



Does Invasion of Eurasian Milfoil *Myriophyllum spicatum* Lead to a “Trophic Dead End” and Reduced Food Web Complexity in Gulf of Mexico Estuarine Food Webs?

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Estuaries of the northern Gulf of Mexico contain an abundance of habitat-forming submerged aquatic vegetation (SAV) that provide refuge and protection for a variety of freshwater, estuarine, and marine organisms. However, many of these estuaries now contain numerous exotic species, the ultimate impacts of which are unclear. In the Mobile-Tensaw Delta, located in the upper portion of Mobile Bay, Alabama (USA), Eurasian milfoil (*Myriophyllum spicatum*, hereafter referred to as *Myriophyllum*) is now the most dominant submerged macrophyte. *Myriophyllum* is a structurally-complex macrophyte with the potential to dramatically alter estuarine food webs through reduced encounter rates between predators and their prey and other mechanisms. Previously, we surveyed faunal communities using throw traps, trawls, cores, and suction sampling to compare milfoil assemblages with other native macrophytes to explore the interactive role of hydrology, diel periodicity, and macrophyte presence in influencing community structure. Here, we use this previously collected data to generate preliminary food web analyses to determine if milfoil, due to its high complexity, creates a “trophic dead end” and limits higher trophic level production. We found the number of nodes, links, linkage density, and connectance to all be greater in milfoil than *Vallisneria americana* (hereafter referred to as *Vallisneria*), indicating that a diverse, productive, and highly connected food web exists in this invasive habitat.

Keywords: *Vallisneria*, watermilfoil, habitat, exotic, network model

INTRODUCTION

Estuarine ecosystems, located in the ecotones between marine and fresh waters and exposed to a range of dynamic stressors, including fluctuating environmental conditions (e.g., tides, salinity) and anthropogenic development (e.g., habitat loss, shoreline modification, altered hydrology), may be at great risk from successful invasions of non-native species. Invasion theory, established by Elton (1958), suggests that the alteration of native ecosystems can reduce invasion resistance of the ecosystem which, when coupled with high invasive propagule pressure from the proximity to urban centers and dispersal vectors such as commercial shipping, may facilitate the establishment of invasive species in estuaries.

After gaining a foothold in these dynamic ecosystems, it is hypothesized that their competitive advantages will further enable their establishment and proliferation, creating a threat to biodiversity (Lodge, 1993; Vitousek et al., 1997; Cohen and Carlton, 1998; Everett, 2000) and ecosystem services provided by species-rich native ecosystems (Mack et al., 2000; Zedler and Kercher, 2004).

In northern Gulf of Mexico estuaries, a variety of invaders are now established at a wide range of trophic levels (Duffy and Baltz, 1998; Hicks et al., 2001; Peterson et al., 2005; Martin et al., 2010) and reported to have a negative impact on biodiversity. At the level of primary producer, however, several recent studies have indicated that plant invasions can supplement species richness in some invaded estuarine ecosystems (Cleland et al., 2004; Smith et al., 2004; Capers et al., 2007; Martin and Valentine, 2012). Invasive species that either create new habitats, or alter environmental conditions in existing habitats, have been hypothesized to have disproportionately negative effects on food webs (Crooks, 2002). In some cases, invasive vegetation can be structurally complex and larger than native species (Posey, 1988; Posey et al., 1993; Duffy and Baltz, 1998; Chaplin and Valentine, 2009). Structurally complex invasive plants can also reduce the foraging efficiency of higher order predators through the creation of interstitial spaces reducing encounter rates between predators and their prey (Nelson, 1979; Heck and Thoman, 1981; Martin and Valentine, 2011; Valinoti et al., 2011). As a result, the invasion of structurally complex macrophytes may limit energy flow to lower levels and alter trophic interactions in estuaries and thus

represent a “trophic dead-end,” with fewer pathways and less energy transfer among adjacent trophic levels in successfully invaded estuarine food webs (Chaplin and Valentine, 2009).

Because estuaries in the northern Gulf of Mexico serve as nursery grounds that fuel some of the most productive commercial and recreational fisheries in the world (Chesney et al., 2000; Lellis-Dibble et al., 2008), the alteration of food web function in this area is of great concern. Here, we use estimates of shelter-seeking fauna from previous literature in Mobile Bay, Alabama (USA) to construct a preliminary food web to assess the impacts of one widespread invasive submerged aquatic vegetation (SAV), Eurasian milfoil *Myriophyllum spicatum*, on oligohaline estuarine food web function via a comparison with an abundant native species of vegetation (wild celery, *Vallisneria americana* hereafter referred to as *Vallisneria*) (Figure 1). The overarching goal of this research is to provide an initial assessment of the potential impacts of invasive Eurasian milfoil (hereafter referred to as *Myriophyllum*) on food web function in the estuaries of the northcentral Gulf of Mexico.

METHODS

Study Site

The Mobile-Tensaw Delta (MTD), located at the upper end of Mobile Bay in lower Alabama, encompasses an area of over 1100 km², from the convergence of the Tombigbee and Alabama Rivers south to Mobile Bay. The watershed drains ~15% of the United States' freshwater, ranking as the fourth largest drainage

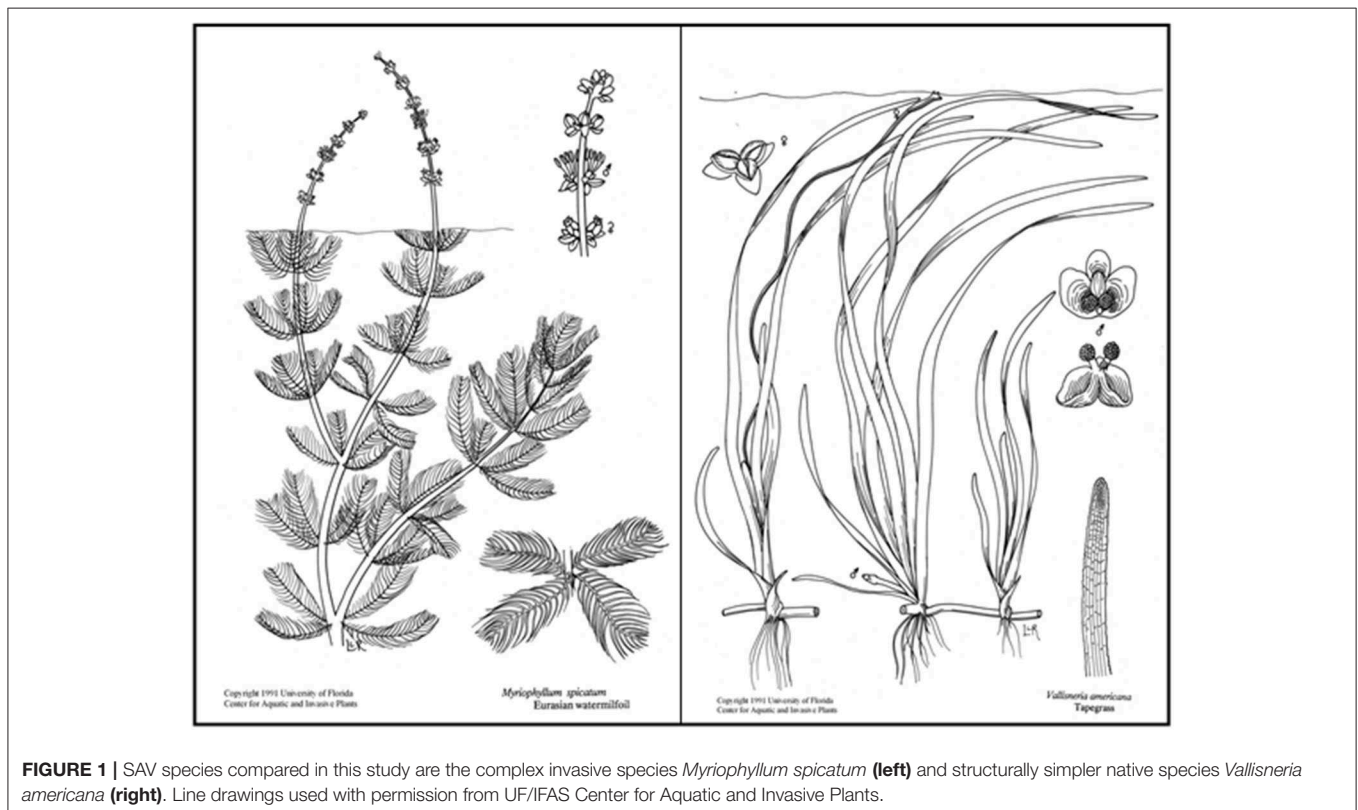


FIGURE 1 | SAV species compared in this study are the complex invasive species *Myriophyllum spicatum* (left) and structurally simpler native species *Vallisneria americana* (right). Line drawings used with permission from UF/IFAS Center for Aquatic and Invasive Plants.

delta in terms of discharge, before entering the Gulf of Mexico (Gastaldo, 1985). The landscape shifts from forested wetlands in the north to tidal freshwater and oligohaline marshes as the MTD empties into Mobile Bay to the south. Salinities in the southernmost portion of the area is highly variable, from freshwater or low salinity (2 Practical Salinity Units, PSU) during the spring to 18 PSU or higher in the fall. Tidal heights vary on average 40-cm (Martin and Valentine, 2014a,b).

Widespread throughout the MTD in shallow waters are as many as 24 species of SAV (Stout et al., 1982; Vittor, 2003), the most abundant of which are *Myriophyllum* and *Vallisneria*. Although annually variable, as much as 80% coverage of the submerged landscape has been estimated to be covered by *Myriophyllum* (Vittor, 2003; Chaplin and Valentine, 2009; Martin and Valentine, 2012). *Myriophyllum* is a structurally complex species of SAV commonly encountered in freshwater and coastal ecosystems in North America, including estuaries of the Gulf of Mexico (Duffy and Baltz, 1998; Frazer et al., 2006; Martin and Valentine, 2011). The dense beds formed by *Myriophyllum* have the potential to alter the composition of faunal assemblages due to their increased complexity and density, especially compared to the structurally simpler native habitats, such as *Vallisneria* (Chaplin and Valentine, 2009; Goecker et al., 2009). While much is known about the aesthetic effects of *Myriophyllum* on freshwater ecosystems, and its effects on food web structure and function in freshwater systems (Smith and Barko, 1990), its food web effects in coastal systems, especially in the Gulf of Mexico, remain less clear and the goal of this study is to perform a preliminary assessment of *Myriophyllum*'s food web.

Previous Literature

Several studies have quantified various aspects of the organisms residing in *Myriophyllum* and *Vallisneria* in the MTD (Table 1). Chaplin and Valentine (2009) quantified secondary production and invertebrate assemblages using cores and found elevated levels driven primarily by very high densities of amphipods. Martin and Valentine (2011) reported that the fishes and macroinvertebrates inhabiting *Myriophyllum*, quantified using throw traps, were more abundant and had a significantly different community structure from those found in native *Vallisneria* beds. Hydrologically isolated areas within the region can also have

impacts on the faunal communities, as demonstrated by a drop sampling approach (Rozas et al., 2013). Finally, the structure provided by *Myriophyllum* can be extremely dense, trapping organic matter which, when coupled with plant respiration, can trigger low oxygen events in some areas and impact organism captured through suction sampling (Kauffman et al., 2018). Generally, this anoxia is limited to nighttime hours and only in *Myriophyllum* beds. Using the data collected for these studies, we used a social network modeling (Borgatti et al., 2002) to perform initial assessments of the food web structure in both *Myriophyllum* and *Vallisneria*.

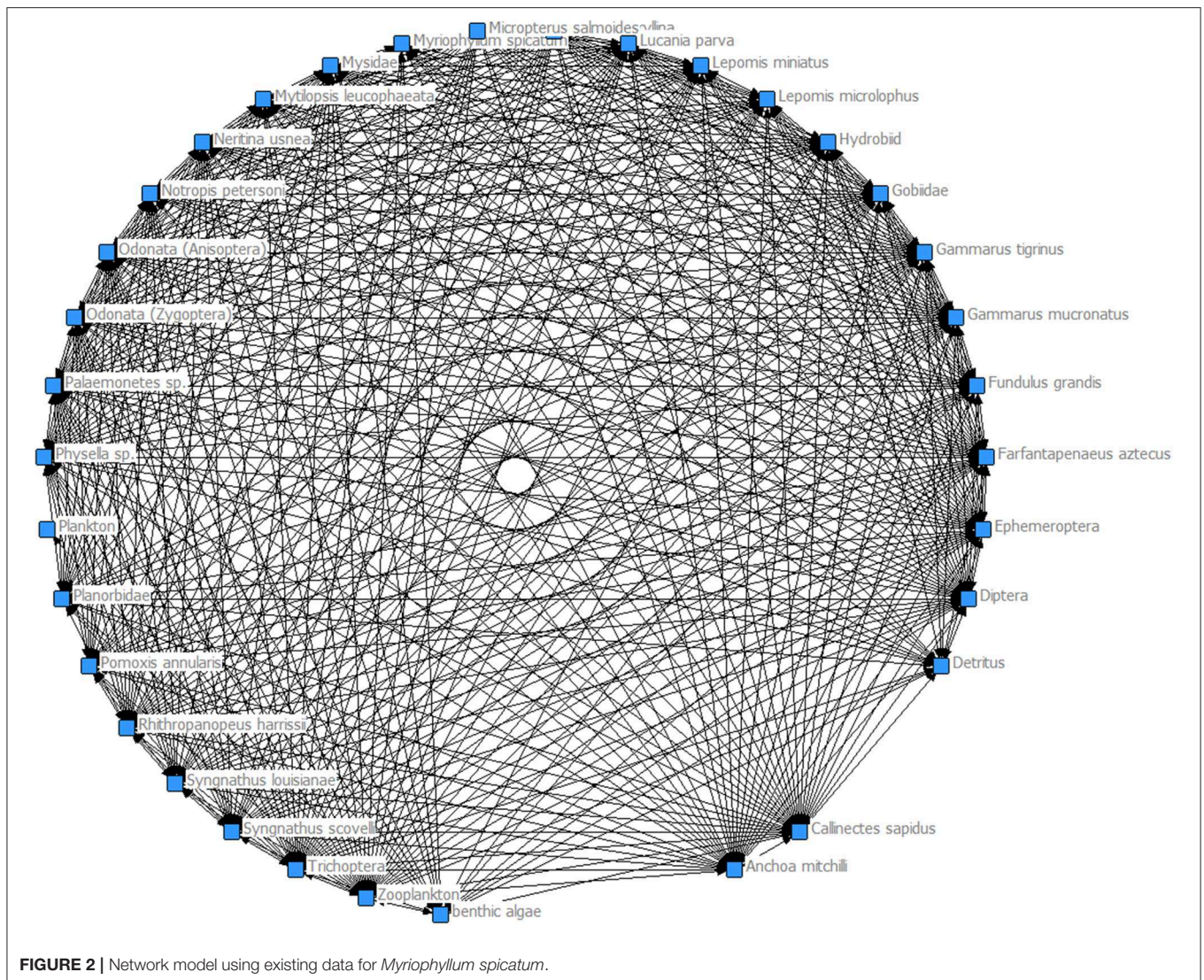
Food Web Analyses

Using presence/absence of species composition, we used the tools of social network analysis to generate a binary food web for organisms captured within each SAV (*Myriophyllum* and *Vallisneria*). Networks were created using UCINET software (Borgatti et al., 2002; McCann et al., 2017). Each network was visualized by creating a circular graph using the NETDRAW feature found in UCINET software. While this approach is most commonly used in social sciences, it has been applied to ecological systems (Christian et al., 2005; Fletcher et al., 2011; McCann et al., 2017). Advantages of this approach are that it provides accurate predictions of structure, requires less data, and is flexible with the types of data used (Fletcher et al., 2011). As a result, this approach may be advantageous for some questions not requiring a full diet model (such as Ecopath with Ecosim). Diet information was attained from the author's unpublished gut content data from this area, literature-based estimates, and best professional judgement (Chaplin, 2002; Christian and Allen, 2014).

From the networks generated by the modeling efforts, a variety of performance metrics were generated for both the *Myriophyllum* and *Vallisneria* habitats. The number of nodes was defined as the number of individual species/taxonomic groups present in each network. The number of links estimated the probable number of trophic interactions (i.e., lines that connect nodes) occurring within the two habitats. The estimated linkage density for each SAV was defined as the average number of links per node, calculated as L/S , where L was the number of links and S was the number of species or nodes. Finally, connectance (or

TABLE 1 | Previous studies used in this analysis.

References	Fauna reported	Collection method	Synopsis
Chaplin and Valentine (2009)	Benthic invertebrates	Cores	Comparison of secondary production in <i>M. spicatum</i> , <i>Heteranthera dubia</i> , and <i>V. americana</i>
Martin and Valentine (2011)	Nekton and macroinvertebrates	Throw trap	Reported differences in community composition in <i>M. spicatum</i> , <i>H. dubia</i> , and <i>V. americana</i>
Rozas et al. (2013)	Benthic invertebrates, fishes	Drop sampler	Assessment of differences in hydrology on assemblages
Kauffman et al. (2018)	Epibenthic invertebrates, fishes	Suction sampler	Comparison of diel variability and causeway location on community composition



the proportion of possible links that are realized) was determined for each network by calculating the maximum connectance as $S(S-1)/2$, where S is the number of species or nodes. Then the connectance in each network was calculated as $L/(S(S-1)/2)$, where S is the number of species or nodes and L is the number of links.

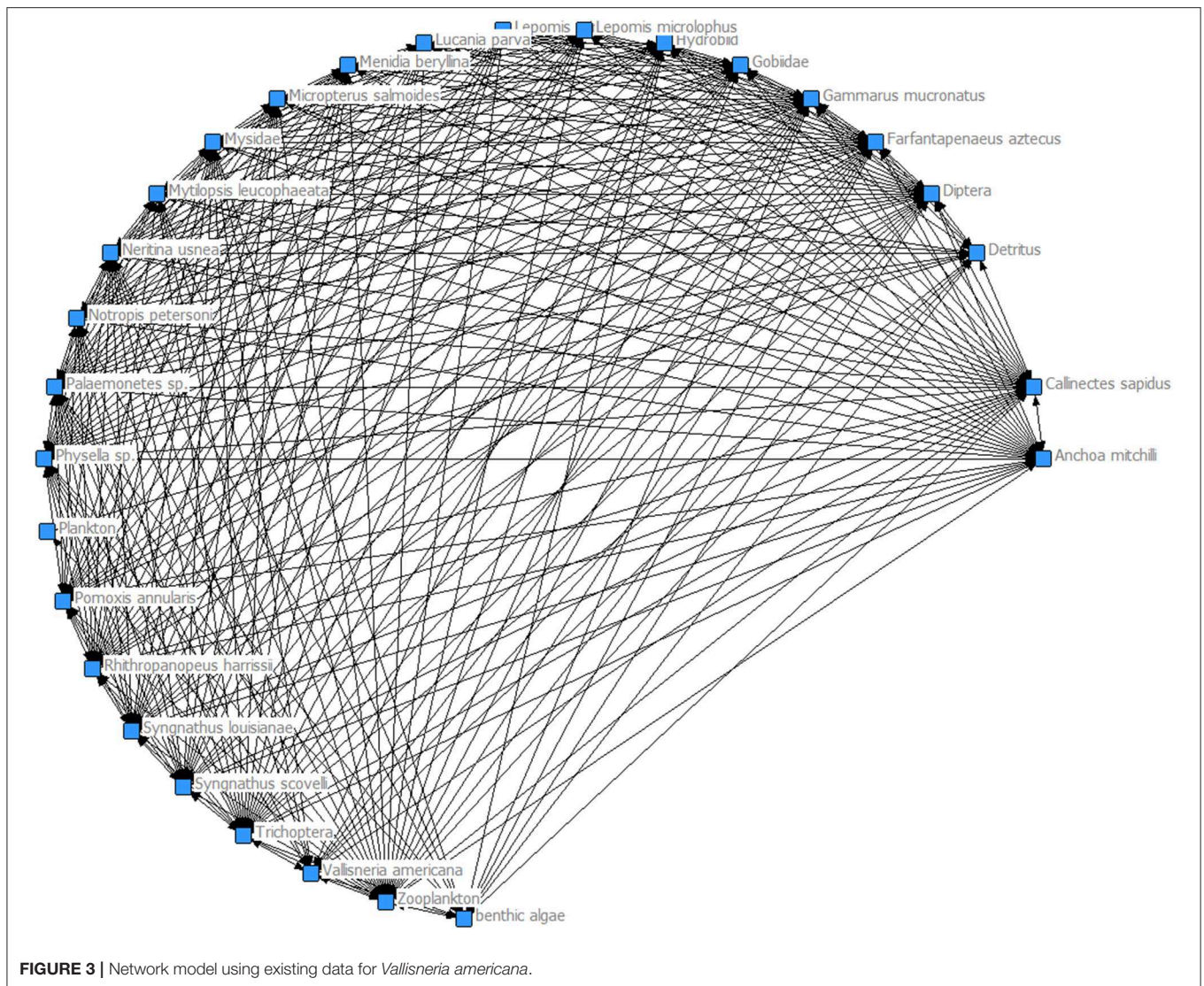
RESULTS

The food webs generated for *Myriophyllum* (Figure 2) and *Vallisneria* (Figure 3) show that each habitat is productive and supports a diverse food web. However, the model-generated food web performance metrics showed that *Myriophyllum* exceeds that of *Vallisneria* in all comparisons. In general, there were more nodes and links in *Myriophyllum* habitats than *Vallisneria* (nodes: 75 compared to 68 and links: 310 compared to 197 respectively). The 9.33% increase in nodes in *Myriophyllum* led to a 36.45% more links. This corresponded to a 29.78% increase in the linkage density in *Myriophyllum* (4.13), when compared

to *Vallisneria* (2.90). Finally, these performance metrics led to a 23.21% increase in connectance for *Myriophyllum* (0.056) over *Vallisneria* (0.043). Given the increased nodes, links, linkage density, and connectance in *Myriophyllum*, we surmise that these initial, preliminary food web metrics indicate that *Myriophyllum* may not be the trophic dead ends as might be predicted based on traditional invasion theory. Rather, *Myriophyllum* seems to support a robust, highly connected food web when compared to the dominant native species, *Vallisneria*.

DISCUSSION

Among the myriad of stressors facing coastal ecosystems, invasive species have been posited to be among the most pervasive consequence of elevated levels of anthropogenic activities in estuaries (Mack et al., 2000). With the increasing human population in coastal areas, and subsequent increases in disturbances accompanying this encroachment, invasive species now join a long list of stressors affecting coastal food webs (Ruiz



et al., 1999) including eutrophication (de Mutsert et al., 2016), climate change (Heck et al., 2015), hurricanes (Anton et al., 2009), and oil spills (McCann et al., 2017; Martin and Swenson, 2018), among others.

Here, we used the results of several recent studies comparing *Myriophyllum* and *Vallisneria* faunal composition in upper Mobile Bay and the lower MTD, Alabama, to evaluate potential food web impacts due to the proliferation of this notorious invader. Given the increased nodes, links, linkage density, and connectance in *Myriophyllum*, we surmise that these initial, preliminary food web performance metrics indicate that *Myriophyllum* may not be a trophic dead end as many predicted and the increased structural complexity does support a highly connected food web compared relative to the dominant native species, *Vallisneria*. We note that the density, and thus structural complexity, of these habitats vary greatly within this invaded system such that a range of complexities are present (Martin and Valentine, 2012; Martin et al., 2012).

We highlight that these analyses are preliminary, with these studies encompassing a large temporal interval (almost a decade), over which changes may have occurred and be integrated within the generated models. Likewise, short-term changes in habitat community composition may also occur, as demonstrated by Kauffman et al. (2018) with migration into/out of these habitats occurring over a diel cycle, further biasing the model. We would contend, however, that this work is conservative to this bias by incorporating presence/absence of all organisms captured over the study period into these analyses. Finally, this study uses a binary, unweighted links to establish food web connections and future research should be aimed at determining carbon flow originating from *Myriophyllum* and true, weighted links in this food web (e.g., using biomarkers such as isotopic and/or fatty acid approaches). Moreover, incorporating abundance into more traditional food web analyses such as Ecopath with Ecosim may yield further insight into ecosystem functioning in these invaded ecosystems.

Throughout the United States, the invasion of *Myriophyllum* has been largely widespread and represents a significant threat to aquatic environments, largely due to the fast growth rates resulting in large canopies and areal coverage of this invader. These changes can impact key ecosystem functions such as environmental conditions and water quality (Frodge et al., 1990; Unmuth et al., 2000) and significantly alter a range of variables impacting community composition and food webs, including habitat preference, herbivory, foraging, and decomposition (Martin and Valentine, 2011; Steele et al., 2018). Based on the impacts to freshwater ecosystems, it is reasonable to assume that *Myriophyllum* might also have negative impacts in estuaries, although to date these have not been observed (Duffy and Baltz, 1998; Martin and Valentine, 2011, 2012). Still, a more detailed assessment of impacts is necessary to gain a more comprehensive view of the ecological impacts of this invader. We suggest that additional food web studies are necessary to fully understand *Myriophyllum*'s impacts in coastal areas, such coupled gut/dietary analyses with biomarker approaches and how ecologically relevant the documented food web changes are for energy flow. Incorporating multiple trophic levels, in addition to spatial and temporal variability in communities and patterns of vegetation will likely significantly enhance our understanding of estuarine invaders and encourage more cognizant management approaches to prevent and eradicate these invaders.

DATA AVAILABILITY STATEMENT

The datasets for this manuscript are not publicly available because Datasets are part of previously published literature found at the following links: <https://link.springer.com/article/10.1007/s12237-010-9274-5>; <https://www.int-res.com/abstracts/meps/v592/p97-108/>; <https://link.springer.com/article/10.1007/s12237-008-9117-9>; [## REFERENCES](https://www.int-res.com/abstracts/</p>
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meps/v492/p9-20/. Requests to access the datasets should be directed to CM, martin.charles.w@gmail.com.

ETHICS STATEMENT

While this manuscript does involve animal subjects, the analysis performed here only used data from previously published literature and no field collections were performed for this modeling approach.

AUTHOR CONTRIBUTIONS

CM and JV conceived the study and contributed to manuscript revision, read, and approved the submitted version. CM performed analysis and wrote the first draft.

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Conflict of Interest: The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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