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Widespread seagrass die-off has no legacy effect on basal resource use of seagrass food webs in Florida Bay, USA

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Macrophyte foundation species provide both habitat structure and primary production, and loss of these habitats can alter species interactions and lead to changes in energy flow in food webs. Extensive seagrass meadows in Florida Bay have recently experienced a widespread loss of seagrass habitat due to a *Thalassia testudinum* mass mortality event in 2015 associated with prolonged hypersalinity and bottom-water anoxia. Using stable isotope analysis paired with Bayesian mixing models, we investigated the basal resource use of seven species of seagrass-associated consumers across Florida Bay in areas affected by the 2015 seagrass die-off. Three years after the die-off, basal resource use did not differ for species collected inside and outside the die-off affected areas. Instead, consumers showed seasonal patterns in basal resource use with seagrass the most important in the wet season (58%), while epiphytes were the most important in the dry season (44%). Additionally, intraspecific spatial variability in resource use was lower in the wet season compared to the dry season. We were unable to detect a legacy effect of a major disturbance on the basal resource use of the most common seagrass-associated consumers in Florida Bay.

Keywords: epiphytes, foundation species, habitat loss, mixing models, stable isotopes.

Introduction

Disturbance events can drastically alter habitat composition (Carlson *et al.*, 2010). Both press (e.g. sea-level rise) and pulse (e.g. drought) disturbances from both natural and anthropogenic sources are becoming more common, especially in coastal ecosystems, leading to drastic alterations in coastal seascapes (Carlson *et al.*, 2010; Santos *et al.*, 2011). For example, the combined effects of long-term stressors such as sea-level rise and decreased sediment supply via river flow modification, as well as pulsed disturbances such as hurricanes and tropical storms, have led to widespread loss of coastal habitats in Louisiana (Couvillion *et al.*, 2016). This is true in other coastal ecosystems as well, such as seagrass beds, which have seen habitat modification through altered light and salinity regimes, as well as by eutrophication from coastal development, human population growth, and water management practices (Waycott *et al.*, 2009; Santos *et al.*, 2011; Hall *et al.*, 2016). Importantly, coastal habitats support many different species, and habitat loss from disturbance events has led to shifts and losses in consumer biomass (Boström *et al.*, 2011; Yeager *et al.*, 2016; Santos *et al.*, 2018).

Macrophyte foundation species for many coastal habitats, serving not only as structural habitat, but also contributing directly or indirectly as primary production sources to the food web (Jones *et al.*, 1994; Boström *et al.*, 2011; James *et al.*, 2019). Any loss in production of foundation species (e.g. seagrass) leads to a loss in secondary production unless consumers compensate by altering basal resource use (Deegan and Garritt, 1997; Smith *et al.*, 2008; Lesser *et al.*, 2020). For example, seagrass omnivores increase variation in basal resource use to compensate for lower production (Lesser *et al.*, 2020; Santos *et al.*, 2022). Habitat loss can also alter species interactions by increasing competition for space and resources and changing prey capture efficiency (Hovel and Lipcius, 2001; Fahrig, 2003; Canion and Heck, 2009). Changes in species interactions can alter energy flow and lead to changes in trophic structure in the food web (Hovel and Lipcius, 2001; Robinson *et al.*, 2015). For example, the loss of seagrass habitat through the invasion of macroalgae leads to increased competition due to altered basal resources compared to food webs in continuous seagrass meadows (Deudero *et al.*, 2014). Therefore, disturbance events that result in losses of foundation species have the potential to significantly alter coastal food webs, and there is a critical need to document and understand the connection between disturbance of macrophyte foundation species and changes to the food webs they support.

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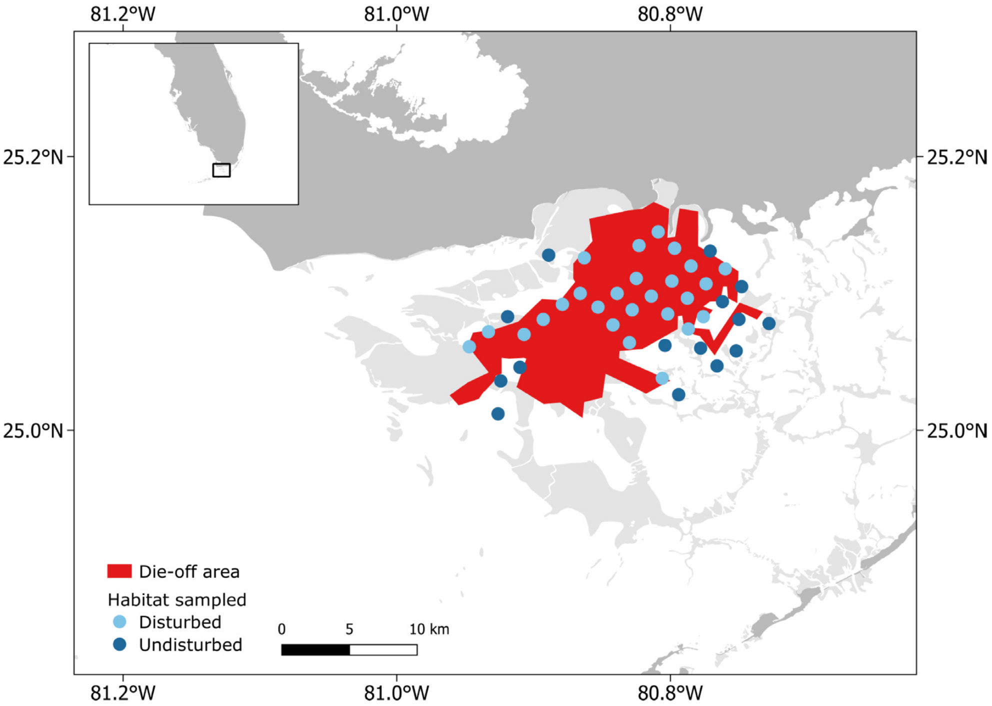

Figure 1. Seagrass die-off area (red) and the trawl sampling locations (blue) in Florida Bay. Die-off footprint is based on initial observations from the beginning of the die-off (Hall *et al.*, 2016). There were 26 sites within the die-off boundary (Disturbed = light blue) and 15 sites outside of the die-off boundary (Undisturbed = dark blue).

Florida Bay is a shallow estuary, located between the Florida Keys and the Everglades, and is home to vast seagrass beds comprised mainly of *Thalassia testudinum* (Fourqurean and Robblee, 1999). These meadows are vital habitat for many ecologically and economically important species and support a lucrative recreational fishery (Kelble *et al.*, 2021; Brown *et al.*, 2018; Stainback *et al.*, 2019). In the Everglades watershed, hydrology and water management have been engineered to allow for urban development, to control flooding, and to support agriculture, resulting in reduced freshwater flow and seasonal hypersalinity (due to seasonality of freshwater flows) in portions of Florida Bay (Marshall *et al.*, 2020). When combined with increasing temperatures, prolonged hypersalinity can lead to hypoxic stress, sulphide intrusion, and mortality of seagrasses (Kelble *et al.*, 2007; Koch *et al.*, 2007). The first well-documented example of widespread seagrass die-off in Florida Bay began in 1987 and continued for ~4 years (Robblee *et al.*, 1991; Fourqurean and Robblee, 1999). Seagrasses had recovered by 2010 (Hall *et al.*, 2021), but in 2015, a second mass mortality event, caused by the same set of stressors, occurred in the same location, resulting in comparable losses of *T. testudinum* (Hall *et al.*, 2016).

Although benthic macrophyte communities in Florida Bay have high ecological and economic importance and have received considerable attention (Zieman *et al.*, 1989; Fourqurean *et al.*, 2001), not much is known about the food webs they support (Chasar *et al.*, 2005; Rezek *et al.*, 2020). The two goals of this study were to (1) characterize the energy flow of seagrass consumers in Florida Bay and (2) determine if energy flow differed in areas that were and were not affected by the 2015 seagrass die-off. Seagrass production is seasonal within Florida Bay (Fourqurean *et al.*, 2001), but we hypothesized that seagrass food webs would be supported mainly from epiphyte production regardless of season (Kitting *et al.*, 1984; Moncreiff and Sullivan, 2001). Additionally, we hypothesized that consumers collected in areas affected by the 2015 seagrass die-off would have shifted resource use away from seagrass-associated basal resources because of spatial differences in resource availability (Deegan and Garritt, 1997; Olin *et al.*, 2012), based on the spatial clustering of the die-off impacts and the degree of recovery thereafter. Seven consumer species were collected from stations inside and outside the die-off boundary throughout Florida Bay, and stable isotope analysis paired with Bayesian mixing models were run to determine resource use of dominant consumer species across sites (Stock *et al.*, 2018).

Methods

Consumer species were collected for stable isotope analysis from 26 sites within the seagrass die-off boundary and 15 sites located in unaffected areas at National Oceanic and Atmospheric Administration (NOAA) long-term Juvenile Sportfish monitoring sites (Figure 1; Kelble *et al.*, 2021; Kearney *et al.*, 2015). The die-off boundary was based on *in-situ* observations described in Hall *et al.* (2016). Areas within the seagrass die-off boundary experienced heavy loss of *T. testudinum* resulting in low seagrass cover compared to areas outside of the boundary (Furman *et al.*, 2021). To represent consumers species abundant in seagrass habitats, bay anchovy (*Anchoa mitchilli*), Silver Jenny mojarra (*Eucinostomus gula*), pigfish (*Orthopristis chrysoptera*), pinfish (*Lagodon rhomboides*), pink shrimp (*Farfantepenaeus duorarum*), rainwater killifish (*Lucania parva*), and silver perch (*Bairdiella chrysoura*) were collected via otter trawl as described in Kelble *et al.* (2021) during the wet (September 2018) and dry seasons (May 2019) both inside and outside the seagrass die-off boundary. Based on salinity trends, the central portion of

Table 1. Isotope values (mean ± *SD*) for each species and season collected inside (disturbed) and outside (undisturbed) the seagrass die-off area in Florida Bay.

Species	Season	Habitat	δ^{13}C	δ^{15}N	δ^{34}S	# of sites
Bay anchovy	Wet	Disturbed	−15.4 ± 0.5	7.9 ± 0.5	6.1 ± 1.7	12
	Wet	Undisturbed	−14.8 ± 0.5	8.2 ± 0.4	5.8 ± 0.8	6
	Dry	Disturbed	−14.9 ± 2.2	6.6 ± 1.9	7.9 ± 0.8	3
Mojarra	Wet	Disturbed	−12.9 ± 0.7	7.1 ± 0.8	1.8 ± 1.4	12
	Wet	Undisturbed	−11.6 ± 1.6	7.1 ± 1.1	1.8 ± 1.0	10
	Dry	Disturbed	−13.7 ± 0.8	7.2 ± 0.6	7.3 ± 2.7	14
	Dry	Undisturbed	−12.4 ± 0.8	7.4 ± 0.1	5.6 ± 3.3	2
Pigfish	Wet	Disturbed	−13.5 ± 1.0	7.5 ± 1.1	2.1 ± 1.0	4
	Wet	Undisturbed	−13.2	6.4	2.4	1
	Dry	Disturbed	−14.3 ± 0.5	7.4 ± 0.3	6.8 ± 1.5	5
	Dry	Undisturbed	−15.4 ± 0.4	8.3 ± 1.2	6.8 ± 1.5	2
Pinfish	Wet	Disturbed	−13.3 ± 1.3	6.8 ± 0.8	4.9 ± 1.7	10
	Wet	Undisturbed	−12.5 ± 1.2	6.4 ± 0.6	4.7 ± 1.3	8
	Dry	Disturbed	−14.2 ± 1.6	7.4 ± 0.6	7.6 ± 2.8	6
	Dry	Undisturbed	−15.8 ± 2.3	7.1 ± 1.0	8.0 ± 2.5	4
Pink shrimp	Wet	Disturbed	−12.2 ± 0.8	5.2 ± 1.3	3.4 ± 1.5	5
	Dry	Disturbed	−14.2 ± 0.9	6.1 ± 0.7	8.2 ± 2.1	7
	Dry	Undisturbed	−15	6.5	5.1	1
Rainwater killifish	Wet	Disturbed	−12.8 ± 0.5	7.4 ± 0.4	7.2 ± 1.8	7
	Wet	Undisturbed	−13.1 ± 0.7	7.0 ± 0.9	7.7 ± 2.3	3
	Dry	Disturbed	−14.2 ± 1.0	6.7 ± 0.9	8.7 ± 1.8	14
	Dry	Undisturbed	−13.1 ± 0.6	7.0 ± 0.2	10.5 ± 1.1	5
Silver perch	Wet	Disturbed	−12.9 ± 0.6	7.5 ± 0.3	7.7 ± 0.6	3
	Wet	Undisturbed	−13.5 ± 0.9	8.1 ± 0.7	10.1 ± 2.7	2
	Dry	Disturbed	−14.3 ± 1.3	7.1 ± 1.4	8.0 ± 2.1	8
	Dry	Undisturbed	−14.9	7.5	5.8	1

Florida Bay likely received more freshwater inflow during the wet season of 2018 than average, while dry season 2019 was similar to historic trends (Supplementary Figure S1). Species collected represent various feeding guilds (e.g. benthic omnivore, pelagic omnivore) and make up the majority of the biomass of lower trophic level consumers in Florida Bay (Sogard *et al.*, 1989; Chasar *et al.*, 2005; Flaherty *et al.*, 2013). Five individuals were pooled for each species collected in a trawl at each sampling location to generate one composite sample for stable isotope analysis (e.g. $n = 1$ pooled sample/species/site; Table 1, Supplementary Figures S1 and S2). Pooling samples is common for isotope samples to control for between-individual variation, as well as ensure that enough tissue is collected for analysis (Phillips *et al.*, 2014; Nelson *et al.*, 2019). Pooling individuals allowed for a better representation of isotope values of species at a given site to compare spatial trends in resource use. Whole individuals were dried at 50°C for 48 h and ground together to make a composite sample that was sent for stable isotope analysis. Grinding whole animals is a common way to process individuals for stable isotope analysis, especially when organisms are smaller (Fry, 2006; Post *et al.*, 2007). Our processing method did not remove the digestive system of the individuals before processing, which could have led to some dietary items being included in the ground sample. However, the amount of potential dietary items being included in the sample is minimal compared to the mass of the whole animal.

Basal resources (i.e. primary producers) were collected at each of the trawl sampling locations in both the wet and dry seasons by hand, with the addition of mangrove leaves collected by hand at mangrove islands throughout the sampling area. Seagrass (*Halodule wrightii* and *T. testudinum*) were rinsed with deionized (DI) water and scraped with the back of a scalpel to remove sediment and epiphytes. Seagrass leaves were then acid washed with 10% HCl and rinsed with DI water, before being dried 50°C for 48 h and ground to be sent for stable isotope analysis. Mangrove leaves (*Rhizophora mangle*) were rinsed with DI water, dried 50°C for 48 h, ground, and sent for stable isotope analysis. Macroalgal thalli (e.g. *Halimeda* spp., *Caulerpa* spp., *Penicillus* spp., and *Batophora oerstedi*) were acid washed with 10% HCl, and rinsed with DI water before being dried 50°C for 48 h, ground, and sent for stable isotope analysis. Each macroalgal species was sent for isotope analysis separately. Particulate organic matter (POM) was not collected in this study and not included as a potential basal resource. However, POM stable isotope values from other studies collected in Florida Bay overlap with those of the macroalgae collected for carbon, nitrogen, and sulphur, and therefore, not isotopically distinguishable from the macroalgal sources collected in this study (Figure 2; Chasar *et al.*, 2005; Eggenberger *et al.*, 2019). Gastropod grazers that specialize in epiphyte consumption (*Turbo castanea*) were collected by hand at the same time as the other primary producers (Frankovich and Zieman, 2005). Grazers were removed from their shells, rinsed with DI water, and dried at 50°C for 48 h before being ground. Each species of primary producer collected at a given site was pooled, so that there was one replicate per site. Each potential basal resource was collected from a minimum of seven sampling locations. All samples were shipped to the Washington State University Stable Isotope Core Facility for analysis of C, N, and S stable isotopes.

Bayesian mixing models were run in R version 4.0.5 (R Core Team, 2021) using the package MixSIAR (v3.1.10, Stock *et al.*, 2018) to determine the relative basal resource contributions to each consumer species. Models were run for each

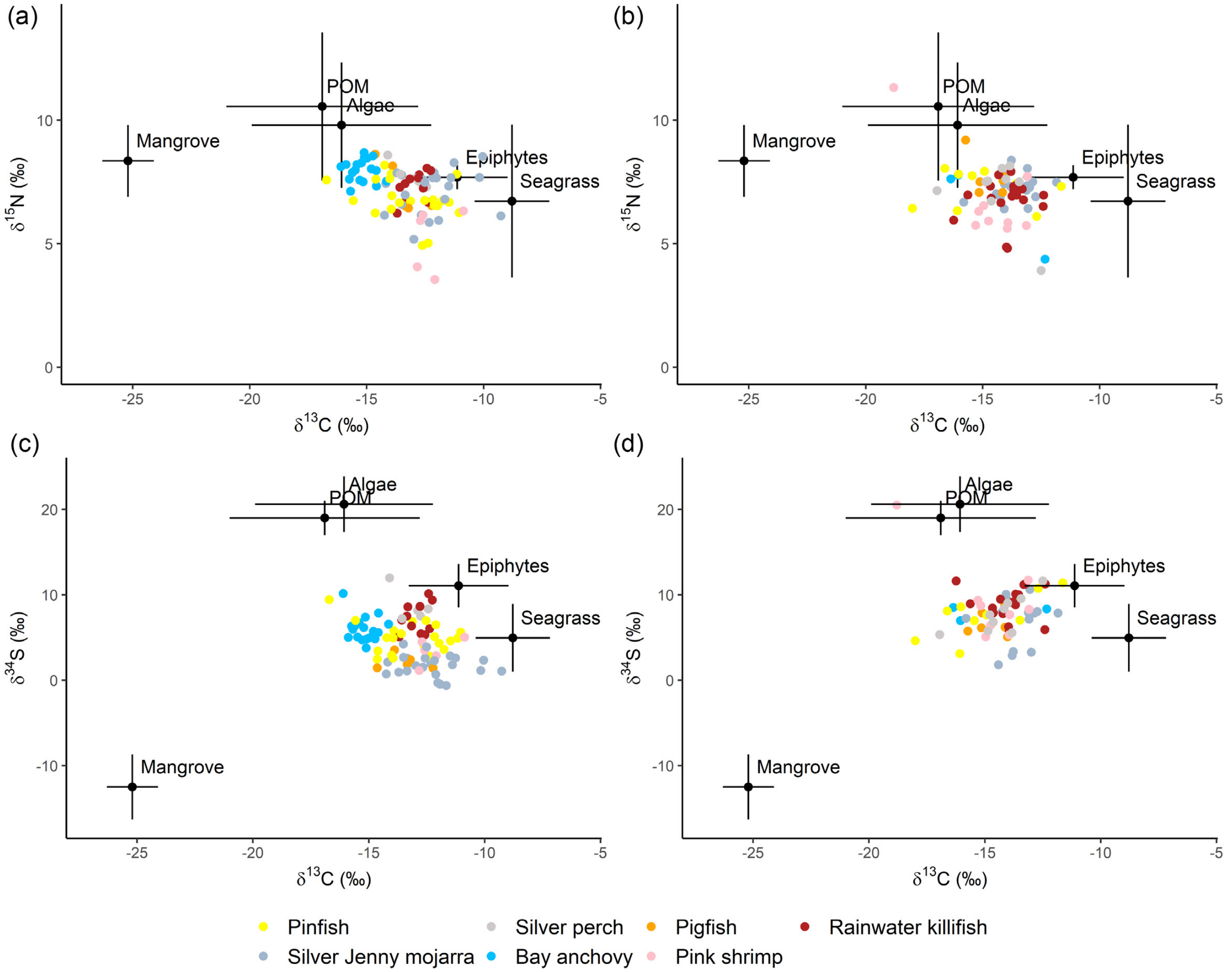

Figure 2. Stable isotope biplots for carbon and nitrogen in the (a) wet and (b) dry season and carbon and sulphur in the (c) wet and (d) dry season collected in Florida Bay. Overlaid source values represent the trophic enrichment corrected mean ± *SD* used in the Bayesian mixing models. POM source values were based on Chasar et al. (2005) and Eggenberger et al. (2019) but were not included as a potential source in the mixing models since they were indistinguishable from macroalgae.

season with consumer species as a fixed factor and sampling location as a random factor nested within species. Macroalgae species could not be distinguished isotopically from one another, and thus, were combined for statistical analyses (hereafter, referred to as algae). Grazers were used as proxies for epiphyte stable isotopes values by trophically-correcting isotope values one trophic level (Frankovich and Zieman, 2005). Using trophically-corrected primary consumers that specialize on a specific primary producer is a common way to obtain stable isotope values of that primary producer, especially when the primary producer is difficult to collect enough organic material for stable isotope analysis (Fry, 2006; Layman *et al.*, 2012; Phillips *et al.*, 2014). Basal resources were averaged across space and season to serve as the source values for consumers in the mixing models. Basal resources were averaged across time and space because, due to tissue turnover times, consumers would likely be assimilating basal resources that from across the year (not just the seasonal time point when sampled), and by averaging our two time points, we would best represent the potential source isotope values. Corrections were made for the elemental concentration in each source to account for differences between sources, and multiplicative error (residual error × process error) was used (Stock and Semmens, 2016). The trophic enrichment for each element was C = 2.5 ± 0.3 (mean ± *SD*), N = 7.25 ± 1, and S = 1 ± 0.2. We chose these values because this enrichment enclosed the consumer isotope values within the mixing polygon and was ecologically relevant to the consumers studied (Figure 2; Phillips *et al.*, 2014; Nelson *et al.*, 2015, 2019). Each model was run with a Markov chain Monte Carlo algorithm that consisted of three chains, chain length of 1000000, burn-in of 500000, and thinning interval of 500 to ensure model convergence.

Results

The four basal resource groups were isotopically distinct (Figure 2). Seagrass stable isotope values had a mean δ^{13}C = −11.1 ± 1.7 (mean ± *SD*), δ^{15}N = −0.3 ± 3.1, and δ^{34}S = 4.1 ± 4.2. Algae had a mean δ^{13}C = −16.2 ± 3.4, δ^{15}N = 1.7 ± 3.0, and δ^{34}S = 19.2 ± 3.0. Epiphytes had carbon and sulphur isotope values that were between the seagrass and algal species, δ^{13}C = −13.1 ± 2.4 and δ^{34}S = 10.3 ± 2.4, and the mean δ^{15}N = 0.5 ± 0.5. Mangrove stable isotope

Table 2. Mixing model results of source contribution (mean ± *SD*) for each species and season collected inside (disturbed) and outside (undisturbed) the seagrass die-off area.

Species	Season	Habitat	Algae	Epiphytes	Seagrass	Mangrove	# of sites
Bay anchovy	Wet	Disturbed	0.02 ± 0.01	0.30 ± 0.01	0.35 ± 0.01	0.33 ± 0.01	12
	Wet	Undisturbed	0.02 ± 0.01	0.30 ± 0.01	0.35 ± 0.01	0.33 ± 0.01	6
	Dry	Disturbed	0.05 ± 0.01	0.33 ± 0.07	0.36 ± 0.12	0.27 ± 0.08	3
Mojarra	Wet	Disturbed	0.01 ± 0.01	0.04 ± 0.01	0.76 ± 0.01	0.19 ± 0.01	12
	Wet	Undisturbed	0.01 ± 0.01	0.04 ± 0.01	0.76 ± 0.01	0.19 ± 0.01	10
	Dry	Disturbed	0.01 ± 0.01	0.58 ± 0.09	0.23 ± 0.07	0.18 ± 0.05	14
	Dry	Undisturbed	0.01 ± 0.01	0.59 ± 0.07	0.22 ± 0.01	0.17 ± 0.07	2
Pigfish	Wet	Disturbed	0.01 ± 0.01	0.08 ± 0.01	0.66 ± 0.01	0.25 ± 0.01	4
	Wet	Undisturbed	0.01	0.08	0.66	0.25	1
	Dry	Disturbed	0.03 ± 0.01	0.53 ± 0.05	0.21 ± 0.02	0.24 ± 0.04	5
	Dry	Undisturbed	0.02 ± 0.01	0.52 ± 0.07	0.22 ± 0.03	0.24 ± 0.04	2
Pinfish	Wet	Disturbed	0.03 ± 0.01	0.10 ± 0.01	0.66 ± 0.01	0.21 ± 0.01	10
	Wet	Undisturbed	0.03 ± 0.01	0.10 ± 0.01	0.66 ± 0.01	0.21 ± 0.01	8
	Dry	Disturbed	0.02 ± 0.01	0.60 ± 0.11	0.14 ± 0.07	0.23 ± 0.05	6
	Dry	Undisturbed	0.02 ± 0.01	0.55 ± 0.10	0.11 ± 0.01	0.32 ± 0.09	4
Pink shrimp	Wet	Disturbed	0.01 ± 0.01	0.05 ± 0.01	0.80 ± 0.01	0.15 ± 0.01	5
	Dry	Disturbed	0.11 ± 0.02	0.13 ± 0.03	0.54 ± 0.06	0.23 ± 0.05	7
	Dry	Undisturbed	0.09	0.12	0.51	0.28	1
Rainwater killifish	Wet	Disturbed	0.02 ± 0.01	0.33 ± 0.01	0.46 ± 0.01	0.19 ± 0.01	7
	Wet	Undisturbed	0.02 ± 0.01	0.33 ± 0.01	0.46 ± 0.01	0.19 ± 0.01	3
	Dry	Disturbed	0.07 ± 0.02	0.38 ± 0.08	0.36 ± 0.08	0.20 ± 0.04	14
	Dry	Undisturbed	0.08 ± 0.01	0.43 ± 0.01	0.34 ± 0.01	0.16 ± 0.02	5
Silver perch	Wet	Disturbed	0.02 ± 0.01	0.54 ± 0.01	0.26 ± 0.01	0.18 ± 0.01	3
	Wet	Undisturbed	0.02 ± 0.01	0.54 ± 0.01	0.26 ± 0.01	0.18 ± 0.01	2
	Dry	Disturbed	0.04 ± 0.01	0.40 ± 0.10	0.34 ± 0.11	0.23 ± 0.06	8
	Dry	Undisturbed	0.04	0.46	0.26	0.24	1

values were the most negative for carbon and sulphur of all basal resources, $\delta^{13}\text{C} = -27.7 \pm 1.1$ and $\delta^{34}\text{S} = -13.5 \pm 3.8$, and the mean $\delta^{15}\text{N} = 1.1 \pm 1.5$ (Supplementary Table S2, Figure 2). Mean consumer isotope values varied between −15.2 (bay anchovy) and −12.2 (pink shrimp) for δ^{13}C (Table 1, Figure 2). Pink shrimp had the lowest δ^{15}N values, while bay anchovy collected in the wet season had the highest δ^{15}N values. For δ^{34}S, consumer species generally had lower values in the wet season, except silver perch which had the highest δ^{34}S values in the wet season (Table 1, Figure 2).

We did not find any differences in resource use between consumers collected inside and outside the die-off area (Table 2, Figure 3). In the wet season, mean basal resource use showed low spatial variability across the bay, with all sites relying mainly on seagrass and low intraspecies spatial variation in basal resource use (Table 2, Supplementary Figure S1, Figure 4). In the dry season, there was more variation in both the mean and intraspecies resource use as compared to the wet season (Table 2, Supplementary Figure S1, Figure 4).

Across all consumer species, seagrass was the most used resource in the wet season, but this switched in the dry season, with epiphytes becoming the most used resource (Table 3). Mean resource use of seagrass was 58% in the wet season and 30% in the dry season, while epiphyte use was 17% in the wet season compared 44% in the dry season. Resource use was similar for mangrove in both seasons (wet = 21%, dry = 23%). Algae use was low in both seasons (wet = 2%, dry = 5%; Table 2).

Each species displayed differential basal resource use in the amount of each resource, but there were trends in seasonal variation of resource use (Table 3). Mojarra, pigfish, pinfish, and rainwater killifish displayed similar seasonal patterns with seagrass being the most used resource in the wet season, while epiphytes were the most used resource in the dry season (Table 3). Bay anchovy displayed low seasonal variation and more equally distributed across epiphytes, seagrass, and mangroves in both seasons (Table 3). Pink shrimp used seagrass most in both seasons but was the only species to use >10% algae in any season (15% in dry season). The most used resource for silver perch was epiphytes in both seasons, but unlike any other species, epiphyte use was higher in the wet season than the dry season (Table 3).

Discussion

The 2015 seagrass die-off in Florida Bay led to the loss of key structural habitat for many consumer species (Hall *et al.*, 2016). The seagrass loss in Florida Bay not only reduced critical habitat for consumer species but also the main energy source, either directly or indirectly (i.e. epiphyte pathway) for seagrass-associated consumers. Contrary to our hypothesis, we were unable to detect a significant, sustained shift in basal resource use between sampling locations that were affected and unaffected by the seagrass die-off 3 years post-disturbance (Table 2, Figure 3). Chasar *et al.* (2005) also found no shift in stable isotope values for consumers before and after the 1987–1991 seagrass die-off in Florida Bay. Therefore, there may not be lasting or legacy effects of seagrass die-off on the basal resource use of mesotrophic seagrass consumers in Florida Bay. Our results confirm that the food web in Florida Bay is driven by benthic production, as has been shown for seagrass food webs generally (Kitting *et al.*, 1984; Moncreiff and Sullivan, 2001; Chasar *et al.*, 2005). We found a consistent pattern of seasonal variation in basal resource use, with seagrass being the most important resource in the wet season and epiphytes being the most important resource in the dry season. Mangroves were a consistent secondary source with similar use in both seasons (~20%), but algal resource use, whether benthic

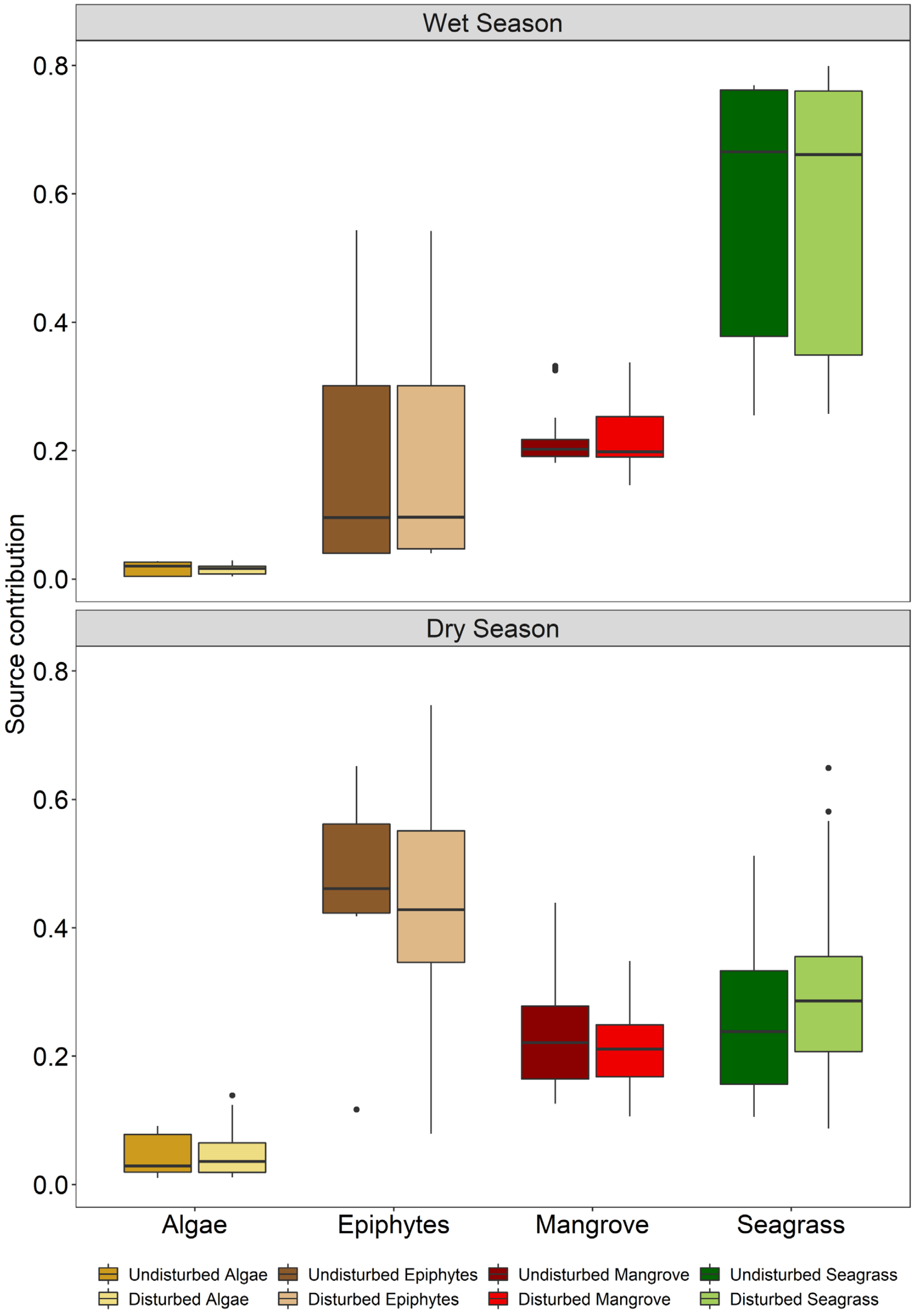

Figure 3. Source contribution across all seven consumer species each season inside (disturbed) and outside (undisturbed) the seagrass die-off area.

or pelagic, was low for all consumer species in both seasons. Overall, there was a lack of spatial structuring and minimal spatial variation in basal resource use across the bay, especially in the wet season.

Many estuarine consumers are opportunistic feeders shifting resource use based on availability (Deegan and Garritt, 1997; Moncreiff and Sullivan, 2001; Olin *et al.*, 2012). Both widespread seagrass die-offs in Florida Bay have likely led to a decline in epiphyte and seagrass production, but consumers do not appear to shift resource use away from these basal resources (Figure 3). One interpretation of this would be that disturbance does not affect the basal resource use of seagrass food webs in Florida Bay. Instead, consumers might concentrate foraging effort into the remnant patches of seagrass, thus increasing competition, with possible negative effects on secondary production (Macreadie *et al.*, 2010). Consumers might also increase movement and home range size or increase variation in resource use in response to lower amounts of basal resources following the die-off in order to meet energetic demands (Schradin *et al.*, 2010; Lesser *et al.*, 2020; Santos *et al.*, 2022). Alternatively, consumers might display shifts in basal resource use immediately following disturbance but display rapid recovery in the timeframe before sampling occurred. Further investigation into these potential hypotheses will provide vital information into the mechanisms leading to a lack in shift of basal resource use following the seagrass die-off found in this study.

Our results reveal that there is a strong seasonal variation in energy flow in the seagrass ecosystems of Florida Bay. Seagrass and mangrove production typically enters the food web

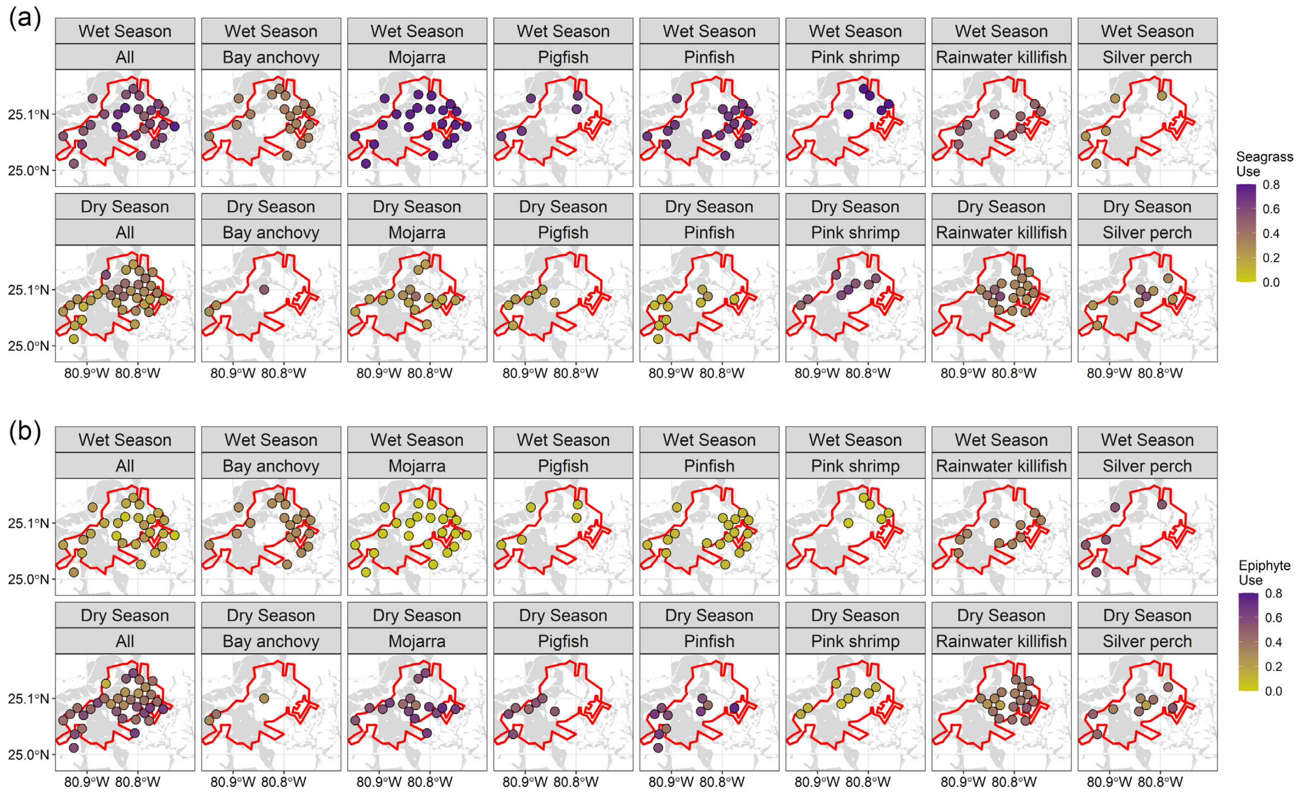

Figure 4. Spatial distribution of (a) seagrass and (b) epiphyte resource use in the wet (top row) and dry (bottom row) seasons. Each dot represents the resource use for seagrass or epiphytes as estimated from the Bayesian mixing models for that species (or if all the average of all species collected at that site) in a given season at that sampling location. The red outline represents the seagrass die-off footprint. All = the average of all species collected at a given sampling location. Mojarra = Silver Jenny mojarra

Table 3. Mixing model results of source contribution (mean ± *SD*) for all species collected in the wet and dry season in Florida Bay.

Species	Season	Algae	Epiphytes	Seagrass	Mangrove	# of sites
Bay anchovy	Wet	0.02 ± 0.01	0.30 ± 0.01	0.35 ± 0.01	0.33 ± 0.01	18
	Dry	0.05 ± 0.01	0.33 ± 0.07	0.36 ± 0.12	0.27 ± 0.08	3
Mojarra	Wet	0.01 ± 0.01	0.04 ± 0.01	0.76 ± 0.01	0.19 ± 0.01	22
	Dry	0.01 ± 0.01	0.58 ± 0.08	0.23 ± 0.06	0.18 ± 0.05	16
Pigfish	Wet	0.01 ± 0.01	0.08 ± 0.01	0.66 ± 0.01	0.25 ± 0.01	5
	Dry	0.02 ± 0.01	0.52 ± 0.05	0.21 ± 0.02	0.24 ± 0.04	7
Pinfish	Wet	0.03 ± 0.01	0.10 ± 0.01	0.66 ± 0.01	0.21 ± 0.01	18
	Dry	0.02 ± 0.01	0.58 ± 0.10	0.13 ± 0.06	0.26 ± 0.08	10
Pink shrimp	Wet	0.01 ± 0.01	0.05 ± 0.01	0.80 ± 0.01	0.15 ± 0.01	5
	Dry	0.11 ± 0.02	0.12 ± 0.03	0.54 ± 0.06	0.23 ± 0.05	8
Rainwater killifish	Wet	0.02 ± 0.01	0.33 ± 0.01	0.46 ± 0.01	0.19 ± 0.01	10
	Dry	0.07 ± 0.01	0.39 ± 0.07	0.35 ± 0.07	0.19 ± 0.04	19
Silver perch	Wet	0.02 ± 0.01	0.54 ± 0.01	0.26 ± 0.01	0.18 ± 0.01	5
	Dry	0.04 ± 0.01	0.40 ± 0.10	0.33 ± 0.11	0.23 ± 0.05	9

through the detrital pool (Cebrian, 1999), and our results reveal that there are seasonal differences in the reliance on brown vs. green energy pathways. Basal resources that enter the food web through the green pathway, in our case epiphyte and algal sources, are generally higher quality with lower C:N and C:P ratios and more readily enter the food web compared to sources that enter the food web through the detrital pool (Cebrian, 1999; Evans-White and Halvorson, 2017). However, in Florida Bay, sources that make up the majority of the detrital pool (seagrass and mangrove) have higher production than basal resources that contribute to the green pathway, with seagrass the highest production of the basal resources (Smith *et al.*, 2020). Seagrass productivity is seasonal, peaking during summer months (Fourqurean *et al.*, 2001), with a lag before it enters the detrital pool and becomes available to consumers (Cebrian, 1999). Although not always equivalent to production, standing stock biomass of epiphytes is highest during the dry season (Frankovich and Zieman, 2005). It is likely that resource use in Florida Bay follows trends in basal resource production availability regardless of the type of pathway, leading to the seasonal patterns observed in this study. Other coastal systems have displayed seasonal shifts in resource use that are likely related to changes in productivity (Olin *et al.*, 2012; Rezek *et al.*, 2017; Jankowska *et al.*, 2019).

In the wet season, there was little spatial variation in intraspecific resource use across the bay, despite variability in both the amount and configuration of seagrass habitat as well as several other environmental variables (Fourqurean *et al.*, 1992; Boyer *et al.*, 1997; Kelble *et al.*, 2007; Herbert *et al.*, 2011). Spatial variation in production, habitat amount, habitat configuration, and environmental factors (e.g. depth, salinity) have all been shown to affect resource use (Livingston, 1984; Deegan and Garritt, 1997; Olin *et al.*, 2012; Nelson *et al.*, 2015; Giraldo *et al.*, 2017; Jankowska *et al.*, 2018; Santos *et al.*, 2022). Our results do not point to these factors influencing basal resource use of seagrass, epiphytes, mangroves, or algae in the wet season as there is little intraspecific spatial variation among the sites sampled, despite broad spatial sampling (Table 3, S1, Figure 4). However, in the dry season, there was more intraspecific spatial variation in basal resource use across all species (Table 3, S1, Figure 4). This variation could be related to seasonal differences in the spatial variation of environmental factors that are known to differ seasonally in our sampling area (Kelble *et al.*, 2007) or related to seasonal differences in productivity as seagrass consumers have been shown to increase spatial variation in resource use under varying levels of primary productivity (Lesser *et al.*, 2020).

Though we found minimal spatial variation in basal resource use, we did find spatial variation in species occurrence, and there was variation in basal resource use among species (Table 3). The seagrass die-off could have altered food web structure, especially at higher trophic levels, through a shift in the amount or configuration of seagrass habitat which has been shown to influence species occurrence through alterations in habitat quality, predation efficiency, and competition (Fahrig, 2003; Boström *et al.*, 2011; Santos *et al.*, 2018). Patterns in species occurrence could also be due to the spatial variability in environmental conditions across the bay (Sheridan *et al.*, 1997; Kelble *et al.*, 2021). Environmental conditions vary naturally across the bay, but the seagrass die-off led to local alterations of environmental conditions and could have influenced species occurrence (Fredley *et al.*, 2019; Rodemann *et al.*, 2021). Therefore, further research is needed into the relationship between species occurrence, environmental variables, and seagrass seascape characteristics to better understand the effect of the seagrass die-off on food web structure through the alteration of species composition across the seascape.

Consumer species were haphazardly collected from trawl samples and were not measured before processing for stable isotope analysis. Because of this sampling, it is possible that differences in resource use could be related to ontogenetic diet shifts that are related to body size and are observed in some of the species sampled (Scharf *et al.*, 2009; Barbosa and Taylor, 2020). For example, pinfish display ontogenetic diet shifts throughout switching from more carnivorous to omnivorous diets throughout their lifecycle (Stoner, 1980; Barbosa and Taylor, 2020). The spatial variation in resource use of pinfish observed in the dry season could be related to spatial differences in size classes of life history stages across Florida Bay.

Contrary to expectations, algal resources were not a major contributor to the food web in Florida Bay (Table 3, Figure 3). Our results are in contrast to food webs from other seagrass ecosystems where algal sources have been shown to be a major energy source for consumers (Deudero *et al.*, 2014; Choi *et al.*, 2017; Lesser *et al.*, 2020). Because POM stable isotope values from other studies throughout Florida Bay overlapped with stable isotope values with the macroalgae (Figure 2; Chasar *et al.*, 2005; Eggenberger *et al.*, 2019), POM falls within the multispecies algal group. We can conclude that this basal resource is not a major contributor to the Florida Bay food web. The low amount of water column production entering the food web is not surprising as Florida Bay is normally a phosphorus limited oligotrophic estuary characterized by having low water column production (Fourqurean *et al.*, 1993; Phlips and Badylak, 1996).

Because all species sampled, including pelagic consumers, are not heavily relying on water column production, there appears to be strong benthic–pelagic coupling in this system (Lawrence *et al.*, 2004; Chasar *et al.*, 2005). For example, bay anchovy are a widely known planktivorous feeder (Sheridan, 1978), but even bay anchovy derived only a maximum of 6% of their energy from algae (Table 3). Our results do not suggest that bay anchovy in Florida Bay are not planktivorous or feeding on zooplankton, but bay anchovy production is not mainly derived from water column production. Bay anchovy have been found to use benthic production as the primary basal resource in other seagrass systems (Wilson *et al.*, 2010), and high reliance on benthic production for pelagic consumers is not unique to our study and has been shown in other studies in Florida Bay (Chasar *et al.*, 2005; Malinowski *et al.*, 2019). Benthic–pelagic coupling of energy can happen in multiple ways, but two common transfers of organic material from benthic into pelagic habitats are through resuspension/bioturbation and movement of organisms (Lawrence *et al.*, 2004; Griffiths *et al.*, 2017). One possible mechanism of benthic–pelagic coupling is through copepod movement. Copepods that live mainly in seagrass beds have been shown to migrate between seagrass beds and pelagic environments, potentially providing a link between benthic productivity to pelagic predators (Walters and Bell, 1994). In Florida Bay, there was a significant number of benthic harpacticoids found in pelagic zooplankton net tows, suggesting this type of migration might be prevalent (Kelble *et al.*, 2010). Determining the mechanism of benthic–pelagic coupling in Florida Bay will be crucial for predicting how food webs will respond to future disturbances.

Our results reveal that there is no shift in basal resource use at the time of sampling across the affected areas, but that does not mean that there was no effect from the die-off. Other studies have shown mixed results regarding changes in trophic contribution in response to changes in seagrass cover; in some cases consumers have shifted trophic pathways (Calizza *et al.*, 2013) or showed no response (Chasar *et al.*, 2005). Samples in this study were taken 3 years after the start of the 2015 die-off (Hall *et al.*, 2016), and it is possible that the food web could have recovered by the time of sampling. Trawl surveys at pre-existing monitoring stations were used to collect consumers (Kelble *et al.*, 2021), which led to the lower sampling stations at undisturbed sites and low sample numbers of some species (Table 2). Possibly, these lower sampling numbers could limit the ability to detect changes in basal resource use. Additionally, areal coverage of *T. testudinum* decreased markedly in the die-off area, but remnant patches remained and in some locations recruitment of *H. wrightii* was rapid, resulting in comparably dense meadows by 2017 (Furman *et al.*, 2021). Thus, enough seagrass and epiphyte production may have been present to prevent basal resource shifts by the consumers sampled in this study, especially those in the eastern portion of the die-off area (Rodemann *et al*., 2021). Future studies should include the areal coverage of seagrass around the sampling locations to test for the effects of seagrass cover and patterning on food web structure.

Stable isotope analysis combined with Bayesian mixing models are a useful tool for estimating the resource use of consumer species, but like all methods are not without limitations. One such limitation is choosing the trophic enrichment factors (TEFs, also referred to as diet discrimination factors) for each stable isotope in the model, as these can vary based on environmental conditions, physiological factors, and diet quality (Vander Zanden and Rasmussen, 2001; McCutchan *et al*., 2003; Caut *et al*., 2009), and these estimates can influence mixing model results (Bond and Diamond, 2011). This variation is particularly true for Δ^{15}N values, which have the largest fractionation and most variation with each trophic compared to carbon and sulphur (Post, 2002; McCutchan *et al*., 2003). Like other studies our estimates are likely influenced by our estimation of TEFs. However, unlike most stable isotope studies our models include δ^{34}S, which is valuable for delineating basal resources in coastal systems (Connolly *et al*., 2004). The variation of δ^{13}C and δ^{34}S of basal resources in our system provide a wide mixing space and combined with the inherent low fractionation values of both carbon and sulphur stable isotopes with each trophic step, our models are likely less sensitive to changes in TEF compared to studies that do not include δ^{34}S. Because Δ^{15}N are so variable, and basal resources can vary little in δ^{15}N values, future research should investigate situations where δ^{15}N values are not useful for estimating resource use of consumers.

We found no differences in resource use of the consumers sampled in Florida Bay inside or outside the die-off area. As seagrass is lost, and epiphytes no longer have a substrate to grow on, seagrass consumers do not appear to change energy use to compensate for this loss in production. These die-off events have a two-fold effect on seagrass consumers as they decrease the critical structural habitat and they decrease the primary production sources that fuel the food web. Based on our results we would expect there to be a decrease in biomass of seagrass nekton that corresponds to the decrease in the production of seagrass and epiphytes. Following the first widespread seagrass die-off in Florida Bay, the densities of seagrass-associated prey species were significantly lower in algae and mud bottom habitats compared to dense seagrass beds (Sheridan *et al*., 1997). Many species (e.g. pinfish) use seagrass beds as nursery habitat and transfer seagrass production to offshore predators when migrating to adult habitats, so a decrease in biomass would not only affect food webs within the seagrass beds (Beck *et al*., 2001; Nelson *et al*., 2012). If consumers respond by decreasing production, then the loss in seagrass could have cascading effects that reach outside of the initial die-off areas (Lesser *et al*., 2021).

This study investigated the seasonal resource use of common seagrass consumers inside and outside the 2015 seagrass die-off area in Florida Bay 3 years after the disturbance. Our results showed that consumer resource use did not differ inside or outside the die-off area, but there were seasonal differences in resource use, as seagrass was the most important resource in the dry season, while epiphytes were the most important resource in the dry season. Intraspecific variation in resource use was low in general, but there was more variation in the dry season compared to the wet season. This study highlights that food webs in Florida Bay display similar spatial characteristics in resource use, and that there appears to be no legacy effect on resource use after a major disturbance event.

Supplementary material

Supplementary material is available at the ICESJMS online version of the manuscript.

Author contributions

WRJ, ROS, ZWF, BTF, MOH, CRK, JSR, and JAN designed the study. WRJ and JRR collected and processed samples. WRJ analysed the data and wrote the first draft. All authors contributed substantially to revising the manuscript. The authors declare no conflicts of interest.

Data availability statement

Data used in this study are available on Github (James *et al*., 2022).

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