Drift macroalgae positively influence seagrass-associated nekton communities of the northern Gulf of Mexico

Kelly M. Correia1,2*, Scott B. Alford3, Benjamin A. Belgrad1, Kelly M. Darnell4, M. Zachary Darnell4, Bradley T. Furman5, Margaret O. Hall5, Christian T. Hayes4†, Charles W. Martin3 and Delbert L. Smee1,2

1Dauphin Island Sea Lab, Dauphin Island, AL, United States, 2Department of Marine Sciences, School of Marine and Environmental Sciences, University of South Alabama, Mobile, AL, United States, 3Nature Coast Biological Station, University of Florida, Cedar Key, FL, United States, 4Division of Coastal Sciences, School of Ocean Science and Engineering, The University of Southern Mississippi, Ocean Springs, MS, United States, 5Florida Fish and Wildlife Conservation Commission, Fish and Wildlife Research Institute, St. Petersburg, FL, United States

Drift macroalgae, often found in clumps or mats adjacent to or within seagrass beds, can provide additional food resources and habitat complexity, leading to increased animal abundance, but large concentrations can also inhibit faunal movements, smother benthic communities, and contribute to hypoxia, reducing nekton abundance. Despite its ubiquity, few studies have quantified drift macroalgal prevalence over large spatial scales or its effects on seagrass-associated nekton, hindering our understanding of the functional role of drift macroalgae in ecosystems. We quantified the relationship between drift macroalgal biomass and the seagrass-associated nekton community within five estuaries spanning 2000 km across the northern Gulf of Mexico. Overall, increases in macroalgal biomass within seagrass meadows significantly influenced community structure, increasing shrimp, crab, and fish abundances, but the effect varied by region. Relationships between species richness, diversity, organism size, and macroalgal biomass were not observed, suggesting that drift macroalgae provide additional habitat but not necessarily new niche space. Small nekton play a vital role in many local fisheries, providing valuable food resources for fish and invertebrates. Increased recruitment into macroalgal can benefit local fisheries by providing shelter and increased food resources, which may increase the survival, growth, and population size of recreationally and economically important species. While excess levels of drift macroalgae can negatively impact benthic plant and animal communities, particularly in eutrophic areas, the moderate levels observed during this survey were associated with positive effects on organismal abundance, suggesting that drift algal dynamics should be considered in habitat-based management strategies for coastal estuaries.

KEYWORDS
habitat complexity, diversity, abundance, Texas, Louisiana, Florida
Introduction

Despite comprising less than 10% of the ocean area, shallow coastal habitats, such as seagrass meadows, salt marshes, mangroves, and oyster reefs, provide extensive benefits that are both ecologically and economically important. Seagrass habitats alone contribute over $19,000 ha⁻¹ yr⁻¹ to local economies (Costanza et al., 1997; Fourqurean et al., 2012; Tuya et al., 2014). When found within seagrass habitats, drift macroalgae can further increase phytobiomass aboveground by 3- to 100-fold (Morris and Hall, 2001), adding to habitat complexity that can support increased animal diversity (Kingsford, 1995).

Drift macroalgae often originate as attached algae on seagrass leaves and other hard substrata before becoming uprooted by various physical disturbances (e.g., currents and waves) (Norton and Mathieson, 1983; Bell and Hall, 1997; Biber, 2002; Lirman et al., 2003). They are classified into three major groups: brown algae (Phaeophyceae), green algae (Chlorophyta), and red algae (Rhodophyta; Norton and Mathieson, 1983; Bell and Hall, 1997; Biber, 2002; Lirman et al., 2003), with rhodophytes being the dominant taxa in the northern Gulf of Mexico (Vörösmarty and Carbonara, 1985; Bell and Hall, 1997; Holmquist, 1997). Seagrass and associated macroalgae create productive ecosystems relative to neighboring unvegetated substrates, providing valuable nursery habitats (e.g., Carr, 1994; Jackson et al., 2001; Heck et al., 2003), enhancing local fisheries, increasing food resources and fish growth rates, and decreasing predation and competition (e.g., Orth et al., 1984; Fraser and Gilliam, 1987; Rooker et al., 1998; Nagelkerken et al., 2002; Jackson et al., 2015).

Drift macroalgae often increase the structural complexity of seagrass habitats (Morris and Hall, 2001) and provide additional refuge, leading to increases in infauna (Hull, 1987), epifauna (Isaksson and Pihl, 1992), and macrofauna, including small crustaceans and mollusks (Norkko et al., 2000; Raffaelli, 2000; Savolius et al., 2005), juvenile blue crabs (Wilson et al., 1990), and small shrimp and fish (Holmquist, 1994; Holmquist, 1997; Kingsford, 1995; Correia, 2021). Relationships between habitat complexity and nekton abundance and species richness have been the focus of many studies, with more complex habitats increasing niche space and leading to increases in the abundance and diversity of animals found there (e.g., Kingsford, 1995; Rozas and Minello, 1998; Minello, 1999). While macroalgae can enhance seagrass ecosystem services, at sufficiently high biomass, they can also lead to hypoxic conditions with resulting declines in animal abundance and species diversity (Hull, 1987; Bonsdorff, 1992; Raffaelli et al., 1998; Cummins et al., 2004; Zajac and McCarthy, 2015). Whether drift macroalgae have positive or negative impacts on the animal community is largely driven by the quantity and type of algae present, with lower drift algal biomass oftentimes leading to higher nekton abundance and species richness (e.g., Everett, 1994; Holmquist, 1997; Norkko et al., 2000; Arroyo et al., 2006) and high biomass leading to a decline in species richness (e.g., Bonsdorff, 1992; Raffaelli et al., 1998). However, understanding the threshold where the net impact of drift algal biomass transitions from positive to negative and the overall role that drift algae play in structuring animal communities remains an ongoing challenge.

Over the past few decades, seagrass cover has declined in the northern Gulf of Mexico, while drift algal abundance has remained constant or increased (Benz et al., 1979; Vörösmarty and Carbonara, 1985; Zieman et al., 1989; Biber and Irlandi, 2006; Kopecky and Dunton, 2006; Fredericq et al., 2009; Correia, 2021). With future climate projections indicating an increase in macroalgae in accordance with higher sea surface temperatures and ocean acidification (Brodie et al., 2014), contemporary studies are needed to assess both the presence and effects of drift macroalgae on seagrass-associated nekton communities. The purpose of this study was to investigate the relationships between drift macroalgal biomass and small nekton communities on a Gulf-wide scale. Previous comparisons across the northern Gulf of Mexico revealed significant differences in algal biomass across the region and sampling period (Correia et al., in press). Because macroalgae were often more abundant during the early summer months, this study primarily focused on data collected during May–June 2018. To determine how drift algal biomass influences nekton community structure, we performed a survey of drift macroalgae across five estuaries spanning 2000 km of the coastline in the northern Gulf of Mexico, measuring macroalgal biomass as well as the nekton community found within the seagrass-macroalgal mosaic. Specifically, we quantified (1) the relationship between algal biomass and nekton community composition (e.g., abundance, diversity, and taxon-specific variations) and (2) regional variation in these relationships across the northern Gulf of Mexico. An epibenthic sled was used during data collection to sample the smaller epibenthic nekton and invertebrates living within the algal-seagrass matrix, which are more likely to be influenced by variations in algal biomass. Because the seagrass percent cover and structure varied across each region, which could affect our interpretation of algal impacts on fauna, a subset of the data was also analyzed to compare nekton community changes across a range of algal weights when the areal coverage of the dominant seagrass turtle grass (Thalassia testudinum) exceeded 75% and canopy heights were between 200 and 400 mm (Correia, 2021). Based on previous findings, we hypothesized that algal biomass would influence the community composition of fauna, increasing the abundance and richness at intermediate algal biomasses.
Materials and methods

Study regions

Five estuaries in the northern Gulf of Mexico, each containing at least 20 sites within seagrass meadows, were surveyed during early (May–June) and late (August–September) summer of 2018 (Supplementary Figure S1). The estuaries sampled included Laguna Madre, TX (LM; \(n = 20\), 26°08′N, 97°14′W), Corpus Christi Bay, TX (CB; \(n = 20\), 27°51′N, 97°08′W), the Chandelier Islands, LA (LA; \(n = 20\), 29°54′N, 88°50′W), Cedar Key, FL (CK; \(n = 25\), 29°05′N, 83°01′W), and Charlotte Harbor (CH; \(n = 25\), 26°04′N, 82°14′W). These estuaries encompass two semi-enclosed bays and one semi-enclosed lagoon with no major freshwater inputs (LM). Sites were selected by overlaying a tessellated hexagonal grid (500 m edge length) on each estuary in ArcGIS (Moore, 2009; Neckles et al., 2012; Wilson and Dunton, 2012). One station was randomly generated within each of the 20–25 grid cells that contained more than 50% seagrass coverage, with a minimum of 500 m distance between sites (Belgrad et al., 2021). Across all regions, turtlegrass (\(T. testudinum\)) was the dominant macrophyte taxa; however, manatee grass (\(Syringodium filiforme\)) and shoal grass (\(Halodule wrightii\)) were also common. At each sampling site, abiotic conditions (i.e., temperature, salinity, dissolved oxygen, and depth) were recorded, drift macroalgal biomass was measured, and seagrass cover/abundance and morphometrics [i.e., percent cover (0–100%), shoot height (mm), and shoot density] were assessed. Because we sampled synoptically using the same methods, we were able to evaluate algal biomass and distribution within and among locations across the northern Gulf of Mexico (Supplementary Table S1; Belgrad et al., 2021; Correia, 2021).

Drift algal biomass and nekton community assessment

Within each hexagon, drift algal biomass and nekton abundance within seagrass meadows were measured using an epibenthic sled, consisting of an aluminum frame (0.75 m wide and 0.6 m high) with two skids on either side (0.7 m in length), and a 2 mm stretch mesh net. The sled captured smaller epibenthic fish and invertebrates living within the algal-seagrass matrix. The sled was towed for 13.3 m at approximately 0.3 m sec⁻¹, covering an area of approximately 10 m². Macroalgae from benthic sled samples were bagged, frozen, and transported to the lab where they were later identified and weighed. Nekton within the sled were identified to the lowest possible classification and counted, and their lengths (i.e., total length for shrimp and fish; carapace width for crabs) were recorded.

Seagrass and algal vegetative sampling (quadrats)

Seagrass structural complexity was assessed using a 1 m² quadrat divided into 100, 10 cm × 10 cm cells. Four quadrats were haphazardly thrown at each sampling location, and the percent cover, shoot count, and canopy height of each seagrass species present in a quadrat were recorded. The seagrass percent cover by species and the cover of drift algae were measured by counting the number of grid cells within each quadrat that contained a particular vegetation type (0–100 grids quadrat⁻¹). Shoot count was calculated for each seagrass species by counting the number of shoots within a random quadrat grid cell. Canopy height was defined as the mean of three randomly selected shoot height measurements.

Statistical analysis

SAS® and Primer™ 7 were used for all statistical analyses. A combination of univariate and multivariate analyses was performed to assess nekton abundance, biodiversity, animal size, and community structure in relation to drift algal biomass. Variables were tested in SAS® for normality, and abundance was log-transformed to mitigate skewness and to achieve normality. Generalized linear mixed models (GLMMs) were used in SAS® to compare nekton abundance (N), species richness (S), and diversity (H') across the region (CB, CH, CK, LA, and LM), to algal weight [g wet weight (ww); Horton and Lipsitz, 2012; Sokal and Rohl, 2013]. The weights of algae collected in the epibenthic sled were then ranked, and multivariate analysis was performed in Primer to compare community differences across these weight classes (0–4), with 0 indicating no algae present (\(n = 70\)), 1 indicating 1–300 g ww of algae (\(n = 77\), mean = 115 ± 83 SD), 2 indicating 301–500 g ww (\(n = 25\), mean = 115 ± 83), 3 indicating 501–1,000 g ww (\(n = 23\), mean = 755 ± 172), and 4 indicating over 1,000 g ww (\(n = 25\), mean = 2,560 ± 1,630). The ranking system was necessary for Primer analysis because this software cannot analyze continuous data as a treatment. Species abundance was square-root-transformed to manage skewness and analyzed using a one-way PERMANOVA design with algal weight class (0–4) as the fixed factor. A canonical analysis of principal coordinates (CAP) plot was also performed to illustrate a pattern of difference across algal weight classes.

To account for the positive relationship between drift macroalgal biomass and increased seagrass percent cover (Correia, 2021; Correia et al., in press), a subset of the data was also analyzed to compare the effects of drift algal biomass to...
nekton community composition while holding seagrass constant (the turtle grass percent cover was greater than 75%, and the canopy heights were between 200 and 400 mm), encompassing 31.8% of the original data set. When analyzing the subset, community or diversity metrics were no longer significantly different across algal weight classes to one another, areas containing 300–500 g of algae (Class 2) showed the most variability in the animal abundance, with significantly higher animal abundances seen at algal biomasses over 500 g ww, compared to those when no algae were present (Figure 1A; Table 1). While algal biomass led to increased nekton species abundance, no clear pattern was found with nekton species richness or diversity ($p = 0.92$; Table 1). Nekton species richness remained relatively stable across algal weight classes, with 49 unique species identified when no algae were present ($n = 19$), 53 species in 1–300 g ww ($n = 37$), 52 species in 301–500 g ww ($n = 19$), 42 species in 501–1,000 g ww ($n = 19$), and 56 species in areas with over 1,000 g ww of algae ($n = 15$). Shannon diversity also did not differ significantly across algal weight and only varied by region ($p = 0.03$; Table 1). When analyzing a subset of the data in turtle grass with a similar coverage and canopy height, similar patterns were observed for animal abundance, with significantly higher animal abundances seen at algal biomasses over 500 g ww, compared to those when no algae were present (Figure 1B; Table 1). Diversity was not significantly different across region ($p = 0.14$) or algal weight ($p = 0.71$; Table 1) in the data subset, and the richness again remained stable across all algal weight classes (Correia, 2021).

Macroalgal biomass significantly influenced overall community structure (Figure 2A; $\text{Pseudo-F} = 3.124$; $p = 0.001$). Pairwise comparisons across the different algal weight classes indicated that small benthic communities were significantly different when algae were present. When comparing algal weight classes to one another, all areas containing algae were significantly different from areas with no algae (Supplementary Table S2). Areas containing smaller concentrations of algae (i.e., Class 1–3) were also significantly different from areas containing over 1,000 g of algae (Class 4; Supplementary Table S2). When analyzing these relationships using a subset of the data to control for seagrass cover and canopy height, macroalgal biomass still significantly influenced community structure (Figure 2B; $\text{Pseudo-F} = 2.24$; $p = 0.002$). Pairwise comparisons across algal weight class indicated that all areas containing algae were significantly different from areas with no algae (Supplementary Table S2). When comparing algal weight classes to one another, areas containing 300–500 g (Class 2) of macroalgae were significantly different from areas containing over 500 g (Classes 3 and 4). Macroalgal concentrations below 300 g showed the most variability in the nekton community and were not significantly different from the other macroalgal classes (Supplementary Table S2).

**Results**

Overall, the mean animal abundance was significantly different across algal weight ($p < 0.001$) and was higher when the algal biomass was greater than 500 g (Figure 1A; Table 1). While algal biomass led to increased nekton species abundance, no clear pattern was found with nekton species richness or diversity ($p = 0.92$; Table 1). Nekton species richness remained relatively stable across algal weight classes, with 49 unique species identified when no algae were present ($n = 19$), 53 species in 1–300 g ww ($n = 37$), 52 species in 301–500 g ww ($n = 19$), 42 species in 501–1,000 g ww ($n = 19$), and 56 species in areas with over 1,000 g ww of algae ($n = 15$). Shannon diversity also did not differ significantly across algal weight and only varied by region ($p = 0.03$; Table 1). When analyzing a subset of the data in turtle grass with a similar coverage and canopy height, similar patterns were observed for animal abundance, with significantly higher animal abundances seen at algal biomasses over 500 g ww, compared to those when no algae were present (Figure 1B; Table 1). Diversity was not significantly different across region ($p = 0.14$) or algal weight ($p = 0.71$; Table 1) in the data subset, and the richness again remained stable across all algal weight classes (Correia, 2021).

Macroalgal biomass significantly influenced overall community structure (Figure 2A; $\text{Pseudo-F} = 3.124$; $p = 0.001$). Pairwise comparisons across the different algal weight classes indicated that small benthic communities were significantly different when algae were present. When comparing algal weight classes to one another, all areas containing algae were significantly different from areas with no algae (Supplementary Table S2). Areas containing smaller concentrations of algae (i.e., Class 1–3) were also significantly different from areas containing over 1,000 g of algae (Class 4; Supplementary Table S2). When analyzing these relationships using a subset of the data to control for seagrass cover and canopy height, macroalgal biomass still significantly influenced community structure (Figure 2B; $\text{Pseudo-F} = 2.24$; $p = 0.002$). Pairwise comparisons across algal weight class indicated that all areas containing algae were significantly different from areas with no algae (Supplementary Table S2). When comparing algal weight classes to one another, areas containing 300–500 g (Class 2) of macroalgae were significantly different from areas containing over 500 g (Classes 3 and 4). Macroalgal concentrations below 300 g showed the most variability in the nekton community and were not significantly different from the other macroalgal classes (Supplementary Table S2).
The largest sources of dissimilarity between communities across the different algal classes, as identified by SIMPER analysis, were nonpenaeid shrimp (Hippolytidae, Palaemonidae, Processidae), penaeid shrimp (Penaeidae), gobies (Gobiidae), pipefish (Syngnathidae), and pinfish (*Lagodon rhomboides*), which collectively made up over 70% of the dissimilarity. Hippolytidae (hippolytid shrimp) were the most abundant organisms collected, with over 1,000 individuals present in some samples. Because of this, Hippolytidae was analyzed separately from other nonpenaeid shrimp. All other nonpenaeid shrimp (Palaemonidae, *Palaemonetes* sp., *Periclimenes* sp., *Processa* sp., *Periclimenes americanus*, *Periclimenes longicaudatus*, *Palaemon floridanus*, *Palaemonetes pugio*, *Palaemonetes vulgaris*, *Tozeuma carolinense*, *Thor* sp., and *Thor dobki*) were grouped together. Penaeid shrimp included Penaeidae, *Farfantepeneaus* sp., *Rimapenaeus* sp., *Farfantepeneaus duroarum*, *Farfantepeneaus azteca*, and *Litopenaeus setiferus*. Gobies included Gobiidae, *Gobiosoma* sp., *Microgobius* sp., *Bathygobius* sp., *Ctenogobius* sp., *Gobionellus* sp., *Gobiosoma robustum*, *Ctenogobius boleosoma*, *Microgobius gulosus*, *Microgobius thalassinus*, *Gobiosoma bosc*, *Evothodus lyricus*, and *Bathygobius saporator*. Pipefish included *Syngnathidae*, *Syngnathus* sp., *Syngnathus floridensis*, *Syngnathus louisiana*, *Syngnathus scovelli*, and *Anarchopterus criniger*.

There was a significant interaction between region and weight class for Hippolytidae shrimp abundance at *α* = 0.1 (*p* = 0.09; Table 2). Other nonpenaeid shrimp abundances were also significantly different across region (*p* < 0.001) and algal weight class (*p* = 0.03; Table 2). The abundances of penaeid shrimp and gobies, however, only differed across region and were not related to algal biomass (Table 2). An overall positive trend in Hippolytidae shrimp was observed in Texas and Florida regions with increasing algal biomass, with a slight negative trend in the Chandeleur Islands, LA. At the highest algal biomass, a slight decline in Hippolytidae abundance was also observed in Laguna Madre, TX, Corpus Christi Bay, TX, and Charlotte Harbor, FL (Supplementary Figure S2). Other nonpenaeid shrimp followed a similar pattern, with an increase in shrimp abundance at all locations except Cedar Key, FL (Supplementary Figure S4). The degree of shrimp increase was regionally dependent (Supplementary Figure S4, S5). While organismal abundance increased, the overall length of shrimp and fish did not change with algal weight (*p* > 0.05; Supplementary Table S3, S4), indicating that the same organismal size classes were accessing structured habitats at all drift algal biomasses.

### Taxon-specific responses to macroalgae

The largest sources of dissimilarity between communities across the different algal classes, as identified by SIMPER analysis, were nonpenaeid shrimp (Hippolytidae, Palaemonidae, Processidae), penaeid shrimp (Penaeidae), gobies (Gobiidae), pipefish (Syngnathidae), and pinfish (*Lagodon rhomboides*), which collectively made up over 70% of the dissimilarity. Hippolytidae (hippolytid shrimp) were the most abundant organisms collected, with over 1,000 individuals present in some samples. Because of this, Hippolytidae was analyzed separately from other nonpenaeid shrimp. All other nonpenaeid shrimp (Palaemonidae, *Palaemonetes* sp., *Periclimenes* sp., *Processa* sp., *Periclimenes americanus*, *Periclimenes longicaudatus*, *Palaemon floridanus*, *Palaemonetes pugio*, *Palaemonetes vulgaris*, *Tozeuma carolinense*, *Thor* sp., and *Thor dobki*) were grouped together. Penaeid shrimp included Penaeidae, *Farfantepeneaus* sp., *Rimapenaeus* sp., *Farfantepeneaus duroarum*, *Farfantepeneaus azteca*, and *Litopenaeus setiferus*. Gobies included Gobiidae, *Gobiosoma* sp., *Microgobius* sp., *Bathygobius* sp., *Ctenogobius* sp., *Gobionellus* sp., *Gobiosoma robustum*, *Ctenogobius boleosoma*, *Microgobius gulosus*, *Microgobius thalassinus*, *Gobiosoma bosc*, *Evothodus lyricus*, and *Bathygobius saporator*. Pipefish included *Syngnathidae*, *Syngnathus* sp., *Syngnathus floridensis*, *Syngnathus louisiana*, *Syngnathus scovelli*, and *Anarchopterus criniger*.

There was a significant interaction between region and weight class for Hippolytidae shrimp abundance at *α* = 0.1 (*p* = 0.09; Table 2). Other nonpenaeid shrimp abundances were also significantly different across region (*p* < 0.001) and algal weight class (*p* = 0.03; Table 2). The abundances of penaeid shrimp and gobies, however, only differed across region and were not related to algal biomass (Table 2). An overall positive trend in Hippolytidae shrimp was observed in Texas and Florida regions with increasing algal biomass, with a slight negative trend in the Chandeleur Islands, LA. At the highest algal biomass, a slight decline in Hippolytidae abundance was also observed in Laguna Madre, TX, Corpus Christi Bay, TX, and Charlotte Harbor, FL (Supplementary Figure S2). Other nonpenaeid shrimp followed a similar pattern, with an increase in shrimp abundance at all locations except Cedar Key, FL (Supplementary Figure S4). The degree of shrimp increase was regionally dependent (Supplementary Figure S4, S5). While organismal abundance increased, the overall length of shrimp and fish did not change with algal weight (*p* > 0.05; Supplementary Table S3, S4), indicating that the same organismal size classes were accessing structured habitats at all drift algal biomasses.
Discussion

Across the northern Gulf of Mexico, the abundance of small epibenthic nekton were positively related to drift algal biomass, but the strength of the effect varied regionally. When the seagrass cover and canopy height were held constant, the same patterns were observed, strengthening our conclusion that changes in macroalgal biomass were the primary driver of organismal patterns. Diversity and species-specific size, however, did not change with macroalgal biomass, indicating an additive role within the seagrass landscape rather than a distinct habitat type, at least for the nekton sampled. Red and brown drift algae, which are common in the Gulf of Mexico and accounted for most of the drift algae in this study, are known to increase faunal abundances (Virmstein and Carbonara, 1985; Bell and Hall, 1997; Holmquist, 1997; Correia, 2021), and thus, our results are consistent with previous findings. In some instances, however, drift algae can smother seagrass beds, cause hypoxia, and ultimately reduce faunal abundance and diversity (Hull, 1987; Isaksson and Pihl, 1992; Norkko and Bonsdorff, 1996a; Norkko and Bonsdorff, 1996b; Raffaelli, 2000). This is commonly seen when nutrient enrichment leads to drastic increases in drift macroalgal biomass, reducing local dissolved oxygen and light concentrations. This effect appears to be dependent on algal biomass and may be species-specific (Hull, 1987; Raffaelli, 2000; Young, 2009). A slight decline in nonpenaeid shrimp was observed at the highest algal biomasses (exceeding 2,000 g ww) in Corpus Christi Bay, TX, Laguna Madre, TX, and Charlotte Harbor, FL, which could be an indicator of algal-mediated habitat degradation (Supplementary Figure S2). Our data are limited at the higher end of algal biomass, although making it difficult to identify a threshold at which algae might begin to have negative effects. Future studies should quantify abundance changes across a larger range of algal biomass to pinpoint such thresholds. With few exceptions, in this study, drift algae were associated with higher animal abundance, driven largely by shrimp species. We believe that this represents an effect of added three-dimensional structure within the seagrass-macroalgal mosaic, allowing more individuals to occupy a given area of seagrass.

Shallow vegetated habitats are commonly associated with increased abundance and diversity of organisms compared to adjacent bare substrates, leading to inferences that structure, regardless of type, is important when determining species occupancy per given area (Heck et al., 2003; Minello et al., 2003; Humphries et al., 2011). Previously, a positive relationship between increased turtle grass percent cover and drift macroalgae percent cover was found (Correia, 2021; Correia et al., in press), which could be influencing the results of this study, due to the overall increase in habitat complexity. However, by analyzing a subset of the data over a narrow range of turtle grass percent cover and canopy heights and coming to similar conclusions, it seems unlikely that seagrass percent cover alone explains the patterns noted between algal biomass and nekton abundance. The added complexity provided by drift macroalgae likely leads to positive changes in nekton abundance by the same mechanism. However, quantification of algal influences on flow, temperature, dissolved oxygen, and recruitment of small nekton organisms would provide additional information regarding the nature of the habitat provided by drift algae relative to seagrass alone.
Macroalgal blooms are more variable than other complex habitats found along the coast (e.g., seagrass meadow, coral reef, and mangrove forest) and are largely dependent on local flow, season, and water quality. Generally, red and brown macroalgae in the Gulf of Mexico are found at peak abundance during the summer (Pihl et al., 1996). Although algae can grow rapidly, storms and currents can displace them quickly (Pihl et al., 1999). Not surprisingly, the ephemeral nature of macroalgal communities makes this a good habitat for smaller, motile, and more opportunistic organisms that can successfully find and use the habitat type when available (Norkko et al., 2000; Camp et al., 2014).

Variation in the positive association between algal biomass and nekton abundance could be related to differences in algal species composition across each region or differences in life history characteristics of both penaeid and nonpenaeid shrimp found in these areas. Changes in macroalgae species composition significantly influenced local animal abundances, with some algal species containing higher abundances than others (Correia, 2021). Spyridia, for example, contained approximately 757 ± 335 individuals when listed as the primary algal taxon in Charlotte Harbor, FL, with 23 unique species identified. Conversely, locations primarily containing Hypnea had 57 ± 39.5 individuals and nine unique species present (Correia, 2021).

However, regardless of region and macroalgal composition, which likely contributed to the variation in our study, higher algal abundances were associated with increased nekton abundances.

Across the northern Gulf of Mexico, the presence of drift macroalgae may have a large, positive effect on smaller nekton organisms, such as shrimp and gobies, with the timing of peak algal abundance often coinciding with the peak in the recruitment of juvenile nekton (Turner and Brody, 1983; Rogers et al., 1993). This increase in recruitment can be beneficial to local fisheries by providing additional food resources, increasing the survival, growth rates, and development of important prey and forage species. It is important, however, to continue to monitor changes in drift macroalgae biomass since they often indicate eutrophication and can quickly transition to nuisance species with well-documented negative effects on the seagrass ecosystems in which they are found.

**Data availability statement**

The data sets presented in this study can be found in online repositories. The names of the repository/repositories and accession number(s) can be found below: http://www.darnellseagrassecologylab.com/turtlegrass.

**Author contributions**

KD and MD conceived and proposed the project, and all authors assisted in planning, coordination, and execution of the project. KC, BB, and DS took samples in the Texas region. KD, MD, and CH collected samples in the Louisiana region, and SA, BF, MH, CM, and AM collected samples in the Florida regions. Data were QA/QGed by CH and KC and analyzed by KC.
coordinated the first draft with writing input by DS. All co-authors contributed to the editing of the subsequent drafts of the manuscript.

Funding

This paper is a result of research funded by the National Oceanic and Atmospheric Administration’s RESTORE Science Program award # NA17NOS4510093 to the University of Southern Mississippi, Dauphin Island Sea Lab, the University of Florida, and Florida Fish and Wildlife Conservation Commission.

Acknowledgments

The authors would like to thank Samantha Smith, Michael Wheeler, and Donna O’Dell for assistance in the field and laboratory, Manuel Merello for identifying macroalgal samples, and the reviewers who provided helpful edits to the manuscript prior to publication.

References


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.

Publisher’s note

All claims expressed in this article are solely those of the authors and do not necessarily represent those of their affiliated organizations or those of the publisher, the editors, and the reviewers. Any product that may be evaluated in this article or claim that may be made by its manufacturer is not guaranteed or endorsed by the publisher.

Supplementary material

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fenvs.2022.939296/full#supplementary-material


Minello, T. J. (1999). "Nekton densities in shallow estuarine habitats of Texas and Louisiana and Identification of essential fish habitat (EFH)." Fish habitat: Essential fish habitat and rehabilitation. Editor L. Benaka (Bethesda, Maryland: Am. Fish. Soc. Symp.), 22, 43–75.


Frontiers in Environmental Science frontiersin.org