Title

Ric DeSantiago1,2,3 Rosa Rodriguez Martinez, Gerardo Castaneda, Aurora Veltran, David Lipson,1 and Jeremy D. Long1,2

1 Department of Biology, San Diego State University, San Diego, CA 98182 USA

2 Coastal and Marine Institute, San Diego State University, San Diego, CA 92106 USA

3 Department of Environmental Science and Policy, University of California Davis, Davis, CA 95616 USA

4Instituto de Ciencias del Mar y Limnología, Universidad Nacional Autónoma de México, Puerto Morelos, Quintana Roo, México

5 Moon Palace

6 Botanical garden / ECOSUR

Abstract

Introduction

Seaweed blooms are ubiquitous

Over the last 15 years, golden tides have increased

Their impacts are widely studied

But we still don’t fully understand their impacts on ecology

Here we looked at \_\_\_\_

Paragraph 1

Golden tides may be a new norm

Causes

Predictions (magnitude and frequency)

Locations expected to continue getting these

Paragraph 2

Beaching events result in impacts on tourism

Efforts to remove them (magnitude that is beached)

Cost to remove them

Paragraph 3

When not removed there is potential to affect human health

Leached chemicals

Gases

Anoxic zones

Paragraph 4

Anoxic zones on the coast

Dead animals as a result of them

Some unnafected (turtles)

More difficult to understand its impact when it is removed

Paragraph 5

Efforts to remove the seaweed have caused locals to move it to forest

Potential impacts in the forest

Fertilization

Aggregation

Macroalgae blooms have increased worldwide, presenting challenges to economies and threatening biodiversity across multiple countries (Lapointe 1997, Teichberg et al. 2010, Smetacek and Zingone 2013, Rodríguez-Martínez et al. 2023). Population growth and urbanization has resulted in escalated nutrient inputs into coastal waters, consequently amplifying eutrophication leading to macroalgae blooms (Teichberg et al. 2010). Beach-cast macroalgae that accumulate along shorelines and can obliterate coastal life by creating anoxic conditions, shading benthic taxa, and changing water chemistry (Hauxwell et al. 2001, Teichberg et al. 2010, Van Tussenbroek et al. 2017, Rodríguez-Martínez et al. 2019). Furthermore, macroalgae blooms can clog fishing nets, impede the passage of boats, and produce foul odors that can be a nuisance and may contribute to human health issues from hydrogen sulfide inhalation when left to decompose on the shore (Teichberg et al. 2010, Smetacek and Zingone 2013, Resiere et al. 2021, Rodríguez-Martínez et al. 2023). However, we still lack a full understanding of the impacts of the decomposing biomass on the ecology of locations where it is discarded after it is removed from beaches. Here, we look at the impacts of macroalgae decomposition on beaches and nearby forests dump sites using manipulative experiments to assess responses by flora and fauna in recipient habitats.

Since 2011, the shores of West Africa, Caribbean islands, and the Gulf of Mexico have experienced unusually elevated quantities of *Sargassum spp.* biomass (*S. fluitans and S. natans*; hereafter referred to as Sargasso; Gower et al. 2013, Rodríguez-Martínez et al. 2020, Chávez et al. 2020). Floating aggregations of Sargasso form extensive patches across the tropical and subtropical North Atlantic (Brooks et al. 2018), a phenomenon observed since the early 1800s (Uribe-Martínez et al. 2022), but massive beach landings are a relatively new occurrence. Both Sargasso species are holopelagic, lacking an attached benthic stage in their life cycle and reproducing vegetatively through fragmentation in the open ocean (Brooks et al. 2018, Uribe-Martínez et al. 2022). Consequently, Sargasso patches can attain sizes of up to 3000 km², with a biomass exceeding 20 million tons in the North Equatorial Recirculating Region of the southern Atlantic Ocean (Chávez et al., 2020, and references therein).

Sargasso has become the largest macroalgae bloom globally, with Mexico ranking among the countries most affected by beaching events (Torres-Conde et al. 2023). The northern sector of the Mexican Caribbean is estimated to receive annual volumes ranging from 10,790 to 40,932 m³ of biomass per kilometer of beach (Rodríguez-Martínez et al., 2023). Like other algae blooms, heightened nutrient loads resulting from deforestation and land-use changes (Wang et al. 2019), escalating oceanic temperatures(Wang et al. 2019, Johns et al. 2020), evolving upwelling patterns along the northeastern African coast (Wang et al. 2019), and mineral inputs from Saharan dust (Johnson et al. 2012), have all been associated with increases of Sargasso (Chávez et al. 2020). Anticipated shifts in climate and eutrophication suggest that these blooms will likely increase in frequency and magnitude (Smetacek and Zingone 2013, Rodríguez-Martínez et al. 2023).

Recent studies have elucidated the potential repercussions of Sargasso beaching events on the tourist industry (Vázquez-Delfín et al., 2021). Much of the Mexican Caribbean is characterized by pristine white-sand beaches, turquoise waters, rich biodiversity, and culture, making the region a hub for tourism (Rodríguez-Martínez et al., 2023). In 2021, the state of Quintana Roo attracted nearly 15 million tourists, generating an income of approximately US$10.8 billion (Rodríguez-Martínez et al., 2023). However, given the region's heavy reliance on the tourism industry, the removal of Sargasso has been imperative to maintaining the economy. Furthermore, it is evident that recipient coastlines have a limited capacity to naturally assimilate current influx magnitudes of Sargasso through natural processes.

Seasonal or periodic landings of macroalgae typically confer benefits to beaches by serving as a foundation for, contributing to the fertilization of coastal dunes, and serve as a resource subsidy to food webs (Polis et al. 1997, Huxel and McCann 1998, Anderson and Polis 1998, Marczak et al. 2007, Yang et al. 2010, Spiller et al. 2010, Williams and Feagin 2010, Wright et al. 2013, Piovia-Scott et al. 2013). Beach dunes reinforced by beach-cast macroalgae play a crucial role in mitigating erosion and enhancing the resilience of coastlines against storm-driven wave action and sea-level rise (Williams and Feagin 2010, Bauer et al. 2023). Furthermore, Sargasso landings can provide a temporary food resource for detritivores and their predators (Spiller et al. 2010, Piovia-Scott et al. 2011, Wright et al. 2013, Kenny et al. 2017) and fertilize plants (Spiller et al. 2010, Piovia-Scott et al. 2013). However, previous studies about the impacts of Sargasso landings used quantities similar to natural deposits prior to current massive blooms. It is likely that some of advantages for recipient beaches are likely lost given the substantial scale of current Sargasso landings.

Without removal of Sargasso biomass from beaches, leachates and organic matter resulting from decomposition induce a reduction in oxygen and pH levels, alongside increased turbidity, sulfur, and ammonia concentrations in coastal waters (Van Tussenbroek et al. 2017, Chávez et al. 2020, Rodríguez-Martínez et al. 2023). For instance, a significant Sargasso beaching event in 2018 was associated with a faunal mortality event, where hypoxic conditions led to the demise of 78 species of neritic fish, crustaceans, echinoderms, mollusks, and polychaetes (Rodríguez-Martínez et al. 2019). Due to the various adverse effects of Sargasso decomposition on the coast, much of the biomass is moved to quarries, garbage dumps, and forest habitats. To this day, we lack an understanding of the ecological impacts of massive Sargasso dumping in these ecosystems.

Ecological theory suggests that local adaptation through coevolution would result in faster decomposition of litter on its own soil over foreign soil, a termed ‘*the home field advantage’* (Bocock et al. 1960, Gholz et al. 2000, Pugnaire et al. 2023). Thus beach-cast Sargasso should decompose more quickly over sand dunes than forest soil. Furthermore, terrestrial predator foraging in beach-cast macroalgae is a common feature in coastal ecosystems (Kirkman and Kendrick 1997, Rose and Polis 1998, Dugan et al. 2003, Colombini and Chelazzi 2003, Kenny et al. 2017), but less is known about terrestrial insect responses to this phenomenon. To our knowledge, this has not been tested with macroalgae deposits in forests. Moreover, previous work with Sargasso biomass showed a fertilization effect on plants on shorelines Bahamian islands and there have been efforts to use Sargasso as a fertilizer for vascular plants. Yet, the fertilization effect of Sargasso in forest has not been tested.

Here, we used manipulative experiments and surveys to test the effects macroalgae deposits on a beach and in a forest. To do this, we created Sargasso piles of realistic magnitudes with paired, unmanipulated controls, at both sites, and surveyed them over the course of a year. We estimated volume over time and sampled CO2 production, nitrate, and ammonium content on sediment below the piles. To test arthropod response, we used sticky traps and pitfall traps to measure flying and crawling abundance on piles and controls. We also conducted point intersect surveys to understand the impacts of this manipulation on plant abundance on plots proper and their perimeter. Furthermore, we measured decomposition of Sargasso at both sites using mesh bags to compare changes in biomass with and without access to arthropods.

**Methods**

**Sargassodecomposition experiments**

*Sargasso piles*

We conducted this study at two sites in Puerto Morelos, Quintana-Roo, Mexico, from August 2022 and August 2023. This region is among those impacted by the invasion of beach-cast Sargasso (Chávez et al. 2020, López-Sosa et al. 2020). We established a beach site on an ungroomed strip of beach north of Moon Palace Resorts (20.99343° N, 86.82442° W). This location is adjacent to a large barrier that prevents Sargasso from accumulating on hotel property and is removed by Sargasso collection vessels owned and operated by the resort. All Sargasso used in this experiment was obtained from drift paddies collected and by Moon Palace Environmental Services.

To simulate a natural deposition of beached Sargasso, we created five Sargasso piles (4.28 ± 0.37 m3) on the beach, parallel to the water line. Sargasso piles were paired with unmanipulated controls (i.e., sections of beach based on the average footprint area of Sargasso piles, 1.88m radius). All plots were separated by a minimum of 9m from the center of the nearest treatment. In order to minimize human disturbance and prevent natural Sargasso deposition from altering the manipulation, we established these plots above the high tide line, in an area not frequented by tourists. The beach at this location is a relatively narrow (~15m) strip adjacent to an unmaintained section of coastal foliage. To simulate sargasso dump sites in the forest, we repeated the experiment along the outer perimeter of a botanical garden (Jardín Botánico ECOSUR “Dr. Alfredo Barrera Marín”; 20.84400° N, 86.90278° W). The botanical garden occupies an area of 65ha of natural forest and consists of 204 species from 64 botanical families (Elizondo 2013). The botanical garden treatments (hereafter “forest”) were located along the outer edge of a clearing, adjacent to a natural forest assemblage similar to areas where sargassois dumped in this region.

To obtain initial volumes of sargasso piles, we measured the longest length, perpendicular width, and height of each pile and estimated volume using the elliptic cone formula (*V=1/3 πabh).* In subsequent sampling trips (November 2022, March, and August 2023), we measured the piles using the same methods and calculated the percent volume relative to original volume in August 2022.

*Mesh bag decomposition experiment*

To test relative contributions of bacterial and arthropod decomposition of sargasso*,* we placed two sizes of mesh bags containing sargasso at the beach and in the forest (sm 180µm, lg 1cm; n=10). Small mesh bags excluded all arthropods larger than 180µm and large mesh bags allowed for decomposition by bacteria and arthropods under 1cm. We placed 234.66 ± 0.42g of sargasso in each bag and measured changes in biomass on subsequent trips. Initially, forest treatments were placed in a forested public area but were later moved to the botanical in November 2022, to ensure they would be left undisturbed. The beach treatment remained in the same location throughout the experiment, however, in March 2023, we were unable to recover the large mesh bags due to vandalism of the experiment.

*Soil nitrification*

To understand if sargasso degradation affects soil nitrification (the oxidation of ammonium into nitrate by bacterial decomposition), we used aquarium water quality test strips (SJ Wave ®) to measure NO3- . We collected sediment samples from all treatments using a modified 50 ml falcon tubes as coring devices (tapered end of the tubes were cut off). All sediment cores were collected from approximately 30 cm from the edge of plots into the interior by temporarily clearing sargassoand leaf litter from the surface and coring the sediment underneath. We homogenized sediment samples and mixed with ?ml of water, then filtered it through filter type. Following instructions included with the test kit, we visually compared the color change of each strip using the chart provided.

*Soil respiration*

We used upside-down 1.87 L plastic containers with an approximate footprint area of 176.72 cm as gas collectors. We drilled a hole in each container and glued rubber septa plug to sample using 10ml syringes. We placed gas collectors approximately 30cm from the edge each plot, directly above the sediment by moving sargasso or leaf litter. We collected gas samples immediately after placing the gas collectors over sediment and after 60 minutes in November 2022. To do this, we penetrated the septa plug with a syringe and pumped it ten times to homogenize the air before extracting a sample. Gas samples were collected in 10 ml vacutainers and transported to San Diego State University for CO2 analysis. In August 2023, we used a respirometer (model #) to obtain *in situ* readings of CO2 at the center and 30cm from the center of each plot.

**Plant surveys**

*Plot interior survey*

To assess the effect of sargassoon plant cover directly on plots, we conducted percent cover surveys on the interior using a 100-point 0.5 x 0.5m PVC quadrats. To estimate plot interior percent cover (August and November 2022), we randomly sampled by blindly tossing a marker over the shoulder and haphazardly placing a quadrat where the marker landed (n=3). We standardized the sampling method (March and August 2023) by placing one quadrat in the center and using two randomly selected cardinal directions (degrees) and placing the next two quadrats at the edge of the first. We decided to sample in this way to fully capture the treatment effect at the center of the plots as sargasso piles as they changed over time. In situations where we encountered multiple species under quadrat cross hairs, we identified and counted the top layer only.

*Plot perimeter survey*

To assess the effect of sargasso beyond piles, we conducted two surveys to look at plant percent cover at the edge of all treatments. For the first survey, we placed a quadrat at the edge of sargasso plots and 1.88m from the centers of control plots, on opposing sides of the plots (“left” and “right”). We measured percent cover using the methods described in the section above. This was repeated at 0.75m and 1.5m (August and November 2022, and March 2023). In March 2023, we did not see variation between sampling distances at 0.75m and 1.5m from the plot and decided to drop this portion of the survey in the interest of sampling efforts and time (supplementary Fig. 1). In the second survey, we placed a quadrat on front and back of each plot (hereafter called “low” and “high”) and conducted percent cover surveys as described above.

Thus, we combined the 0 m points of both surveys to create a perimeter survey to detect the effect of sargasso directly adjacent to the piles. Additionally, because Bermuda grass (hereafter “grass”) was so prevalent at the beach sites and there were no obvious patterns observed in the forest or with other plants in general, we decided to score these surveys by collapsing all non-Bermuda grass plants into one category in the forest (March 2023), and both sites in August 2023. Furthermore, the sargasso treatments had decreased in volume and area footprint which meant that quadrats placed on the edge of sargasso had been moving over sampling periods, thus in August 2023 we decided to sample at 1.88m from the centers of sargasso piles in the same way we sampled control plots.

It should be noted that the beach site was located in an area that is not typically used by beachgoers, however, between November 2022 and March 2023, we found recreational vehicles tracks that disturbed the edge of two sargassopiles*.* Due to this disturbance, surveys were adjusted to avoid these areas by moving quadrats to an adjacent side where the piles were undisturbed. Thus, the “low” quadrats were placed approximately 0.5m closer to the left side of these plots. We did not see any signs of unnatural disturbance on treatments in the forest.

**Arthropod Surveys**

*Crawling arthropods*

To assess the effect of sargassoon crawling arthropod abundance, we placed yellow plastic cups (210 ml) at the edge of the lowest and highest points of each plot. Pitfall traps were buried flush with the substrate and filed approximately halfway with water and ~5 drops of dish soap to break the surface tension and prevent arthropods from escaping. We collected the entire contents of each trap after 24 hours, counted and identified arthropods to order.

*Flying arthropods*

To assess the effect of sargassoon flying arthropod abundance, we placed two double-sided sticky cards (127mm x 76mm brand), attached to wire rods, on each plot. The sticky traps were placed ~130mm above the substrate or sargassopiles, ~1m from the center to the “high” and “low” sides of the plot. After 24 hours, we photographed all sticky traps *in-situ* to process at a later time. Arthropods were counted on both sides of sticky traps and identified to order.

**Analysis**

**Results**

*Sargasso piles*

Sargasso piles at the beach were initially larger than those in the forest in August 2022 ( 5.25 ± 0.03 m3 beach, 3.31 ± 0.09 m3 forest; rm-ANOVA, Estimate = -1.9320, p<0.001). Both treatments decreased the most between August and November 2022, but their volumes converged in subsequent trips (Fig. 1). A pairwise post-hoc test revealed that there was no difference in pile volumes between sites over time (beach-forest November 2022, Estimate=-1.94, p=0.99; beach-forest March 2023, Estimate=0.21, p=0.97, beach-forest August 23, Estimate=0.038, p=1.00). Beach pile volumes significantly decreased between sampling periods, with an average reduction of 3.98 m3 in November 2022, 4.48 m3 in March 2023, and 4.93 m3 in August 2023 compared to the initial measurements (all p<0.001). Forest pile volumes also decreased over time, with an average reduction of 1.86 m3 in November 2022, 2.76 m3 in March 2023, and 3.03 m3 in August 2023 (all p<0.001).

*Mesh bag decomposition experiment*

Figure 2

*Soil nitrification*

Nitrate levels generally followed the same pattern and peaked in March 2023 at both sites. We did not detect nitrate levels in any control plot at either site (Fig. 3A, B, C, D). Nitrate levels under sargasso piles at the beach were initially 6.5 ± 2.3 mg/L after deployment and continued to increase to 18.6 ± 5.2 mg/L in November 2022, peaked at 79.5 ± 44 mg/L in March 2023, and declined to 24 ± 10.8 in August 2023 (Fig. 3A, C). Due to logistical and time constraints, we were unable to sample the sediment under the forest treatments after installation in August 2022 (Fig. 3B). Forest nitrate levels were lower than those at the beach but generally followed the same pattern (i.e., peaked in March 2023). In forest treatments, levels were 7.5 ± 4.03 mg/L in November 2022, increased to 20 ± 5.2 mg/L in March 2023, and declined to 10 mg/L in August 2023 (Fig. 8B, D).

*Soil respiration*

Using gas collectors, we measured generally higher levels of CO2 production in sargasso plots (Fig. 4A, B); However, our analysis revealed no statistical significance in CO2 production over an hour period between treatments (ANOVA: F=1.679, p=0.219), sites (F=0.953, p=0.348), or their interaction (F=0.025, p=0.878) in November 2022. We measured zero CO2 production in control plots and 0.156 ± 0.0557 grams of CO2 m-2 hour-1 in sargasso plots at the beach (Fig. 4A). In forest treatments, control plots produced 0.122 ± 0.0536 g CO2 m-2 hour-1 and sargasso plots produced 0.244 ± 0.148 g CO2 m-2 hour-1 (Fig. 4B).

There was no clear pattern in CO2 production using the respirometer in the center or edge of plots (Fig. 4C, D). CO2  production was not statistically significant between position of respirometer (F=1.770, p=0.192) and treatment was marginally significant (F=3.971, p=0.0549). Further, there was a significant interaction between position and site (F=13.532, p<0.001), thus, we analyzed sites separately. CO2 production did not differ between respirometer position at the beach (F=3.873, p=0.067) but was higher in sargasso plots than controls (F=5.593, p=0.031. In sargasso plots, CO2 production measured 1.43 ± 0.601 on the center and 0.266 ± 0.0509 on the edge, and 0.146 ± 0.0354 on the center and 0.124 ± 0.0175 of control plots )(Fig. 4C). CO2 production in the forest did not differ by treatment (F=0.089, p=0.769) or position (F=0.063, p=0.804). In sargasso plots, CO2 measured 1.40 ± 0.310 on the center and 1.13 ± 0.335on the edge, and 0.986 ± 0.187 on the center and 1.38 ± 0.152 on the edge of control plots (Fig. 4D).

**Plant surveys**

*Plot interior*

The beach floor was primarily sand with few plants, including Bermuda grass and some dead plant litter (supplementary Fig. 2). Sargasso positively affected grass percent cover on sargasso plots throughout the experiment (Fig. 5A, C). Grass cover on control plots at the beach was 5 % ± 2.79% when the experiment was installed and remained at similar levels for the duration of the experiment. During the second sampling period (November 2022), grass percent cover on sargasso plots was 17.40 ± 6.6% (7.6 ± 3.37% control; *d*=0.483) and increased to 72.47 ± 4.31 % (7 ± 3.31% control; *d*=4.373) in March 2023 and 81.73 ± 7.26 % (6.8 ± 1.88% control; *d*=3.648) August 2023. When all plants (non-grass) were grouped together, percent cover was below 5% in both treatments for all sampling periods August 2023, when plant cover was higher in control plots, resulting in a small, negative effect size (3.2 ± 1.32% sargasso, 6.33 ± 3.76% control; *d*=-0.287).

The forest floor was primarily leaf litter and bare ground with a high plant diversity compared to the beach (supplementary Fig. 3). Sargasso addition in the forest did not positively impact percent cover of grass or any other plant during any sampling periods (Fig. 5B, D). Grass cover was relatively low in the forest compared to the beach during initial installation of the experiment (0.14 ± 0.09 %) and was only present again in one control plot in November 2022 (0.2 %). Plant percent cover in control plots in the forest during the initial installation was 3.86 ± 1.77%. Plant percent cover in sargasso plots in November 2022 was 0.74 ± 0.35 (6.13 ± 1.52 % control; *d*= -1.25), increased to 11.13 ± 5.86% (9.47 ± 2.58 control; *d*=0.95) in March 2023, decreased to 1.6 ± 0.87% (14.2 ± 3.35% control; *d*= -.1.33) in August 2023.

*Plot perimeter*

Percent cover of grass also increased at the perimeter of sargasso plots at the beach over time (Fig. 6A, C). Initially, grass percent cover was higher on the perimeter of sargasso plots than controls (16 ± 6.05% sargasso, 5.6 ± 2.28% control; *d*=0.51) but decreased in November 2022, resulting in a small negative effect size (1.15 ± 1.05% sargasso, 440 ± 3.24% control; *d*=-0.30). Sargasso had a medium effect on grass percent cover in March 2023 (18.80 ± 6.33% sargasso, 6.69 ± 3.97% control; *d*=0.71) and the largest effect in August 2022 (34.60 ± 6.87% sargasso, 9.15 ± 3.84% control; *d*=1.02). Other plant (non-grass) percent cover in the perimeter of control plots was slightly higher in control plots in August 2022 (7.95 ± 3.46% sargasso, 11.15 ± 4.29% control; *d*=-0.18) but increased in perimeters sargasso plots by November 2022 (16.65 ± 4.95% sargasso, 8.49 ± 2.91% control; *d*=45). Sargasso had a small effect on plant cover in March 2023 (8.50 ± 4.44% sargasso, 6.10 ± 3% control; *d*=0.20) and negligible effect in August 2023 (8.35 ± 2.99% sargasso, 5.85 ± 2.33% control; *d*=0.16).

Overall, percent cover of grass in the forest was initially minimal (0.05 ± 0.05% sargasso, 0.75 ± 0.61% control) and only appeared in one sargasso plot in November 2022 (0.90%), thus, sargasso had little to no effect on grass in the perimeter of any plots (Fig. 6B, D). Percent cover of all other plants in August 2022 was 3.70 ± 1.07% in sargasso plots and 8.95 ± 2.75% in control plots and generally increased over time in the forest. Sargasso had a small effect on plant cover in November 2022 (6.75 ± 2.88% sargasso, 2.65 ± 0.70% control; *d*=0.44) and March 2023 (10.20 ± 5.17% sargasso, 6.30 ± 2.44% control; *d*=0.30) and a medium effect in August 2023 (27.05 ± 7.98% sargasso, 11.25 ± 3.97% control; *d*=0.56). Percent cover of plants and other categories are included in the supplementary materials (supplementary Fig. 4 and 5).

**Arthropod Surveys**

*Crawling arthropods*

Crawling arthropods in pitfall traps consisted of various arachnids and hymenopterans, mainly wolf spiders and ants at both sites, and tilirid amphipods at the beach (Fig. 7A, B). Sargasso addition at the beach initially had a large effect on amphipod abundances in August 2022 (4.60 ± 0.93 control 195.3 ± 57.11 sargasso; *d*=1.49)(Fig. 7A, C, E) but only 1 amphipod was found in a control plot in November 2022 (Fig. 7A) and 1 in a sargasso plot in March 2023 (Fig. 7C). Arachnids were more abundant on sargasso plots in August 2022 ( 0.70 ± 0.26 controls, 1.90 ± 0.51 sargasso; *d*=0.95), and were less abundant in November 2022 (1.00 ± 0.26 control, 0.60 ± 0.16 sargasso , *d*=-0.59) and March 2023 (1.60 ± 0.43 control, 0.70 ± 0.26 sargasso,=; *d*=-0.80) (Fig. 7A, C, E). The effect of sargasso on hymenoptera abundance at the beach was initially small in August 2022 (4.60 ± 1.94 control, 3.70 ± 1.94 sargasso; *d*= 0.35), medium in November 2022 (0.70 ± 0.40 control, 16.70 ± 10.55 sargasso; *d* = 0.68) and medium in March 2023 (5.90 ± 3.26, 12.80 ± 3.62 sargasso; *d* = 0.63) (Fig. 7A, C, E).

No amphipods were found in forest pitfall traps during any of the sampling periods (Fig. 7 B, D). Sargasso addition had negligible effects on arachnid abundance in August 2022 (0.67 ± 0.49 control, 0.67 ± 0.33 sargasso,; *d*=0) and November 2022 (1.20 ± 0.33 control, 1.30 ± 0.26 sargasso; *d*=0.11) and a small but negative effect in March 2023 (0.60 ± 0.27, 0.40 ± 0.16 sargasso; *d*=-0.29) (Fig. 7B, D, F). Sargasso effects on hymenoptera in the forest were also negligible in August 2022 (1.67 ± 0.61 control, 2.11 ± 1.20 sargasso; *d*= 0.15) and November 2022 (5.20 ± 1.60 control, 5 ± 1.53 sargasso; *d*=-0.04), but we detected a small effect in March 2023 (5.50 ± 1.45 control, 11.70 ± 6.14 sargasso; *d*=0.44) (Fig. 7B, D, F).

*Flying arthropods*

Flying arthropods on traps consisted of various dipterans and hymenopterans, mostly various species of flies and wasps at the beach (Fig. 8A,C). On the initial deployment of the experiment, amphipods were also captured on sticky traps. Sargasso addiction had a large effect on amphipod abundance in August 2022 (0.90 ± 0.48 control, 21 ± 7.10 sargasso; *d*=0.89) but no amphipods were captured on sticky traps in November 2022 or March 2023. Diptera abundances were initially higher on sargasso piles plots (10.35 ± 2.12 control, 223.75 ± 57.33 sargasso; *d*=1.18) but the effect was reduced in November 2022 (48.95 ± 8.08 control, 96.30 ± 22.63 sargasso; *d=*0.62) (Fig. 8A, C, E). In March 2023, diptera abundance was higher in control plots (25.05 ± 4.12 control, 12.9 ± 1.98 sargasso; *d*=-1.57) but were an order of magnitude lower than abundances in August 2023 (Fig. 8A, C, E).

No amphipods were found in forest sticky traps, however, one individual on a sargasso pile resulted in a small effect size (*d=*0.32; Fig. 8F). Sargasso addition initially had a small effect on diptera abundance in August 2022 (3.00 ± 0.91 control, 4.10 ± 0.59 sargasso; *d*=0.35) and peaked in November 2022 (3.90 ± 0.60 control, 14.95 ± 1.62 sargasso; *d*=2.02)(Fig. 8B, D, F). Diptera abundance was similar between treatments in March 2023, resulting in a small effect size (2.10 ± 0.38 control, 2.85 ± 1.04 sargasso; *d=*0.50)(Fig. 8B, D, F). Sargasso initially had a negligible effect on hymenoptera abundance in the forest (1.05 ± 0.33 control, 0.85 ± 0.27 sargasso; *d=-*0.15*)*, increased in November 2022 (2.25 ± 0.46 control, 7.65 ± 2.21 sargasso; *d=*0.76) and decreased in March 2023 (2.65 ± 0.50 control, 5.6 ± 1.33 sargasso; *d*=0.64) (Fig. 8B, D, F).

**Figure legends**

**Figure 1**

Sargasso pile volume loss over sampling periods (August and November 2022, March and August 2023) as a percent (%) of original volume calculated for sargasso treatments in August 2022. Individual dots represent replicates at the beach (black) and the forest (white).

**Figure 2**

Percent decomposition of initial dry mass of large (gray bars) and small (white bars) mesh bags at beach (left column) and the forest (right column) in November 2022 (A) and March 2023 (B). Error bars represent mean ± SE. Note that no values are reported for large mesh bags at the beach in March 2022 due to vandalism, the lack of a bar does not indicate zero decomposition.

**Figure 3**

Nitrate content (mg/L) over sampling periods (August and November 2022, March and August 2023) by site (beach A,C and forest B,D). Nitrate content in the top panels (A,B) were extracted from tissue in sargasso plots (gray bars) and nitrate content in the bottom panels (C,D) were extracted from sediment in sargasso and control (black bars) treatments. Error bars represent mean ± SE. Note that control plots did not produce measurable levels of nitrates, thus, they are shown as solid black lines rather than bars.

**Figure 4**

Grams of CO2 per m2 over an hour in control and sargasso plots at the beach (A) and forest (B) from samples collected with ‘gas collectors’ November 2022. Respirometer CO2 (units) readings from beach (C) and forest (D) control and sargasso plot centers (gray bars) and edges (white bars) in August 2023. Error bars represent mean ± SE.

**Figure 5**

Mean percent cover of plot interiors over sampling period (August and November 2022, March and August 2023) at the beach (A) and forest (B). Shapes represent grass (▲) and other plants (●) and colors represent control plots (gray) and sargasso plots (black). Error bars represent mean ± SE. Lower panels show the effect sizes by sampling period associated with the panel above (i.e., panel C effect sizes associated with panel A, and panel D effect sizes are associated panel B). Effect sizes were calculated using Cohen’s d (sargasso vs. control) for grass (▲) and other plants (●).

**Figure 6**

Mean percent cover of plot perimeter over sampling period (August and November 2022, March and August 2023) at the beach (A) and forest (B). Shapes represent grass (▲) and other plants (●) and colors represent control plots (gray) and sargasso plots (black). Error bars represent mean ± SE. Lower panels show the effect sizes by sampling period associated with the panel above (i.e., panel C effect sizes associated with panel A, and panel D effect sizes are associated panel B). Effect sizes were calculated using Cohen’s d (sargasso vs. control) for grass (▲) and other plants (●).

**Figure 7**

Mean crawling arthropod abundance in pitfall traps over sampling period (August and November 2022, and August 2023) in the beach (left column, panels A, C, E) and the forest (right column, panels B, D, F). Arthropod abundances are separated by controls (A, B) and sargasso (C, D). Effect size plots are associated with plots above (i.e., panel E effect sizes are associated with panels A and C, panel F effect sizes are associated with panels B and D). Effect sizes were calculated using Cohen’s d (sargasso vs. control). Shapes represent Amphipoda (●), Arachnida (▲), and Hymenoptera (■) and error bars represent mean ± SE.

**Figure 8**

Mean flying arthropod abundance in pitfall traps over sampling period (August and November 2022, and August 2023) in the beach (left column, panels A, C, E) and the forest (right column, panels B, D, F). Arthropod abundances are separated by controls (A, B) and sargasso (C, D). Effect size plots are associated with plots above (i.e., panel E effect sizes are associated with panels A and C, panel F effect sizes are associated with panels B and D). Effect sizes were calculated using Cohen’s d (sargasso vs. control). Shapes represent Amphipoda (●), Arachnida (▲), and Hymenoptera (■) and error bars represent mean ± SE.

**Supplementary Figure 1**

Percent cover of grass (light gray bars) and other plants (dark gray bars) over sampling periods (August 2022, November 2022, and March 2023). Sargasso treatment panels (A) include beach (left column) and forest (right column). Control treatment panels (B) include beach (left column) and forest (right column). Panel rows indicate distance from treatment plots (0m, 0.75m, and 1.5m). Error bars represent mean ± SE.

**Supplementary Figure 2**

Proportion of cover categories in plot interiors over sampling periods 1 (August 2022), 2 (November 2022), 3 (March 2023), and 4 (August 2023) in the beach site. Columns designate treatment type (left is control and right is sargasso) and rows represent treatment block.

**Supplementary Figure 3**

Proportion of cover categories in plot interiors over sampling periods 1 (August 2022), 2 (November 2022), 3 (March 2023), and 4 (August 2023) in the forest site. Columns designate treatment type (left is control and right is sargasso) and rows represent treatment block.

**Supplementary Figure 4**

Proportion of cover categories in plot perimeter over sampling periods 1 (August 2022), 2 (November 2022), 3 (March 2023), and 4 (August 2023) in the beach site. Columns designate treatment type (left is control and right is sargasso) and rows represent treatment block.

**Supplementary Figure 5**

Proportion of cover categories in plot perimeter over sampling periods 1 (August 2022), 2 (November 2022), 3 (March 2023), and 4 (August 2023) in the forest site. Columns designate treatment type (left is control and right is sargasso) and rows represent treatment block.

**Figures**

Figure 2. Mesh bag decomposition

A graph of different sizes of trees

Description automatically generated

Figure ???? Mesh bag arthropod counts

A white rectangular object with black text

Description automatically generated with medium confidence

Figure 3. Nitrate content

**A graph of different sizes and shapes

Description automatically generated with medium confidence**

Figure 4. Soil respiration

A graph of different types of plants

Description automatically generated with medium confidence

Figure 5. Plot interior percent cover and effect sizes

A graph of different types of data

Description automatically generated with medium confidence

Figure 6. Plot perimeter percent cover and effect sizes

A graph of different types of data

Description automatically generated with medium confidence

Figure 7. Crawling arthropod counts and effect sizes

A graph of different types of growth

Description automatically generated with medium confidence

Figure 8. Flying arthropod abundance and effect sizes

A graph of different sizes and numbers

Description automatically generated with medium confidence

**Supplementary**

Figure 1. Plant percent cover from edges of sargasso piles

**A graph of different sizes and colors

Description automatically generated with medium confidence**

Figure 2. Plot interior percent cover categories (beach)

A chart of different colored squares

Description automatically generated

Figure 3. Plot interior percent cover categories (forest)

A chart with different colored squares

Description automatically generated

Figure 4. Plot perimeter percent cover categories (beach)

A chart of different colored squares

Description automatically generated

Figure 5. Plot perimeter percent cover categories (forest)

A chart with different colored squares

Description automatically generated

**Lit review**

**Marczak et al. 2007**

Meta-Analysis: Trophic Level, Habitat, and Productivity Shape the Food Web Effects of Resource Subsidies (see note later in this document)

Focused on biomass or density response of consumers in recipient habitats to a resource subsidy.

Excluded studies if they did not report consumer response OR if they reported consumer response in units other than density or biomass

Included studies that manipulated either subsidy amount OR used natural gradient in a subsidy as a proxy for manipulation.

|  |  |  |
| --- | --- | --- |
| Study | Donor | Responder |
| Gende and Willson 2001 | Salmon | Forest birds |
| Marczak unpublished data | stream insects | Forest spiders |
| Sabo and Power 2002 | stream insect | Forest lizard |

Note that in this meta-analysis, there was an emphasis on forest predators (spiders, birds, lizards). The meta-analysis revealed that subsidy effects were neutral for birds and spiders  (the exception being horizontal orb weavers). Further, subsidies had weaker effects on predators than detritivores. I think the fact that such few studies could indicate a lack of subsidies (studies would be rare if there weren’t suspected roles of subsidies). Also, this table was edited because I had to remove riparian forest subsidies (where impacts were much greater).

**Recalde et al. 2016**

Impacts of subsidies in the tropical forests.

Subsidy impacts were seen on vegetation-associated arthropods, not ground-associated. The lack of effect on ground-associated guys sounds like our pitfall trips. But the lack of effect in this study could because subsidy was aquatic insects. “We also predicted that vegetation-dwelling predators are more responsive to allochthonous inputs than those living on the ground (leaf litter), because the flow of emerging insects is likely intercepted higher in the air column (vegetation stratus) than close to the ground.”

**Collins and Baxter 2014**

"Salmon carcasses in un-vegetated habitats desiccated whereas in vegetated habitats  
they remained moist which likely facilitated rapid consumption"

And from that same paper "Similar effects have been

observed in tropical habitats, where desiccation

of reptile carcasses inhibited rates of consumption

by arthropods in dry versus wet habitats

(Cornaby 1974)."

**Anderson and Polis 1998**

-coastal individuals exhibited more strongly marine-based diets than inland individuals (using stable isotopes)

-“Flow of energy and nutrients across habitat boundaries is ubiquitous, and spatial subsidization of less productive habitats by more productive habitats often influences population and community dynamics of the less productive habitat (Polis et al. 1996, 1977a, Oksanen et al. 1997).”

“During years of high precipitation, for example the 1992-93 El Nino event, population dynamics and community interactions are different from those in dry years (Polis et al. 1997b, c). Increases in land plant biomass following heavy rains increase the absolute contribution of terrestrial productivity and diminish the relative importance of marine input to island and coastal communities.”

In a water limited system, adding water increases plant biomass, thus, reducing marine subsidy impact on arthropods. We have forests that are not water limited and little response from arthropods

**Greig et al 2012**

Human mediated climate change changes subsidies between aquatic and terrestrial habitats. Using mesocosm experiments they showed predatory fish reduce arthropod emergence and terrestrial detritus decomposition. Warming and nutrients resulted in higher emergence and decomposition rate especially without predators.

**Helfield and Naiman 2001**

Salmon carcasses subsidize trees which then improve stream quality through sediment and nutrient filtration and woody detritus production (which then maybe loops back to providing better spawning habitat for fish?). Uses stable isotope enrichment.

**Holt 2008**

Recurrent resource pulses can alter community structure, permitting coexistence that otherwise would not occur, or hamper coexistence mechanisms effective in stable environments.

**Jeffreis 2000**

Where large amounts of agricultural resources are transferred to natural habitats, trophic dynamics change: trophic cascades can occur and rare or uncommon species can become invasive.

Non native, nuisance grasses fertilized in dunes in our system…

**Kenny et al 2017**

Seaweed subsidies changed perching heights and movement rates of lizards on Bahamian islands. Terrestrial predators forage on seaweed subsidies (i.e. predator release to terrestrial prey).

**Marcarelli et al. 2011**

Literature review of studies (>90) about open water metabolism in lakes and streams. They concude that animals select higher quality food regardless of allochthonous vs autochthonous.

“ecosystem and food web effects of a subsidy depend on its quality and its quantity, yet the role of subsidies cannot be understood via either of these characteristics by themselves.”

**Zelnik et al. 2023**

Modeling paper using methods from a previous study (zelnik 2023) and data from Cebrian (199, 2004).

“The subsidies provide food for detritivores, which in turn increases predator populations, and lead to a trophic cascade where plants grow more as herbivory pressure is reduced by predators.”

The positive trend in the terrestrial ecosystem occurs because organic nitrogen supports a large detritivore community, which feeds the predators that in turn reduce the herbivores, thereby allowing plants to grow more. At higher organic fractions outside the coexistence range, NPP decreases when larger amounts of nitrogen flow into the brown food web instead of being used by primary producers.

“emphasizing that benefits of organic subsidies to primary production are context dependent”

**Reshamwala et al 2018**

Terrestrial to terrestrial subsidies via human trash as fox food. Foxes consumed less natural prey where there was an abundant human-produced subsidy.

**Piovia-Scott et al. 2013**

We found that both top-down, lizard-mediated, and bottom-up, plant-mediated pathways contributed to the long-term effect of chronic seaweed deposition on herbivory. ry. However, the bottom-up fertilization pathway overshadowed the effects of the top-down lizard-mediated pathways, resulting in a positive association between seaweed deposition and herbivory. In contrast, our previous experimental study indicated that a short-term increase in herbivory in response to a single, large pulse of seaweed deposition was due to the lizard diet-shift pathway. Thus, even though both chronic and pulsed subsidies increased herbivory, the mechanism underlying this response depended on the temporal pattern of subsidy inputs, with a predator-mediated pathway dominating short-term responses to pulsed subsidies and a plant-mediated pathway dominating long-term responses to chronic subsidy inputs.

**Piovia-Scott et al 2019**

Looked at the impact of seaweed deposition on the effect of lizards on the food web (insects and plants). Long-term strengthening of lizard effects was associated with lizard numerical responses and plant fertilization. Increased pulse frequency reinforced the strengthening of lizard effects on spiders and plants. These results underscore the temporally variable nature of top–down effects and highlight the role.

**Riggi and Bommarco 2018**

Effect sizes (log-ratio) of top-down (predation) and bottom-up (fertilization) forces across three fertilization treatments on aphid density per plant biomass and on plant biomass.

Subsidy is fertilizer and the treatment is Removal of the subsidy.

Leroux and Loreau, 2008

**Schnidler and Smits 2017**

“The lateral extent of biological aquatic subsidies is typically small, extending only a few meters into riparian habitat; however, terrestrial consumers often aggregate on shorelines to capitalize on these high-quality resources.”

Aquatic to terrestrial subsidies delivered hydrologically (floods, complex drainage), biologically (bears, salmon, insects, bats, lizards). Introduced lizards to island and fond that they have a top-down effect on leaf damage (reduce it).

“Lizards reduced leaf damage significantly; because they consume numerous kinds of arthropods, including many herbivores”

Note that, for a between-subjects effect, repeated-measures analysis is equivalent to using the time average in a simple analysis. The between-subjects statistics are used to test hypotheses about magnitudes; within-subject statistics (i.e., those involving time) are used to test hypotheses about temporal changes. Initially, we performed an ANCOVA with the premanipulation value on each island as the covariate. If the P value for the covariate was !.10, the ANCOVA, which adjusts for premanipulation plot differences, was given in the results. If (true for all variables except small P ∏ .10 aerial arthropods), the covariate was omitted from the analysis. Treatment (1–3) was a fixed effect. All analyses used Type III sums of squares and were executed with SAS software (Littell et al. 1991).

**Spiller et al. 2010**

For each response variable, mean values for each plot on each post-manipulation date were analyzed using repeated-measures MANOVA with block (island) and treatment (seaweed added, removed) as the main (between-subjects) factors and time (sampling date) as the repeated (within-subject) factor. We used rmMANOVA because it contains fewer assumptions (e.g., sphericity) than does rmANOVA.

To test each hypothesis, the P value for the overall treatment effect was used when the time 3 treatment interaction P value was .0.10. When the interaction P value was ,0.10, treatment effects from separate ANOVAs on each sampling date were used; significance levels were then adjusted for multiple comparisons using the step-down Bonferroni method (SAS Institute 1999).

A page of a book

Description automatically generated

Relevant…see last sentence from Marczak et al. (No effect of subsidies on spiders for studies like ours).