

## LETTER

**Body size, trophic position, and the coupling of different energy pathways across a saltmarsh landscape**

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**Scientific Significance Statement**

Landscape theory for food web architecture (LTFWA) suggests that food webs are hierarchically organized with larger consumers coupling energy from different habitats that would otherwise be functionally isolated. Empirical tests of this theory remain rare and support differs among terrestrial, freshwater, and marine systems. Saltmarshes and their associated habitats represent a transitional ecotone where food webs may be organized differently than in neighboring terrestrial, freshwater, and open marine habitats. Here we provide such an empirical test by correlating body size, trophic position (TP), and the coupling of different energy channels using stable isotope data from saltmarsh-dependent species. Consistent with the LTFWA, we found a gradual increase in the coupling of phytoplankton and C4-marsh plant energy channels with larger body sizes and higher TPs.

**Abstract**

Body size is considered an important structuring mechanism of food webs because consumers are usually larger and more mobile than their prey and may couple energy among habitats. We explored the links among trophic position (TP), body size, and the coupling of different energy channels (phytoplankton and C4-marsh plants) in a saltmarsh landscape in the northern Gulf of Mexico—a dynamic system considered weakly shaped by biotic interactions. Body size was positively associated with TP, and this relationship was stronger in the phytoplankton pathway vs. the C4-marsh pathway. There was a gradual increase in the coupling of phytoplankton and C4-marsh plants at larger body sizes and higher TP. Phytoplankton supported longer food chains and larger body sizes than C4-marsh

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**Data Availability Statement:** Data are available in the Dryad repository at <https://doi.org/10.5061/dryad.5dv41ns6f>.

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plants. Results support predictions of the landscape theory for food web architecture and indicate that the role of body size in determining trophic interactions may vary across food web compartments.

## Introduction

Trophic interactions vary in space and time, leading to changes in the structure and dynamics of food webs (Winemiller 1990). However, historically, food webs constructed from empirical data lacked spatial and temporal components, and models were constructed as static entities (e.g., Cohen 1978). Recently, a landscape theory for food web architecture (LTFWA) was proposed (Rooney et al. 2008). This theory is based on empirical evidence from macroecology and behavioral ecology, mainly associated with body size and foraging behavior.

Consumers are typically larger than their prey and, consequently, food webs are expected to be size-structured, with larger consumers occupying higher trophic positions (TPs) (Riede et al. 2011). Larger consumers are more mobile and have larger home ranges because they spend less energy per unit of mass to move (Reiss 1988). Indeed, evidence indicates that small consumers from lower TP occupy smaller activity spaces and are often supported by a single basal resource, whereas large consumers from a high TP explore space at larger scales, relying on multiple energy channels to support their higher energetic costs (e.g., Arim et al. 2010).

The close association among body size, TP, and the access to multiple food webs or trophic resources assumed by the LTFWA (Rooney et al. 2008) does not always hold. In the Serengeti, for example, large herbivores couple resources in space while top predators are more sedentary with sit-and-wait foraging strategies (Dobson 2009; McCann 2011). Flying insects are also more mobile than fishes in pond meta-communities (De Bie et al. 2012). Passive dispersion (e.g., plankton) is ultimately determined by vectors (e.g., water flow) where the efficiency of dispersal is inversely related to size (Vagvolgyi 1975; Villarino et al. 2018). Strong positive TP–body size relationships tend to occur in marine ecosystems but not in freshwater and terrestrial ecosystems (Potapov et al. 2019; Keppeler et al. 2020). Pelagic marine food webs are mainly supported by phytoplankton that are relatively nutrient rich, easy to digest, and hard to handle by large animals, leading to long and efficient size-based food webs (Tucker and Rogers 2014; McGarvey et al. 2016). Conversely, multicellular autotrophs are important sources supporting freshwater and terrestrial ecosystems. In these systems, animals of many sizes have evolved to feed on plants and detritus, weakening TP–body size relationships (Shurin et al. 2006; Keppeler et al. 2020). Although poorly studied, the strength of TP–body size relationship likely varies between fast-energy channel (i.e., high production–biomass ratios, e.g., phytoplankton) and slow-energy channel (i.e., low

production–biomass ratios, e.g., many vascular plants) within food webs (Rooney et al. 2008; Potapov et al. 2019).

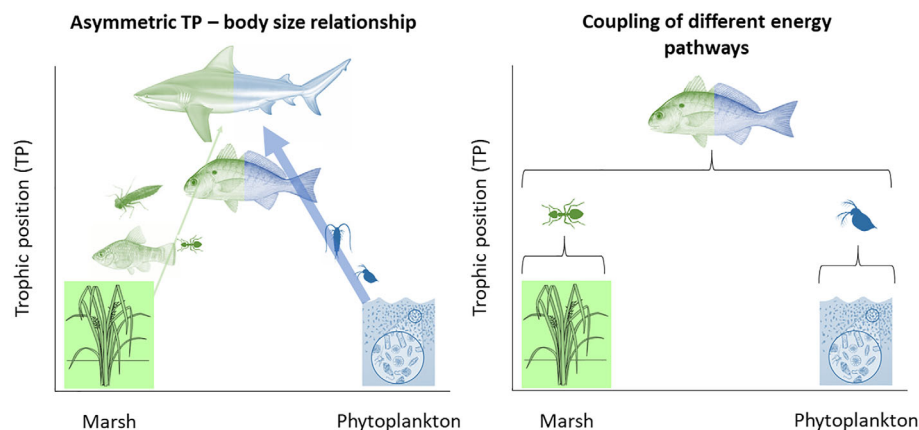
Estuarine marshes are dynamic and productive systems at the transition of marine–freshwater and terrestrial–aquatic realms (Elliott and McLusky 2002; Hill and Roberts 2017). The associated biota is strongly influenced by environmental variables (e.g., salinity) that fluctuate over short spatial–temporal scales (Telesh and Khlebovich 2010). Consequently, it is believed that communities are weakly shaped by biotic interactions (Elliott and Whitfield 2011). Previous studies have found divergent associations (including positive, flat, and even negative relationships) between TP and body size in adjacent estuarine areas (Akin and Winemiller 2008; Keppeler et al. 2020). Data from the Chesapeake Bay indicate that high TP consumers couple phytoplankton and detritus channels (Rooney et al. 2006). However, to our knowledge, no study has investigated the coupling of phytoplankton and marsh plant compartments across multiple TP and body sizes. Also, we are not aware of any study that has explored differences in TP–body size relationships between resource compartments in estuaries or saltmarshes.

We explored the association among TP, body size, and the coupling of two energy channels, phytoplankton (fast-energy channel) and C4-marsh plants (a slower-energy channel), in a saltmarsh-dominated landscape of Barataria Bay, Louisiana. We expected that body size was positively related to TP with a stronger relationship associated with the phytoplankton pathway (Hypothesis 1; Fig. 1a); and that body size and TP covaried with the relative contributions of phytoplankton and C4-marsh plants as small consumers at lower TP are more isolated in space than large consumers at higher TP (Hypothesis 2; Fig. 1b).

## Material and methods

### Study area

We analyzed data (Keppeler et al. 2021) from three sites located in northeastern Barataria Bay (Data S1). The area is in a subtropical zone with shallow and turbid waters, diurnal tide range of ~0.3 m, and salinities varying from fresh to salt-water (Conner and Day 1987; Marton et al. 2015). The study sites are immersed in a saltmarsh landscape composed of macrophytes and their associated microhabitats (e.g., ponds, tidal creeks, and subtidal edge), as well as surrounding open waters. C4-plants (e.g., *Spartina alterniflora*) usually dominate the vegetation with C3-marsh plants (primarily *Juncus roemerianus*) less abundant and mainly restricted to the highest elevations in the marshes.



**Fig. 1.** A schematic description of two possible relationships between trophic position and food sources. **(a)** An asymmetric TP–body size relationship with a stronger correspondence associated with the phytoplankton channel. **(b)** Larger organisms couple C4-marsh plants and phytoplankton channels while smaller organisms are more restricted to single-energy channels.

## Data

Data consisted of 1563 samples from 77 taxa, including basal sources, fishes, invertebrates, birds, and mammals. Samples were collected in May (2015, 2016) and October (2015) from a variety of saltmarsh microhabitats (e.g., ponds, tidal creeks) and their surrounding open waters.

$\delta^{15}\text{N}$  ( $^{15}\text{N} : ^{14}\text{N}$  ratio) and  $\delta^{13}\text{C}$  ( $^{13}\text{C} : ^{12}\text{C}$  ratio) were available for all samples.  $\delta^{15}\text{N}$  is correlated with TP due to its natural enrichment with trophic interactions.  $\delta^{13}\text{C}$  differs mainly among producers and is associated with differences in photosynthetic pathways and inorganic sources of carbon assimilated (Peterson and Fry 1987).

Body size measurements were available for 59% of all samples (52 taxa). For the remaining taxa ( $n = 19$ , 18 being small invertebrates), we either measured preserved specimens sampled in the same region ( $n = 7$ ) or estimated body mass using published data ( $n = 12$ ). For details about sampling protocols, isotope analysis, and measurements, see Data S1.

## Data analysis

We carried out Two Baselines Full Bayesian models (herein called TBF models; Quezada-Romegialli et al. 2018) to estimate relative TP and the contribution of C4-marsh plants and phytoplankton (baselines) pathways using  $\delta^{15}\text{N}$  and  $\delta^{13}\text{C}$  (Data S2). In TBF models, coupling is inferred by the parameter alpha which varies from 0 (supported only by C4-marsh plants) to 1 (supported only by phytoplankton). Alpha and TP generated by TBF models are not correlated unless there is an underlying association between  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  (Data S3).

Given that  $\delta^{15}\text{N}$  and  $\delta^{13}\text{C}$  may vary in space and time, and that there is uncertainty in consumers' space use, TP and alpha were estimated at four different scales: broad, with single estimates for each species, across all years, seasons, and sites (Scale 1); intermediate, with TP and alpha estimates for each species at either each site (Scale 2) or each site and

season (Scale 3); and specific, with TP and alpha estimates for each species at each site, season, and year (Scale 4). We also calculated averages of species body mass for each site, season, and year, depending on the scale being analyzed. The exceptions were averages measured from preserved specimens and estimates obtained from the literature. In addition, we used TBF models to estimate TP and alpha values for each individual sample in our dataset (herein referred as individual level analysis). This was necessary to investigate whether the patterns at the interspecific level were still consistent after accounting for intraspecific variation.

Bayesian generalized linear multilevel models (Bürkner 2018) were conducted to estimate the associations among body size, TP, and alpha. To test Hypothesis 1 (Fig. 1a), we considered TP as our response variable, and alpha, body mass, and the interaction between alpha and body size as our predictors. For Hypothesis 2 (Fig. 1b), TP and body size were considered as our response variables, and the quadratic term of alpha as our predictor. The quadratic term implies a U-shaped or dome-shaped relationship among the variables, which is in line with our expectations (Fig. 1b). Site, season, and years were included as random effects in models conducted at intermediate and specific scales to incorporate the nested structure of the data. All hypotheses were tested with species average estimates, but only the association between TP and alpha was explored with individual estimates as body size was only available for a limited number of species. For models using individual sample data, we weighted the contribution of each individual sample in the analysis according to the sample size of its respective species (i.e.,  $1/\text{species sample size}$ ). This was necessary to ensure that all species contribute equally to the analysis. We did not consider microhabitats in our analyses because (1) microhabitat boundaries are often not well defined and species are not expected to be restricted to them; and (2) sampling design varied across taxonomic groups and, therefore, the sample size of each microhabitat was unbalanced.

For each hypothesis, we compared the global model (with all variables) against a nested model without either the interaction term (Hypothesis 1) or the quadratic effect (Hypothesis 2), and against a null model without any predictors. Models were ranked according to their predictive accuracy, which was estimated through approximate leave-one-out (LOO) cross-validation (Vehtari et al. 2017). More details are in Data S2 and S4.

Some caveats are important to note. First, although phytoplankton samples were sieved (105- $\mu\text{m}$  mesh) to remove large particles and likely reflect phytoplankton production ( $\sim 93\%$  of algae chlorophyll; Data S1), they may contain a fraction of other sources (e.g., detritus). Second, basal sources experience higher isotope variability than consumers, which might cause a mismatch in the TBF models and affect our results (Post 2002). In addition, our analysis focused on the coupling of two major sources with distinct isotope signal, but there are other basal resources (e.g., microphytobenthos) that may be relevant for consumers. We conducted two complementary approaches to address these issues. First, we investigated whether replacing C4-marsh plants and phytoplankton (baselines) in our TBF models with primary consumers associated with open waters (*Geukensia granosissima* and *Crassostrea virginica*, two filter-feeding bivalves) and C4-marsh plants (*Prokelisia* and *Ischnodemus*, two terrestrial heteropterans) would lead to different alpha and TP values. This was accomplished by correlating alpha/TP values generated by each type of TBF model. Second, we conducted a multi-source mixing model (herein called MS models; Stock et al. 2018) to generate contribution values of C4-marsh plant, phytoplankton, microphytobenthos, and detritus for each consumer (Data S2).

Then, we calculated the Shannon index ( $H_k = -\sum_{i=1}^S p_i \ln p_i$ ), where  $p_i$  is the proportion contribution of basal source  $i$ ,  $S$  is the number of basal sources, and  $H_k$  is the diversity index associated with consumer  $k$ ) and correlated it against TP and body mass to check whether larger predators are supported by a higher diversity of energy sources. Results of this analysis were used to complement results from the TBF model and to provide more evidence that large predators are important couplers in our saltmarsh system.

Finally, although our study encompassed a variety of vertebrates (particularly fish) and invertebrates, we did not sample some resident and transient species that occur in saltmarsh landscapes. These include aquatic (e.g., dolphins, zooplankton), semiaquatic (e.g., snakes, muskrats, waterfowl), and terrestrial organisms (e.g., racoons, white-tailed deer).

## Results

Alpha and TP values generated by the TBF models using different pairs of baselines were strongly correlated ( $r > 0.92$ ). Overall, we found a consistent isotope gradient with C3

photosynthesis mainly related to aquatic (algae) production and C4 photosynthesis with terrestrial (marsh plants) production. Analyses conducted at different scales led to similar results. Thus, hereafter, we provide results associated with the analysis conducted at the lowest scale (Scale 4; see Data S4 for results of Scales 1, 2, and 3) and with C4-marsh plant and phytoplankton as baselines because (1) it incorporates spatial and temporal variations in resource use; and (2) C4-marsh plant and phytoplankton are the producers in the system.

The difference among models containing only the fixed effects (body mass + alpha) and the models containing the interaction terms (body mass \* alpha) was small; however, the latter explained a slightly larger proportion of variation in species TP (LOO- $R^2 = 0.39$  vs. LOO- $R^2 = 0.41$ , respectively; Table 1). Both models had consistently higher predictive power than the null model (LOO- $R^2 = 0.05$ ; Table 1). TP-body mass associations were positive but steeper when alpha values were high (Fig. 2; Table 2), indicating stronger relationships in phytoplankton pathways.

Alpha was related to TP and body size. Models containing the linear (TP: LOO- $R^2 = 0.29$ , TP [individual level]: LOO- $R^2 = 0.22$ ; body size: LOO- $R^2 = 0.32$ ) and the quadratic term of alpha (TP: LOO- $R^2 = 0.34$ , TP [individual level]: LOO- $R^2 = 0.26$ ; body size: LOO- $R^2 = 0.44$ ) performed consistently better than null models (TP: LOO- $R^2 = 0.05$ , TP [individual level]: LOO- $R^2 = 0.03$ ; body size: LOO- $R^2 = -0.01$ ; Table 1). The models with the quadratic term had a better fit than the model with the linear term, indicating highest TP and larger body sizes at intermediate values of alpha, although TP and body size were generally lower at low alpha values (C4-marsh plants pathway) than at high alpha values (phytoplankton pathway; Fig. 3; Table 2). The MS models indicated that the diversity of energy sources supporting consumers also increased with TP ( $r = 0.56$ , 95% confidence interval [CI]: 0.38–0.70) and body size ( $r = 0.57$ , 95% CI: 0.39–0.71).

## Discussion

TP was positively correlated with body size corroborating previous studies conducted in estuaries (Akin and Winemiller 2008) and marine ecosystems (e.g., Romero-Romero et al. 2016). TP-body size relationships were steeper in the food chain supported by the fast-energy channel (phytoplankton) than in the slower-energy channel (C4-marsh plants). The slope difference mainly reflected the large proportion of consumers with different body sizes at low TP in the C4-marsh plant pathway (max = marsh rice rat [47 g], min = delphacid planthoppers [0.2 mg]). This corroborates our hypothesis that phytoplankton pathways have stronger TP-body size relationships due to the challenge for larger consumers (excluding filter feeders, such as mussels) to meet their energy requirements through capture of small food particles. The presence of small intermediate consumers that often present disproportionately low predator-prey mass ratios also

**TABLE 1.** List of Bayesian regression models used to estimate the association among trophic position (TP), body size, and alpha values. Models were ranked according to their prediction accuracy. Body mass values are averages of individuals of the same species/ taxa collected at each season, site, and year (Scale 4 approach). TP and alpha values were generated for each species or individual sample (individual level) using the “Two Baselines Full” Bayesian models (TBF models; Scale 4 approach). Each model includes a random intercept term to account for the potential season, site, and year effect. Species were weighted according to their sample size (1/n) in the individual level model to ensure that each species contribute the same to parameter estimates.

Model	ELPD	LOOIC	LOO-R <sup>2</sup>	R <sup>2</sup> marginal	R <sup>2</sup> conditional
<i>Asymmetric TP–body size relationship</i>					
TP ~ body mass * alpha	–173.97 (11.05)	347.94 (22.09)	0.41	0.38 (0.04)	0.44 (0.04)
TP ~ body mass + alpha	–177.34 (10.72)	354.69 (21.44)	0.39	0.35 (0.04)	0.42 (0.04)
TP ~ 1	–229.24 (9.89)	458.49 (19.78)	0.05	0 (0)	0.08 (0.04)
<i>Coupling of different energy pathways—TP</i>					
TP ~ alpha + alpha <sup>2</sup>	–187.1 (11.54)	374.2 (23.07)	0.34	0.3 (0.04)	0.37 (0.04)
TP ~ alpha	–195.49 (11.97)	390.99 (23.93)	0.29	0.25 (0.04)	0.32 (0.04)
TP ~ 1	–229.24 (9.89)	458.49 (19.78)	0.05	0 (0)	0.08 (0.04)
<i>Coupling of different energy pathways—TP (individual level)</i>					
TP ~ alpha + alpha <sup>2</sup>	–171.71 (8.04)	343.42 (16.08)	0.26	0.26 (0.04)	0.3 (0.04)
TP ~ alpha	–179.09 (8.91)	358.18 (17.82)	0.22	0.26 (0.04)	0.3 (0.04)
TP ~ 1	–215.91 (8.71)	431.83 (17.42)	0.03	0 (0)	0.06 (0.03)
<i>Coupling of different energy pathways— body size</i>					
Body mass ~ alpha + alpha <sup>2</sup>	–626.58 (11.71)	1253.16 (23.42)	0.44	0.46 (0.04)	0.46 (0.04)
Body mass ~ alpha	–649.99 (11.22)	1299.99 (22.44)	0.32	0.33 (0.04)	0.34 (0.04)
Body mass ~ 1	–696.63 (9.29)	1393.27 (18.59)	–0.01	0 (0)	0.01 (0.01)

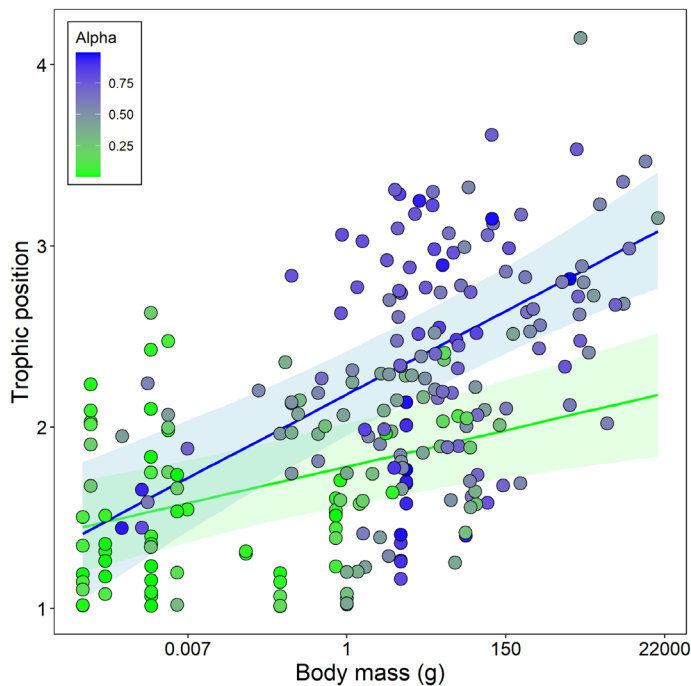
ELPD, expected log pointwise predictive density; LOOIC, leave-one-out information criterion; LOO-R<sup>2</sup>, R<sup>2</sup> for leave-one-out cross-validation.

\*Interaction between the left and right side variables; ~, indicates that the variable on the left side is modeled by the variable on the right side; ~ 1, indicates the null model (without explanatory variables); +, addition of a new exploratory variable.

**TABLE 2.** Parameter estimates for the Bayesian regression models used to estimate the association among trophic position (TP), body size, and alpha values. Only the models with the best prediction accuracy are shown. Body mass values are averages of individuals of the same species/taxa collected at each season, site, and year (Scale 4 approach). TP and alpha values were generated for each species or individual sample (individual level) using the “Two Baselines Full” Bayesian models (TBF models; Scale 4 approach).

Fixed parameter	Estimate	Est. error	I-95% CI	u-95% CI
<i>Asymmetric TP–body size relationship</i>				
Intercept	1.653	0.126	1.413	1.91
Alpha	0.661	0.141	0.383	0.933
Body mass	0.023	0.015	–0.005	0.052
Alpha * body mass	0.086	0.03	0.028	0.145
<i>Coupling of different energy pathways—TP</i>				
Intercept	2.039	0.108	1.82	2.25
Alpha	5.067	1.053	2.946	7.152
Alpha <sup>2</sup>	–2.496	0.705	–3.904	–1.029
<i>Coupling of different energy pathways—TP (individual level)</i>				
Intercept	0.695	0.045	0.603	0.781
Alpha	5.459	0.835	3.884	7.128
Alpha <sup>2</sup>	–2.372	0.730	–3.766	–0.931
<i>Coupling of different energy pathways—body size</i>				
Intercept	0.49	0.275	–0.036	1.014
Alpha	41.1	4.795	31.853	51.117
Alpha <sup>2</sup>	–25.543	3.784	–32.981	–18.238

\*Interaction between the left and right side variables.



**Fig. 2.** Relationship between body mass (log scale) and trophic position (TP). Dots are colored according to their alpha value. TP and alpha values were generated for each species at each season, site, and year using TBF models (Scale 4 approach). Similarly, body mass values are averages of individuals of the same species/taxa collected at each season, site, and year. The blue trend line represents the effect of body mass on TP when alpha is equal to 0.8 (consumers predominantly associated with the phytoplankton pathway). The green trend line represents the effect of body mass on TP when alpha is equal to 0.2 (consumers predominantly associated with the C4-marsh plant pathway). Ribbons around the trend lines indicate uncertainty intervals (i.e., 95% CI) associated with the model. Predictions are based on the best Bayesian regression model (see Tables 1 and 2).

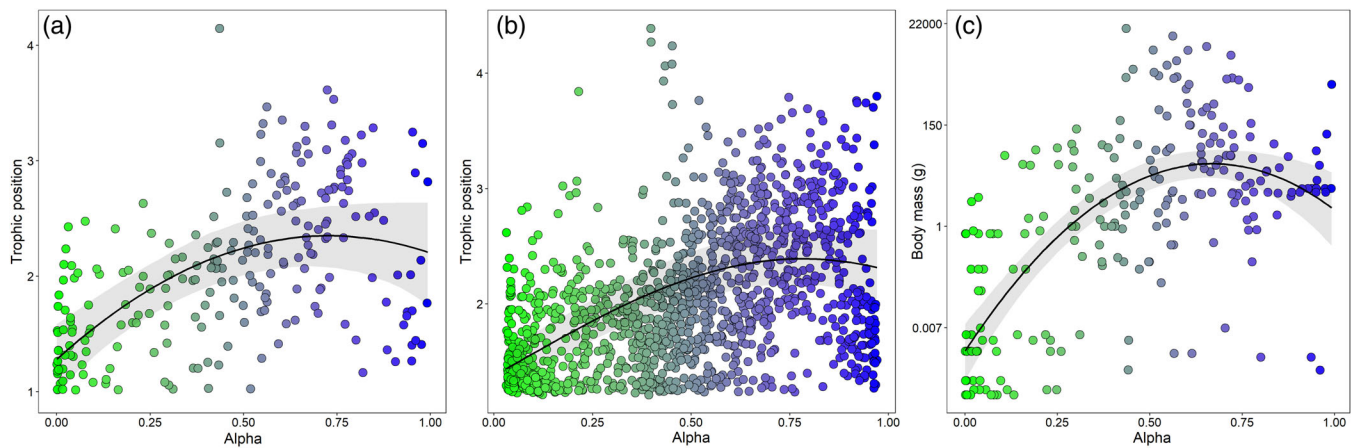
weakened the TP-body size relationship in the C4-marsh plant pathway. These include ants and spiders that can feed on disproportionately large prey (via cooperative hunting and spiderwebs, respectively) and that rely on marsh plants to provide the structure necessary to host their colonies and support spiderwebs. Thus, higher habitat structural complexity provided by multicellular producers may be linked to higher trophic specialization (Shurin et al. 2006), generating more variability in stable isotope data and further weakening TP-body size relationships.

The TP/body size-alpha relationships formed an asymmetrical humped-shaped curve where maximum TP/body size values were found at intermediate alpha values (0.5–0.75). MS models also suggested that larger body sizes and higher TP are associated with a higher diversity of energy sources. These results support our hypothesis that organisms lower in the food chain are more isolated in space whereas higher-order consumers progressively couple phytoplankton and C4-marsh plant pathways. The main couplers were large carnivorous

fishes, such as bull sharks, gars, and spotted sea trout, which are known to have large home ranges and forage across multiple habitats (Matich and Heithaus 2014; Moulton et al. 2017; Wegener et al. 2017). These predators are expected to be important stabilizers in spatially expansive ecosystems, such as Barataria Bay, by responding to asynchronous production in space (McCann et al. 2005). Interestingly, some small-bodied organisms (e.g., amphipods) at low TP seem to be supported by both C4-marsh plants and phytoplankton. One explanation is the exchange of materials between marshes and nearby open waters via tidal movements and wind (Childers and Day 1990). Small animals, such as grass shrimps, are known to move in and out of marshes following tide movements (Bretsch and Allen 2006). Another possibility is the presence of spatial overlap between producers since there can be considerable algae production beneath the C4-marsh plant canopy (Pomeroy 1959).

The hump-shaped relationship between TP and alpha was also found when analysis incorporated individual data. However, the amount of TP variation explained was lower. This may be linked with the higher uncertainty associated with TP and alpha estimates generated by the TBF models due to the lack of replicates per individual. Analysis at the individual level also incorporates more variation associated with ontogenetic changes in habitat use and diet. For instance, some herbivorous species (e.g., pinfishes) feed primarily on small invertebrates at early life stages (Horn 1989). Conversely, as carnivorous species (e.g., ladyfish, snappers) grow they tend to progressively replace a diet focus on small invertebrates with a more diversified diet that includes larger macroinvertebrates and fishes (Costa 2009). Several large-bodied fishes (e.g., tarpons) inhabit the saltmarsh platform at younger ages and later move to open waters (Boesch and Turner 1984), which possibly leads to important changes in trophic interactions. Unfortunately, we were unable to assess the association between body size and alpha using individual data, but results are likely to be consistent given the significant association among TP, body size, and alpha at the species level.

Phytoplankton pathways had longer food chains and supported animals with larger body sizes than C4-marsh plant pathways. Phytoplankton are smaller, more nutritious, and easily digestible which leads to more efficient energy and mass transfers (Lindeman 1942; Shurin et al. 2006). Systems supported by phytoplankton tend to have rapid trophic energy transfers due to faster biomass turnover rates and this may be linked with longer food chains (McGarvey et al. 2016). Alternatively, the association of larger predators (mainly fish) with the phytoplankton pathway may indicate limited on-marsh foraging (Ziegler et al. 2019) due to harsher environmental conditions (e.g., lower oxygen levels; Domenici et al. 2007), lower depth (Ruiz et al. 1993), and higher habitat structural complexity (Crowder and Cooper 1982). Indeed, saltmarshes are recognized as important refuges for many species (Chabreck 1988; McDevitt-Irwin



**Fig. 3.** Relationships between (a,b) alpha and trophic position (TP), and between (c) alpha and body mass (log scale). Dots are colored according to their alpha value and represent species average estimates in panels a and c, and individual estimates in panel b. The quadratic relationships are predicted by the best Bayesian regression models (see Tables 1 and 2). Gray ribbons around the trend lines indicate uncertainty intervals (i.e., 95% CI) associated with the models. TP and alpha values were generated for each species in each site, season, and year (a,c) or individual sample (b) using “Two Baselines Full” Bayesian models (Scale 4 approach). Body mass values are averages of individuals of the same species/taxa collected at each season, site, and year.

et al. 2016). If the limited on-marsh foraging hypothesis is correct, the hump-shaped curve described above may result from predators feeding on prey that move off the marsh platform rather than predators actively foraging on the marsh platform.

Top predators are expected to respond rapidly to fluctuations in resource abundance under the LTFWA, coupling different habitats and energy channels at time scales shorter than population dynamics (Rooney et al. 2008). However, the isotopic signature of an animal tissue does not immediately reflect what has been eaten but rather integrates the animals' diet over some period (half-life). The half-life of the isotopic signal generally varies among ectotherms and endotherms and increases with the organism's body size (Vander Zanden et al. 2015). In our data set, this half-life signal is estimated to vary from ~ 4 days to ~ 4 months (Data S5). Thus, the increase in carbon signature mixing of C4-marsh plants and phytoplankton with body size could also reflect different temporal scales of resource assimilation between consumers. Although the strong association between body size and isotopic turnover in our data set ( $r = \sim 0.8$ ) prevented us from conclusively separating their associations with alpha, exploratory analyses indicated that alpha is slightly more associated (~ 9.5%) with body size than with isotopic turnover (Data S5). The isotopic turnover time is probably not the main driver of alpha variation because smaller organisms tend to have shorter life spans (Speakman 2005) and, consequently, smaller home ranges (Reiss 1988) and dispersal capabilities (Jenkins et al. 2017). Previous studies (Rooney et al. 2006, 2008) have assessed habitat coupling across consumers using diet and published semi-quantitative data, which also have their own limitations, including uncertainty regarding resource origin (Keppeler and Winemiller 2020). Thus, we are confident that our results

provide one of the strongest pieces of evidence thus far in support of the LTFWA.

The LTFWA (Rooney et al. 2008) provides an elegant view of food webs structure and dynamics. Here, we used stable isotope data from a saltmarsh landscape to show that body size is positively associated with TP, and that these two variables are positively associated with coupling of different energy channels as predicted by LTFWA. In addition, compartments supported by phytoplankton have a stronger TP–body size relationship than compartments supported by C4-marsh plants. This observation supports the hypothesis that food webs with weak TP–body size relationship may be size-compartmentalized rather than size-unstructured (Potapov et al. 2019). Thus, we reconcile previous studies with contrasting results and highlight the role of body size in structuring saltmarsh food webs. Our findings should matter for estuary managers because (1) the disappearance of large predators may increase the isolation of habitats and food web compartments (McCann et al. 2005), and (2) the loss of saltmarshes will homogenize basal production in the system (Rooney et al. 2006). Both processes are expected to lead to unstable food web states and ultimately loss of species diversity (Rooney et al. 2008).

## References

- Akin, S., and K. O. Winemiller. 2008. Body size and trophic position in a temperate estuarine food web. *Acta Oecol.* **33**: 144–153. doi:10.1016/j.actao.2007.08.002
- Arim, M., S. R. Abades, G. Laufer, M. Loureiro, and P. A. Marquet. 2010. Food web structure and body size: Trophic position and resource acquisition. *Oikos* **119**: 147–153. doi:10.1111/j.1600-0706.2009.17768.x

- Boesch, D. F., and R. E. Turner. 1984. Dependence of fishery species on salt marshes: The role of food and refuge. *Estuaries* **7**: 460–468. doi:[10.2307/1351627](https://doi.org/10.2307/1351627)
- Bretsch, K., and D. M. Allen. 2006. Tidal migrations of nekton in salt marsh intertidal creeks. *Estuar. Coast.* **29**: 474–486. doi:[10.1007/BF02784995](https://doi.org/10.1007/BF02784995)
- Bürkner, P.-C. 2018. Advanced Bayesian multilevel modeling with the R Package brm. *R. J.* **10**: 395–411. doi: [10.32614/RJ-2018-017](https://doi.org/10.32614/RJ-2018-017)
- Chabreck, R. A. 1988. *Coastal marshes: Ecology and wildlife management*. Univ. of Minnesota Press.
- Childers, D. L., and J. W. Day Jr. 1990. Marsh-water column interactions in two Louisiana estuaries. II. Nutrient dynamics. *Estuaries* **13**: 404–417. doi:[10.2307/1351785](https://doi.org/10.2307/1351785)
- Cohen, J. E. 1978. *Food webs and niche spaces*. Princeton Univ. Press.
- Conner, W. H., and J. W. Day Jr (eds). 1987. The ecology of Barataria basin, Louisiana: An estuarine profile. U.S. Fish and Wildlife Service. Biological Report 85: 7.13.
- Costa, G. C. 2009. Predator size, prey size, and dietary niche breadth relationships in marine predators. *Ecology* **90**: 2014–2019. doi:[10.1890/08-1150.1](https://doi.org/10.1890/08-1150.1)
- Crowder, L. B., and W. E. Cooper. 1982. Habitat structural complexity and the interaction between bluegills and their prey. *Ecology* **63**: 1802–1813. doi:[10.2307/1940122](https://doi.org/10.2307/1940122)
- De Bie, T., and others. 2012. Body size and dispersal mode as key traits determining metacommunity structure of aquatic organisms. *Ecol. Lett.* **15**: 740–747. doi:[10.1111/j.1461-0248.2012.01794.x](https://doi.org/10.1111/j.1461-0248.2012.01794.x)
- Dobson, A. 2009. Food-web structure and ecosystem services: Insights from the Serengeti. *Philos. T. Roy. Soc. B* **364**: 1665–1682. doi:[10.1098/rstb.2008.0287](https://doi.org/10.1098/rstb.2008.0287)
- Domenici, P., C. Lefrançois, and A. Shingles. 2007. Hypoxia and the antipredator behaviours of fishes. *Philos. T. Roy. Soc. B* **362**: 2105–2121. doi:[10.1098/rstb.2007.2103](https://doi.org/10.1098/rstb.2007.2103)
- Elliott, M., and D. S. McLusky. 2002. The need for definitions in understanding estuaries. *Estuar. Coast. Shelf S.* **55**: 815–827. doi:[10.1006/ecss.2002.1031](https://doi.org/10.1006/ecss.2002.1031)
- Elliott, M., and A. K. Whitfield. 2011. Challenging paradigms in estuarine ecology and management. *Estuar. Coast. Shelf Sci.* **94**: 306–314. doi:[10.1016/j.ecss.2011.06.016](https://doi.org/10.1016/j.ecss.2011.06.016)
- Hill, T. D., and B. J. Roberts. 2017. Effects of seasonality and environmental gradients on *Spartina alterniflora* allometry and primary production. *Ecol. Evol.* **7**: 9676–9688. doi:[10.1002/ece3.3494](https://doi.org/10.1002/ece3.3494)
- Horn, M. H. 1989. Biology of marine herbivorous fishes. *Oceanogr. Mar. Biol.* **27**: 167–272.
- Jenkins, D. G., and others. 2017. Does size matter for dispersal distance? *Global Ecol. Biogeogr.* **16**: 415–425. doi:[10.1111/j.1466-8238.2007.00312.x](https://doi.org/10.1111/j.1466-8238.2007.00312.x)
- Keppeler, F. W., C. G. Montaña, and K. O. Winemiller. 2020. The relationship between trophic level and body size in fishes depends on functional traits. *Ecol. Monogr.* **90**: e01415. doi:[10.1002/ecm.1415](https://doi.org/10.1002/ecm.1415)
- Keppeler, F. W., and others. 2021. Data from: “Body size, trophic position, and the coupling of different energy pathways across a saltmarsh landscape”. Dryad Dataset. doi:[10.5061/dryad.5dv41ns6f](https://doi.org/10.5061/dryad.5dv41ns6f)
- Keppeler, F. W., and K. O. Winemiller. 2020. Can ancestry and morphology be used as surrogates for species niche relationships? *Ecol. Evol.* **10**: 6562–6578. doi:[10.1002/ece3.6390](https://doi.org/10.1002/ece3.6390)
- Lindeman, R. 1942. The trophic-dynamic aspect of ecology. *Ecology* **23**: 399–418. doi:[10.2307/1930126](https://doi.org/10.2307/1930126)
- Matich, P., and M. R. Heithaus. 2014. Multi-tissue stable isotope analysis and acoustic telemetry reveal seasonal variability in the trophic interactions of juvenile bull sharks in a coastal estuary. *J. Anim. Ecol.* **83**: 199–213. doi:[10.1111/1365-2656.12106](https://doi.org/10.1111/1365-2656.12106)
- Marton, J. M., B. J. Roberts, A. E. Bernhard, and A. E. Giblin. 2015. Spatial and temporal variability of nitrification potential and ammonia-oxidizer abundances in Louisiana salt marshes. *Estuar. Coast.* **38**: 1824–1837. doi:[10.1007/s12237-015-9943-5](https://doi.org/10.1007/s12237-015-9943-5)
- McCann, K. S. 2011. *Food webs*. Princeton Univ. Press.
- McCann, K. S., J. B. Rasmussen, and J. Umbanhowar. 2005. The dynamics of spatially coupled food webs. *Ecol. Lett.* **8**: 513–523. doi:[10.1111/j.1461-0248.2005.00742.x](https://doi.org/10.1111/j.1461-0248.2005.00742.x)
- McDevitt-Irwin, J. M., J. C. Iacarella, and J. K. Baum. 2016. Reassessing the nursery role of seagrass habitats from temperate to tropical regions: A meta-analysis. *Mar. Ecol. Prog. Ser.* **557**: 133–143. doi:[10.3354/meps11848](https://doi.org/10.3354/meps11848)
- McGarvey, R., N. Dowling, and J. E. Cohen. 2016. Longer food chains in pelagic ecosystems: Trophic energetics of animal body size and metabolic efficiency. *Am. Nat.* **188**: 76–86. doi:[10.1086/686880](https://doi.org/10.1086/686880)
- Moulton, D. L., M. A. Dance, J. A. Williams, M. Z. Sluis, G. W. Stunz, and J. R. Rooker. 2017. Habitat partitioning and seasonal movement of red drum and spotted seatrout. *Estuar. Coast.* **40**: 905–916. doi:[10.1007/s12237-016-0189-7](https://doi.org/10.1007/s12237-016-0189-7)
- Peterson, B. J., and B. Fry. 1987. Stable isotopes in ecosystem studies. *Annu. Rev. Ecol. Evol. S.* **18**: 293–320. doi:[10.1146/annurev.es.18.110187.001453](https://doi.org/10.1146/annurev.es.18.110187.001453)
- Pomeroy, L. R. 1959. Algal productivity in salt marshes of Georgia. *Limnol. Oceanogr.* **4**: 386–397. doi:[10.4319/lo.1959.4.4.0386](https://doi.org/10.4319/lo.1959.4.4.0386)
- Post, D. M. 2002. Using stable isotopes to estimate trophic position: Models, methods, and assumptions. *Ecology* **83**: 703–718. doi:[10.2307/3071875](https://doi.org/10.2307/3071875)
- Potapov, A. M., U. Brose, S. Scheu, and A. V. Tiunov. 2019. Trophic position of consumers and size structure of food webs across aquatic and terrestrial ecosystems. *Am. Nat.* **194**: 823–839. doi:[10.1086/705811?af=R&mobileUi=0](https://doi.org/10.1086/705811?af=R&mobileUi=0)
- Quezada-Romegialli, C., A. L. Jackson, B. Hayden, K. K. Kahilainen, C. Lopes, and C. Harrod. 2018. tRophicPosition, an R package for the Bayesian estimation of trophic position from consumer stable isotope ratios.



- Methods Ecol. Evol. **9**: 1592–1599. doi:[10.1111/2041-210X.13009](https://doi.org/10.1111/2041-210X.13009)
- Reiss, M. 1988. Scaling of home range size: Body size, metabolic needs and ecology. *Trends Ecol. Evol.* **3**: 85–86. doi:[10.1016/0169-5347\(88\)90025-0](https://doi.org/10.1016/0169-5347(88)90025-0)
- Riede, J. O., U. Brose, B. Ebenman, U. Jacob, R. Thompson, C. R. Townsend, and T. Jonsson. 2011. Stepping in Elton's footprints: A general scaling model for body masses and trophic levels across ecosystems. *Ecol. Lett.* **14**: 169–178. doi:[10.1111/j.1461-0248.2010.01568.x](https://doi.org/10.1111/j.1461-0248.2010.01568.x)
- Romero-Romero, S., A. Molina-Ramírez, J. Höfer, and J. L. Acuña. 2016. Body size-based trophic structure of a deep marine ecosystem. *Ecology* **97**: 171–181. doi:[10.1890/15-0234.1](https://doi.org/10.1890/15-0234.1)
- Rooney, N., K. McCann, G. Gellner, and J. C. Moore. 2006. Structural asymmetry and the stability of diverse food webs. *Nature* **442**: 265–269. doi:[10.1038/nature04887](https://doi.org/10.1038/nature04887)
- Rooney, N., K. S. McCann, and J. C. Moore. 2008. A landscape theory for food web architecture. *Ecol. Lett.* **11**: 867–881. doi:[10.1111/j.1461-0248.2008.01193.x](https://doi.org/10.1111/j.1461-0248.2008.01193.x)
- Ruiz, G. M., A. H. Hines, and M. H. Posey. 1993. Shallow water as a refuge habitat for fish and crustaceans in non-vegetated estuaries: An example from Chesapeake Bay. *Mar. Ecol. Prog. Ser.* **99**: 1–16. doi:[10.3354/MEPS099001](https://doi.org/10.3354/MEPS099001)
- Shurin, J. B., D. S. Gruner, and H. Hillebrand. 2006. All wet or dried up? Real differences between aquatic and terrestrial food webs. *P. Roy. Soc. B Biol. Sci.* **273**: 1–9. doi:[10.1098/rspb.2005.3377](https://doi.org/10.1098/rspb.2005.3377)
- Speakman, J. R. 2005. Body size, energy metabolism and lifespan. *J. Exp. Biol.* **208**: 1717–1730. doi:[10.1242/jeb.01556](https://doi.org/10.1242/jeb.01556)
- Stock, B. C., A. L. Jackson, E. J. Ward, A. C. Parnell, D. L. Phillips, and B. X. Semmens. 2018. Analyzing mixing systems using a new generation of Bayesian tracer mixing models. *Peer J* **6**: 5096. doi:[10.7717/peerj.5096](https://doi.org/10.7717/peerj.5096)
- Telesh, I. V., and V. V. Khlebovich. 2010. Principal processes within the estuarine salinity gradient: A review. *Mar. Pollut. Bull.* **61**: 149–155. doi:[10.1016/j.marpolbul.2010.02.008](https://doi.org/10.1016/j.marpolbul.2010.02.008)
- Tucker, M. A., and T. L. Rogers. 2014. Examining predator-prey body size, trophic level and body mass across marine and terrestrial mammals. *P. Roy. Soc. B-Biol. Sci.* **281**: 20142103. doi:[10.1098/rspb.2014.2103](https://doi.org/10.1098/rspb.2014.2103)
- Vagvolgyi, J. 1975. Body size, aerial dispersal, and origin of the Pacific land snail Fauna. *Syst. Zool.* **24**: 465–488. doi:[10.2307/2412906](https://doi.org/10.2307/2412906)
- Vander Zanden, M. J., M. K. Clayton, E. K. Moody, C. T. Solomon, and B. C. Weidel. 2015. Stable isotope turnover and half-life in animal tissues: A literature synthesis. *PLoS One* **10**: e0116182. doi:[10.1371/journal.pone.0116182](https://doi.org/10.1371/journal.pone.0116182)
- Vehtari, A., A. Gelman, and J. Gabry. 2017. Practical Bayesian model evaluation using leave-one-out cross-validation and WAIC. *Stat. Comput.* **27**: 1413–1432. doi:[10.1007/s11222-016-9696-4](https://doi.org/10.1007/s11222-016-9696-4)
- Villarino, E., and others. 2018. Large-scale ocean connectivity and planktonic body size. *Nat. Commun.* **9**: 142. doi:[10.1038/s41467-017-02535-8](https://doi.org/10.1038/s41467-017-02535-8)
- Ziegler, S. L., K. W. Able, and F. J. Fodrie. 2019. Dietary shifts across biogeographic scales alter spatial subsidy dynamics. *Ecosphere* **10**: e02980. doi:[10.1002/ecs2.2980](https://doi.org/10.1002/ecs2.2980)
- Wegener, M. G., K. M. Harriger, J. R. Knight, and M. A. Barrett. 2017. Movement and habitat use of alligator gars in the Escambia River, Florida. *N. Am. J. Fish. Manage.* **37**: 1028–1038. doi:[10.1080/02755947.2017.1342722](https://doi.org/10.1080/02755947.2017.1342722)
- Winemiller, K. O. 1990. Spatial and temporal variation in tropical fish trophic networks. *Ecol. Monogr.* **60**: 331–367. doi:[10.2307/1943061](https://doi.org/10.2307/1943061)

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