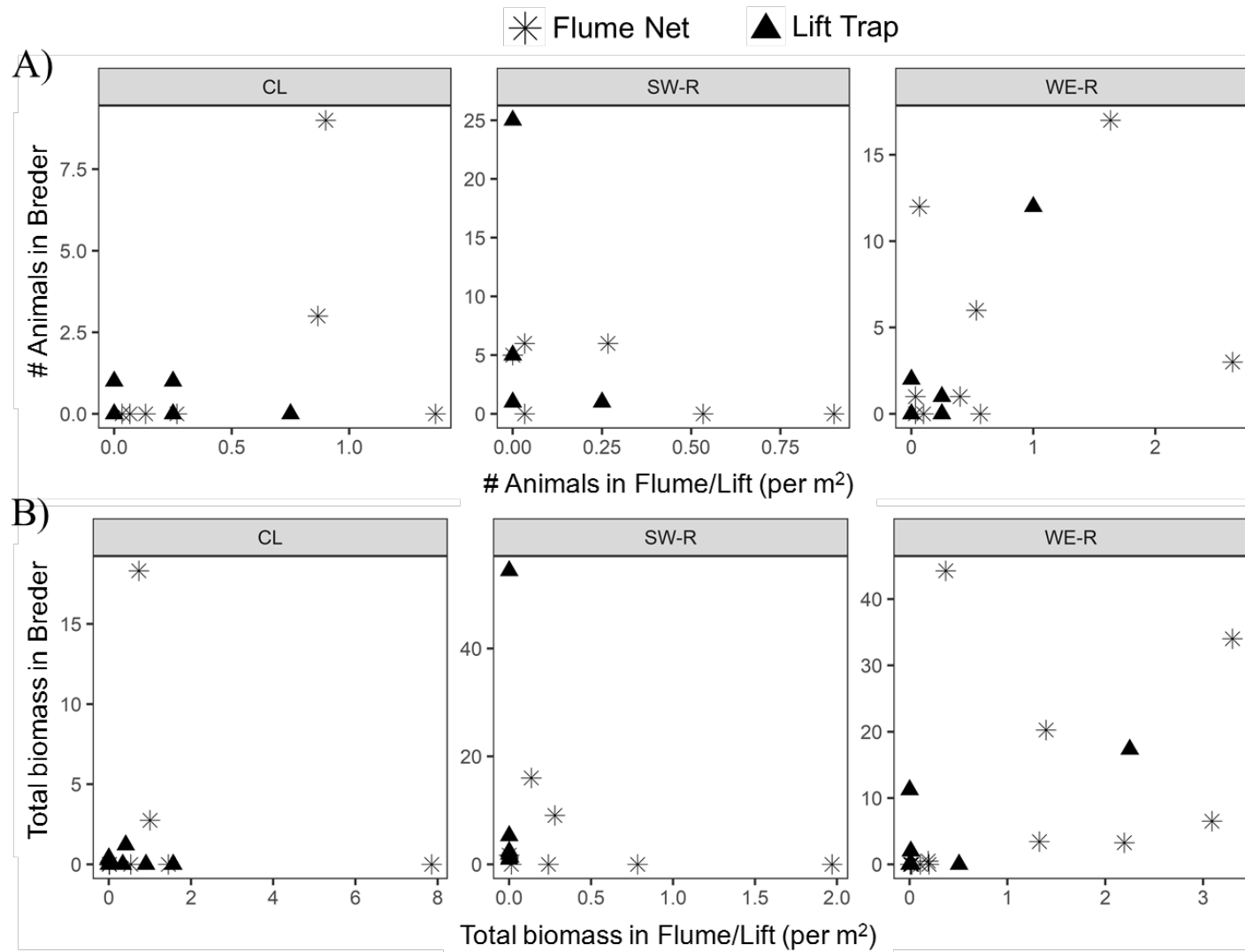


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648 B)

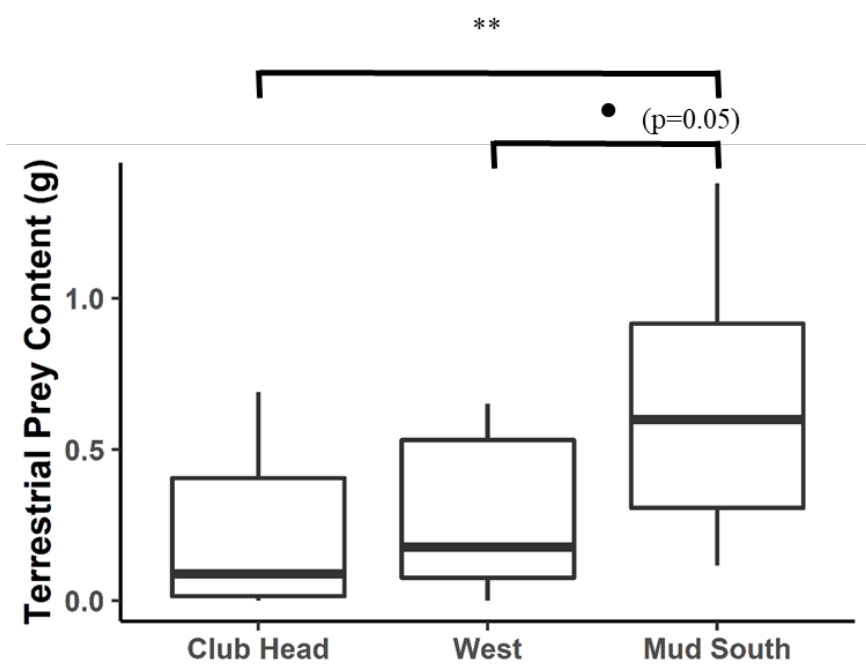


658 **Figure 2**

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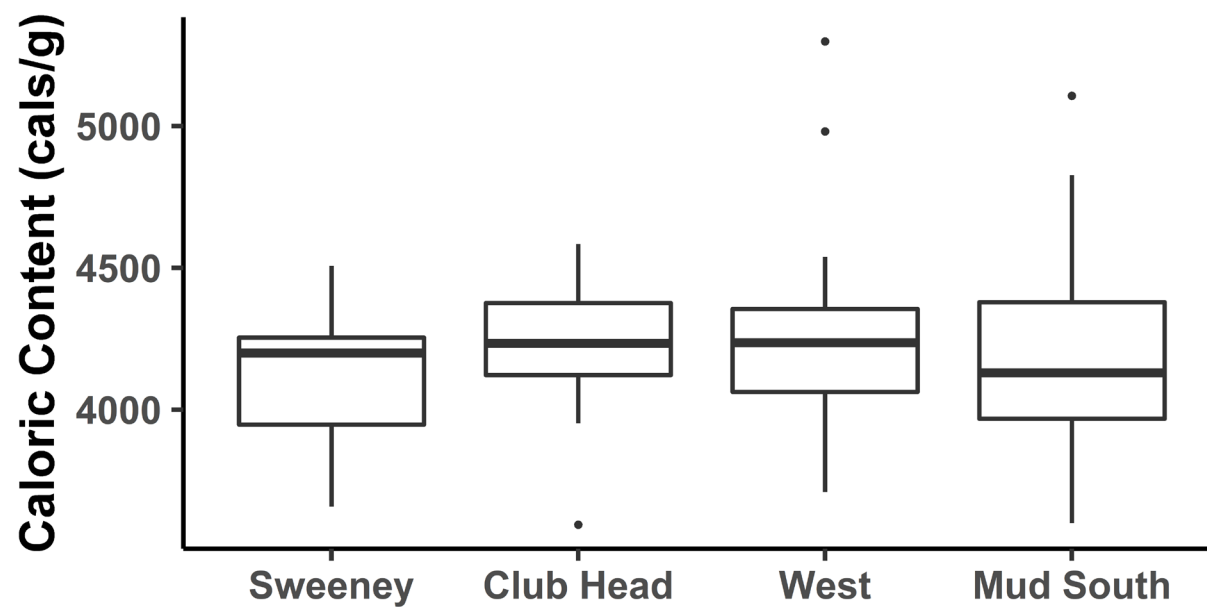
660 **Figure 3**

661 A)



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663 B)

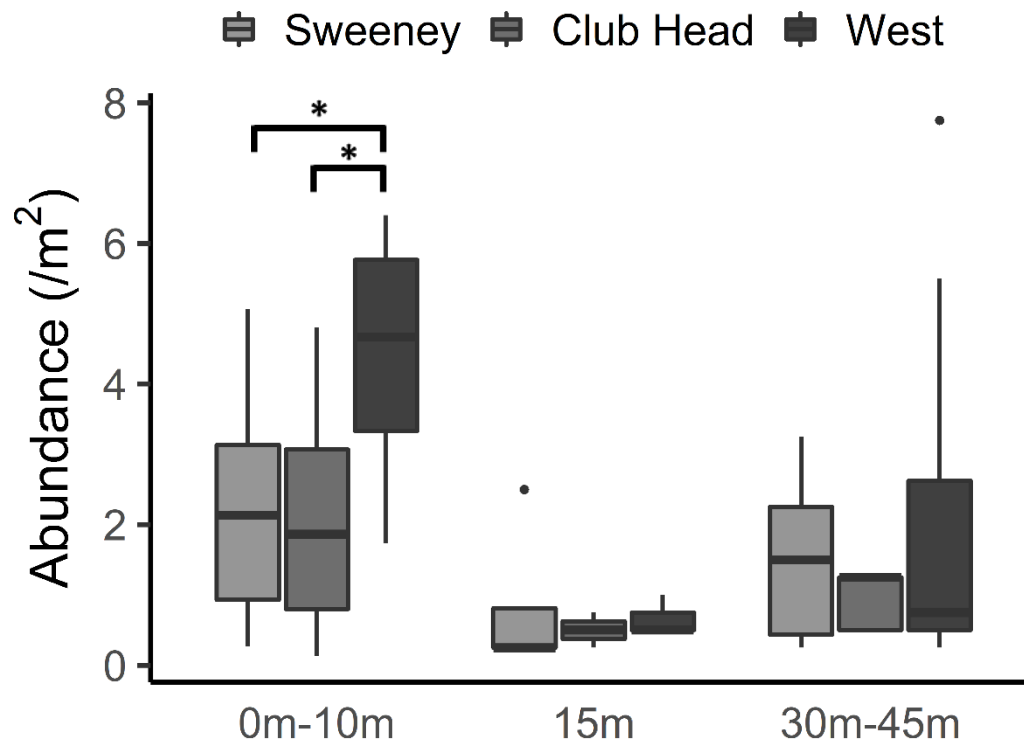


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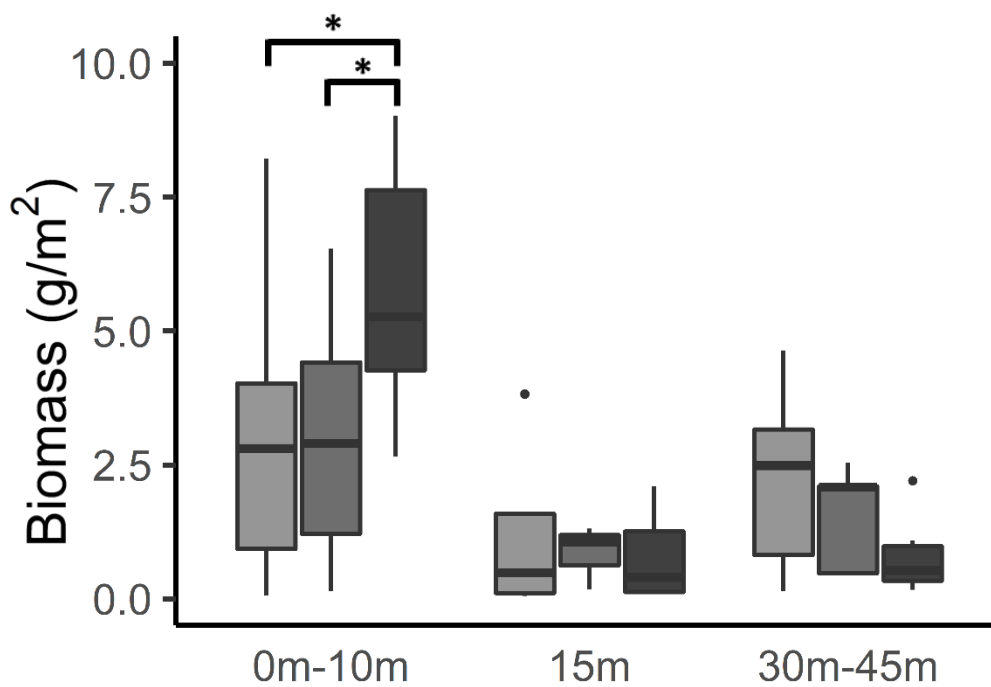
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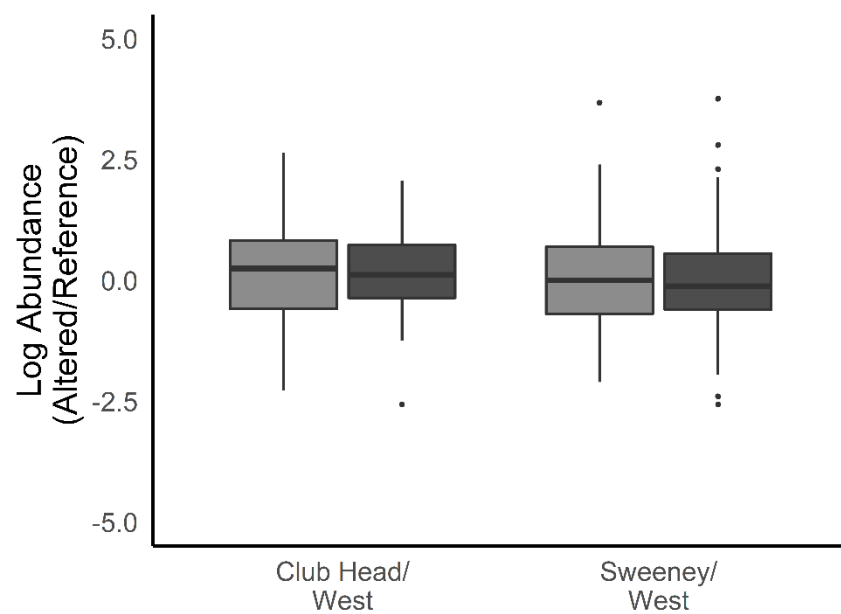
Figure 4

A)



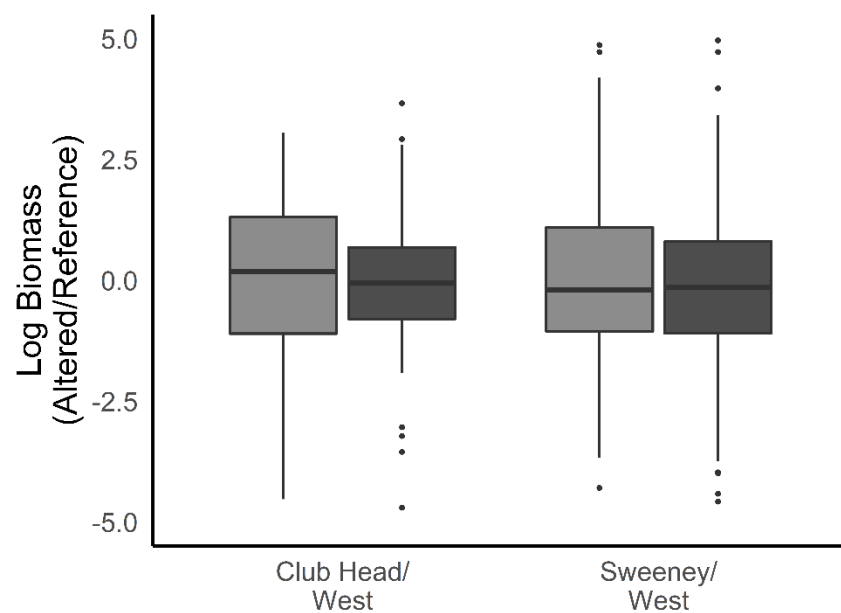
B)



689 **Figure 5**690 A) 

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692 B)

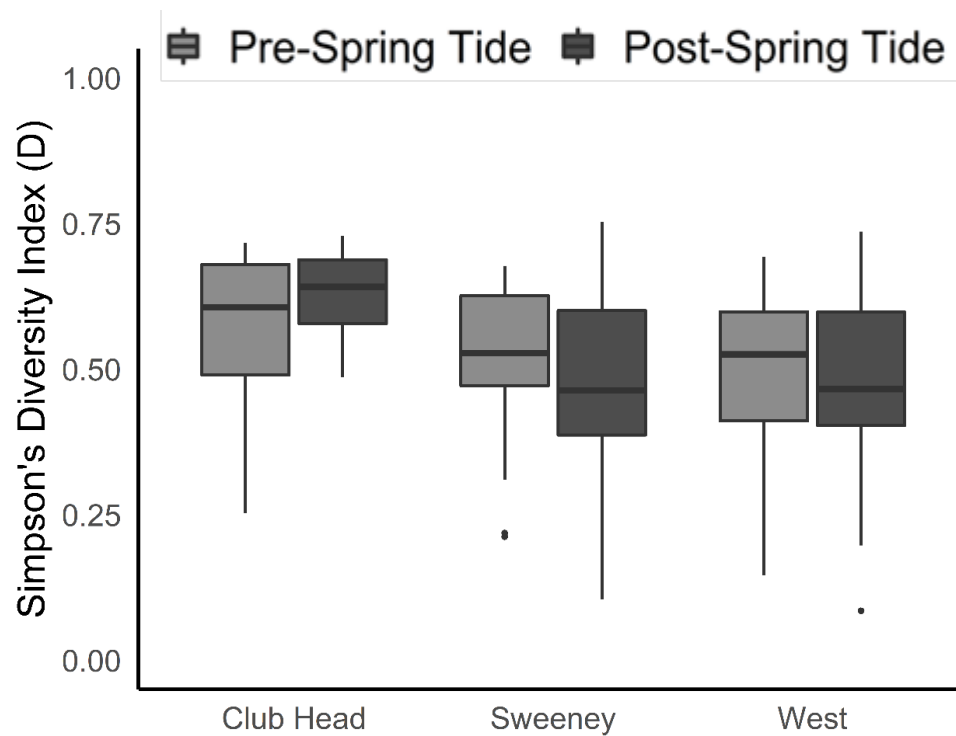


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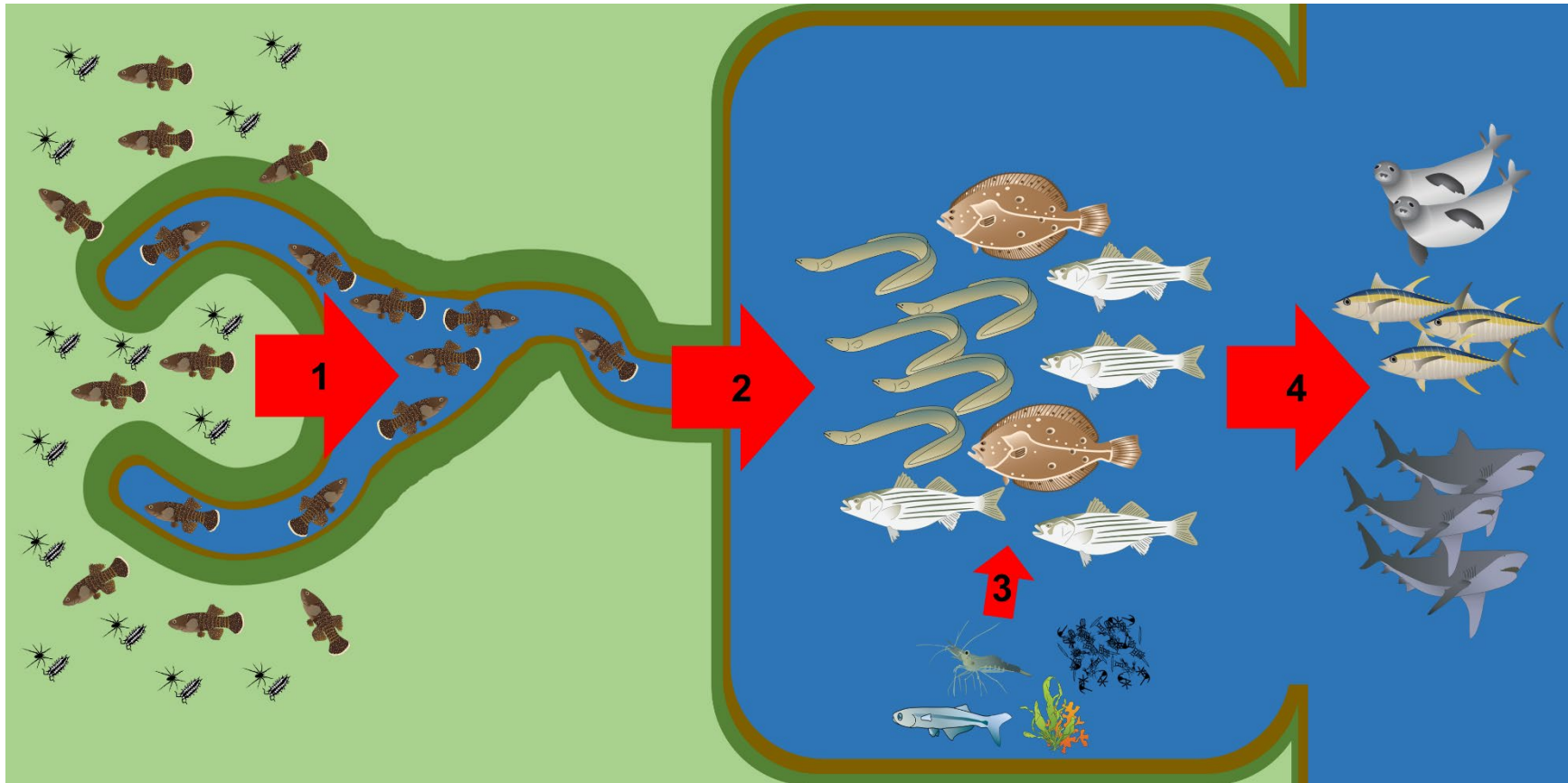
695 C)

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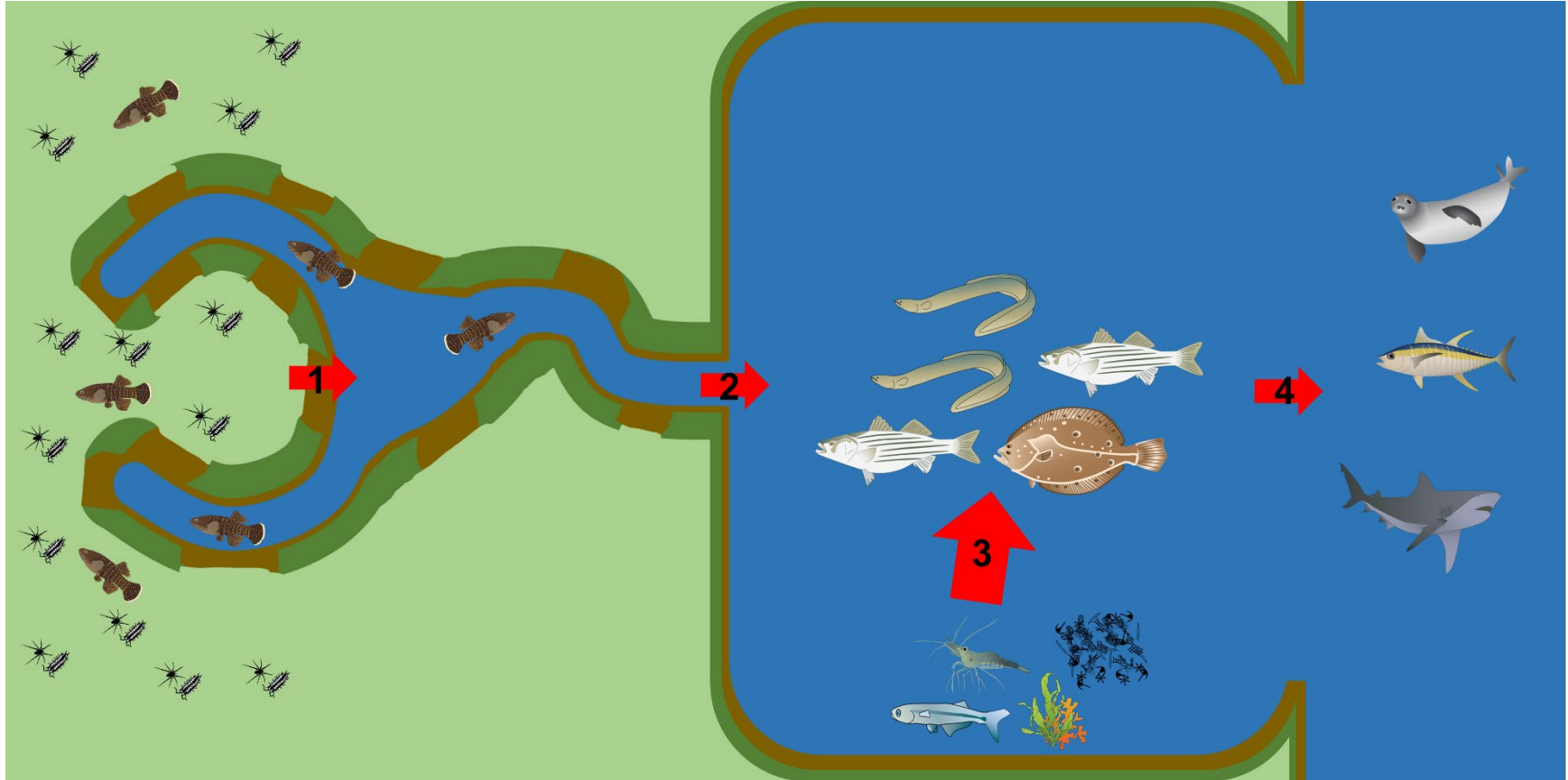
697 **Figure 6**

698 **A)**



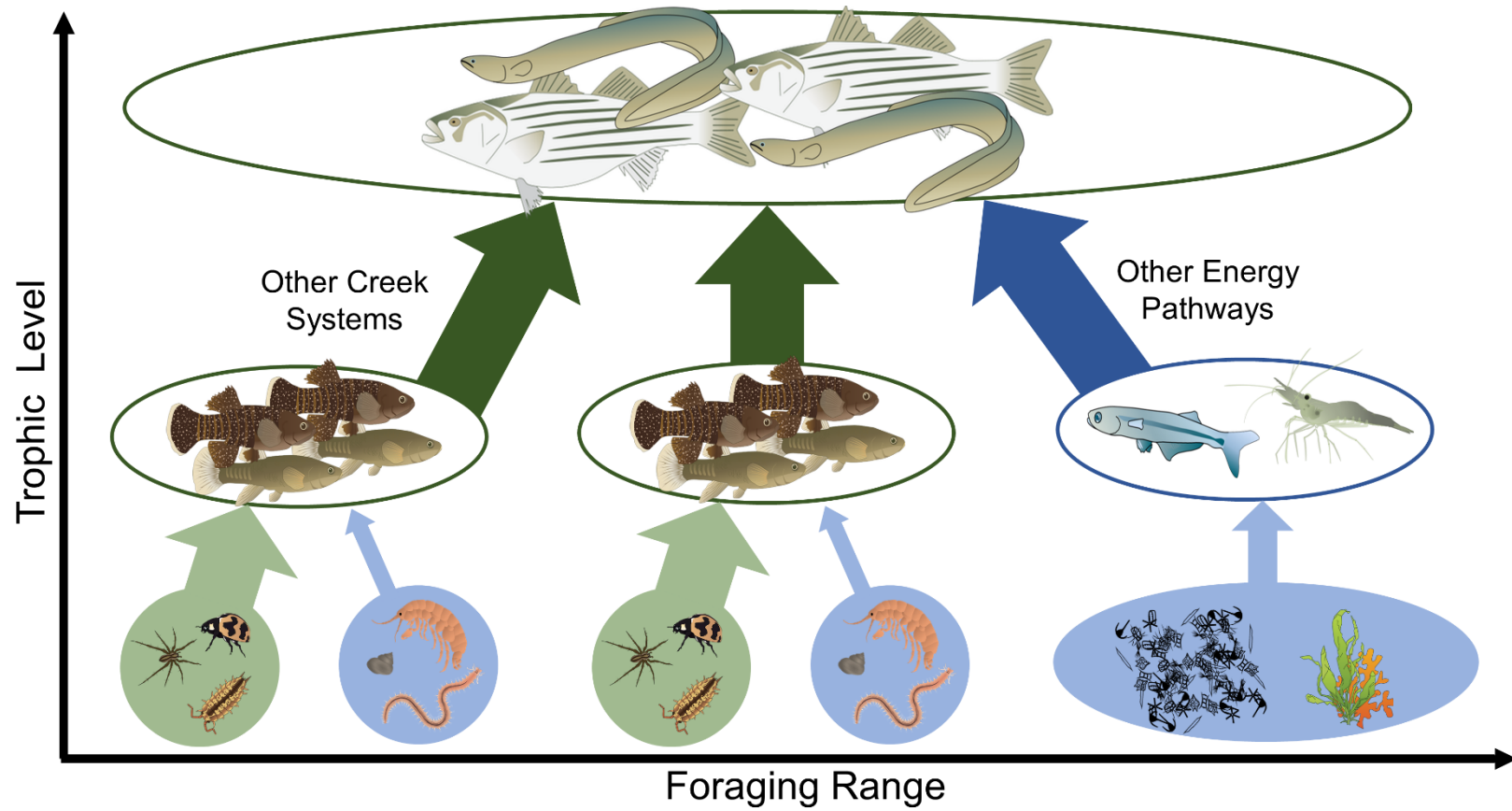
700 B)

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704 **Figure 7**705 **A)**

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707

708 B)

