

# Long-Term Persistence of Propeller and Anchor Damage to Seagrass Canopy and Demersal Biodiversity in Puerto Rico

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**How to cite this paper:** Hernández-Delgado, E.A. (2023) Long-Term Persistence of Propeller and Anchor Damage to Seagrass Canopy and Demersal Biodiversity in Puerto Rico. *Open Journal of Ecology*, 13, 671-710. <https://doi.org/10.4236/oje.2023.1310042>

**Received:** July 5, 2023

**Accepted:** October 21, 2023

**Published:** October 24, 2023

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## Abstract

Seagrass ecosystems support high biodiversity and productivity and constitute critical links to adjacent ecosystems. However, there is a growing concern that increasing recreational navigation may affect its ecological processes and functions, which may affect its recreational and tourism values, compromising local economies and livelihoods. The long-term impacts (1996-2011) of recreational navigation on seagrass benthic community structure were assessed by addressing the question of whether long-term effects of recreational navigation had a significant impact on seagrass community structure and on its benthic faunal assemblages. Findings evidenced: 1) a consistent spatio-temporal gradient in the ecological conditions of seagrasses across the scoured areas, with increased percent seagrass cover, density and canopy height, and seagrass benthic biodiversity with increasing distance from disturbed areas; 2) a decline in percent seagrass cover, and an increased macroalgal and cyanobacterial percent cover through time around the disturbed areas; 3) a significant shift in seagrass assemblage biodiversity as a response to boating that followed the intermediate disturbance hypothesis; 4) an adverse effect on the spatial distribution and survival of multiple benthic invertebrate taxa; and 5) a significant decline in cnidarians, echinoids, ophiuroids, holothurians, and gastropods, and an increase in polychaetes, platyhelminths, and hermit crabs, particularly in areas exposed to boating. Spatio-temporal variation in seagrass community structure explained the observed variation in benthic faunal assemblages. The long-term consequences on ecosystem functions and management needs are discussed to foster the conservation of seagrasses.

## Keywords

Benthic Faunal Communities, Community Trajectory, Ecological

## 1. Introduction

Seagrasses form extensive meadows on unconsolidated sediments over shallow tropical and temperate waters. Tropical seagrass communities provide critical ecological services. They can significantly modify the physical, chemical, and geological properties of coastal areas [1] and constitute a fundamental source of nutrients [2], in support of coastal primary productivity [3] [4]. Organic matter and decaying seagrass roots initiate sulfate reduction and maintain the sulfur cycle [5]. Seagrasses also support a high biodiversity [6] [7], multi-species fishery resources [8] [9] [10], function as nursery habitat for juveniles of a myriad of commercially important species [11] [12] [13] [14], and provide foraging grounds for some threatened and endangered species [15] [16] [17] [18]. They constitute a critical steppingstone in the natural connectivity between terrestrial, estuarine, and coastal marine ecosystems [19] [20], fundamental for the conservation of coral reef communities [21] and fishery- and tourism-dependent community-based livelihoods.

Seagrasses also play a critical role in reducing the concentration of suspended particulate matter and land-based pollutants in the water column [22], function as a sink of dissolved nutrients [23] [24], damp wave action [25] [26] [27], contribute to reducing shoreline erosion [28] [29] [30], and minimize the impact of natural disasters such as hurricanes [31]. Furthermore, seagrasses play a vital role in filtering the effects of land-based source pollution on adjacent coastal ecosystems [32], and promote climate regulation through carbon dioxide (CO<sub>2</sub>) sequestration [4] [33] [34] [35]. They play an unequivocal role in supporting multiple ecosystem processes and services, contributing to coastal social-ecological resilience in the tropics [36] [37] [38] [39] [40], which is fundamental for the conservation and sustainability of community-based livelihoods and often weak economies of small island development states (SIDS).

Tropical seagrass meadows are threatened by multiple local-scale, regional- and global-scale anthropogenic factors. Local factors often include a combination of water pollution [41] [42], eutrophication [43] [44] [45], sewage discharges [43] [46], land-based source pollutants [47], catchment disturbance [48], sedimentation [49], dredging [50], turbidity [51] [52], unsustainable coastal development practices [53], trawling [54], gillnetting [55], scallop harvesting [56], and recreational navigation impacts [57] [58] [59]. Regional- and global-scale factors are often associated with climate change-related sea surface warming trends [60] [61] [62] [63] [64], ocean acidification [65] and extreme weather events, such as hurricanes [66] [67] [68]. Also, invasive species [67] [69] [70] [71] and other ecological surprises have also become a recent concern across Caribbean SIDS [72]. In combination, these factors may jeopardize seagrass eco-

logical benefits [37] [40], their socio-economic value [73], ecological resilience and persistence, as well as the socio-economic resilience of adjacent coastal human communities.

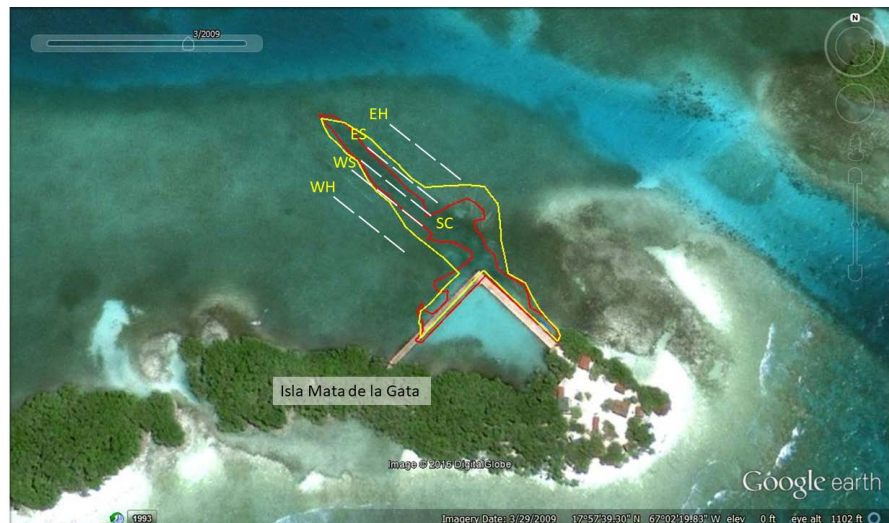
The usually calmer oceanographic conditions of shallow tropical seagrass meadows often attract many recreationists. Aquatic recreational activities may include navigation (*i.e.* power boating, jet skiing, parasailing, anchoring), sailing, kayaking, snorkeling, SCUBA diving, swimming, and trampling [74]-[79]. Most of the attention to recreational impacts on coastal communities has been put on SCUBA diving impacts on coral reefs [80] [81] [82]. However, there is limited information regarding recreational impacts on seagrass assemblages, particularly in the tropics. Vessel-generated wave action can resuspend sediments, enhance sediment-derived ammonia, and reduce water transparency over seagrasses [57]. Major landscape-level fragmentation was documented affecting *Posidonia australis* by vessel moorings and propeller scouring [77]. Widespread, dense seagrass scarring has been documented on shallow depths, near navigational channels, and around areas heavily frequented by boats [76] [83]. Physical disturbance on seagrasses can alter demersal faunal assemblages and can foster the blooming growth of cyanobacteria [84]. Even moderate seagrass trampling can create significant disturbances on demersal invertebrate assemblages [85] [86]. Also, dock shadows can significantly reduce seagrass biomass, affecting its productivity [87].

There is a growing concern that increasing recreational navigation impacts may affect the ecological processes and functions of seagrass habitats. In the long term, such effects could magnify potential climate change-related impacts on seagrass communities [88]. If the species and the natural environment are not appropriately conserved and protected under projected climate changes, recreational and tourism values might be lost, affecting local economies and livelihoods [67] [89]. This study assessed the long-term impacts (1996-2011) of power boat propeller scouring and anchoring on seagrass benthic community structure by addressing the question of whether long-term effects of recreational navigation had a significant impact on seagrass community structure and on its benthic faunal assemblages.

## 2. Methods

### 2.1. Study Site

This study was conducted at Mata de la Gata Island, off the fishing village of La Parguera, at the municipality of Lajas, within La Parguera Natural Reserve in southwestern Puerto Rico (Figure 1). Mata de la Gata is a 320 m-long × 40 m-wide key surrounded by mangrove and formed on top of a backreef coral rubble habitat and is highly frequented by recreational navigators, snorkelers, and beach enthusiasts. No carrying capacity or limits of acceptable change associated with the number of visitors or vessels arriving to the island are strictly enforced. Data were collected during 1996 and 2011 on seagrass communities adjacent to



**Figure 1.** Study site at Mata de la Gata Island, La Parguera Natural Reserve, Puerto Rico. Red polygon = scoured channel during 1996 (1784 m<sup>2</sup>); Yellow polygon = scoured channel during 2011 (2388 m<sup>2</sup>). SC = scoured channel; ES = eastern scoured edge (5 m); EH = eastern healthy (15 m); WS = western scoured edge (5 m); WH = western healthy (15 m). Aerial image source: Google Earth.

the recreational navigation scoured channel approaching Mata de la Gata Island's pier. Based on aerial imagery photointerpretation, there was a ~34% expansion in the spatial extent of the scoured channel between year 1993 (1783.85 m<sup>2</sup>) and 2010 (2387.77 m<sup>2</sup>). The scoured channel expanded to 2682 m<sup>2</sup> by 2022, which represents a ~50% increase in relation to 1996. There has always been a major concern regarding the magnitude of recreational navigation impacts on Mata de la Gata's seagrass ecosystems as recreational navigation has represented a major governance challenge within La Parguera Natural Reserve (**Figure 2**).

Sampling was conducted across five fixed sampling zones located within the scoured channel (SC), the eastern scoured edge of the seagrass stand within 5 m off the scoured channel (ES), the western scoured edge of the seagrass within 5 m off the scoured channel (WS), the eastern healthy seagrass at 15 m off the scoured channel (EH), and the western healthy seagrass at 15 m off the scoured channel (WH).

## 2.2. Sampling Design

Triplicate 10 × 1 m belt transects were sampled using a 1 m<sup>2</sup> quadrat subdivided in 100 replicate 10 × 10 cm sub-quadrats. Ten replicate quadrats were sampled per transect. Data were collected in 1996 and in 2011 on each zone to address seagrass benthic community structure. Data included seagrass species richness and percent coverage, as well as percent coverage of other components, including macroalgae, cyanobacteria, and open sandy substrate. *Thalassia testudinum* shoot density (#/m<sup>2</sup>) and canopy height (cm) were obtained from ten replicate haphazard counts determined from each transect using a 15 × 15 cm sub-quadrat. Seagrass community data were also used to calculate species richness (*S*), the



**Figure 2.** Example of uncontrolled recreational navigation impacts at Cayo Caracoles, La Parguera Natural Reserve, Puerto Rico, just east of Mata de la Gata Island. Excessive propeller wash, scouring and anchoring effects have resulted in the nearly total extirpation of nearly 11,000 m<sup>2</sup> of seagrass habitat, raising an increasing concern regarding the consequences of recreational navigational impacts to essential fish habitats within the natural reserve. Image source: Edwin Rodríguez-Sánchez (PR Department of Natural and Environmental Resources).

Shannon-Weaver diversity index ( $H'_n$ ), the Simpson's diversity index ( $1 - \lambda$ ), and the Pielou's evenness index ( $J'_n$ ).

Drop traps (0.5 × 0.5 m) were used in triplicates along each transect to sample benthic invertebrates using a 0.5 × 0.5 scooping net, with a maximum of ten replicate scoops per sample. Organisms were counted and identified to the lowest taxon possible, at least to the level of class. Fish counts were conducted in triplicate 10 × 10 m plots per zone and analyzed at the species level.

### 2.3. Statistical Analysis

All statistical tests were done through the Plymouth Routines in Multivariate Ecological Research (PRIMER) software v7.021 + PERMANOVA 1.0 [90] [91]. A lack of a significant difference in the spatio-temporal variation in seagrass benthic community structure among sampling sites in 1996 and 2011 was tested using a two-way crossed permutational analysis of variance (PERMANOVA), with time and zone (arranged by distance from the scoured navigational channel) as main factors for 9999 random permutations. A balanced experimental design and the data's lack of normality suit the strengths and limitations of this test. PERMANOVAs yielded the traditional Fisher's F-value, yet without assuming normal distributions [92]. Two-way tests were carried out in Bray Curtis dissimilarity space, a widely applied for biological assemblages [93] to understand the interacting factors that most explained variances in the community structure. A similar procedure was used to test spatio-temporal variation in *T. testudinum* shoot density and canopy height, and in benthic habitat's  $S$ ,  $H'_n$ ,  $1 - \lambda$ , and  $J'_n$ . Permutational distance-based tests for homogeneity of multivariate dispersions (PERMDISP) were done to measure spatio-temporal variation in benthic invertebrates and fish  $\sqrt{}$ -transformed  $\beta$ -diversity [94]. Principal compo-

ment ordination (PCO) was used to identify which benthic community components influenced spatio-temporal patterns based on  $\sqrt{\cdot}$ -transformed species abundances.

### 3. Results

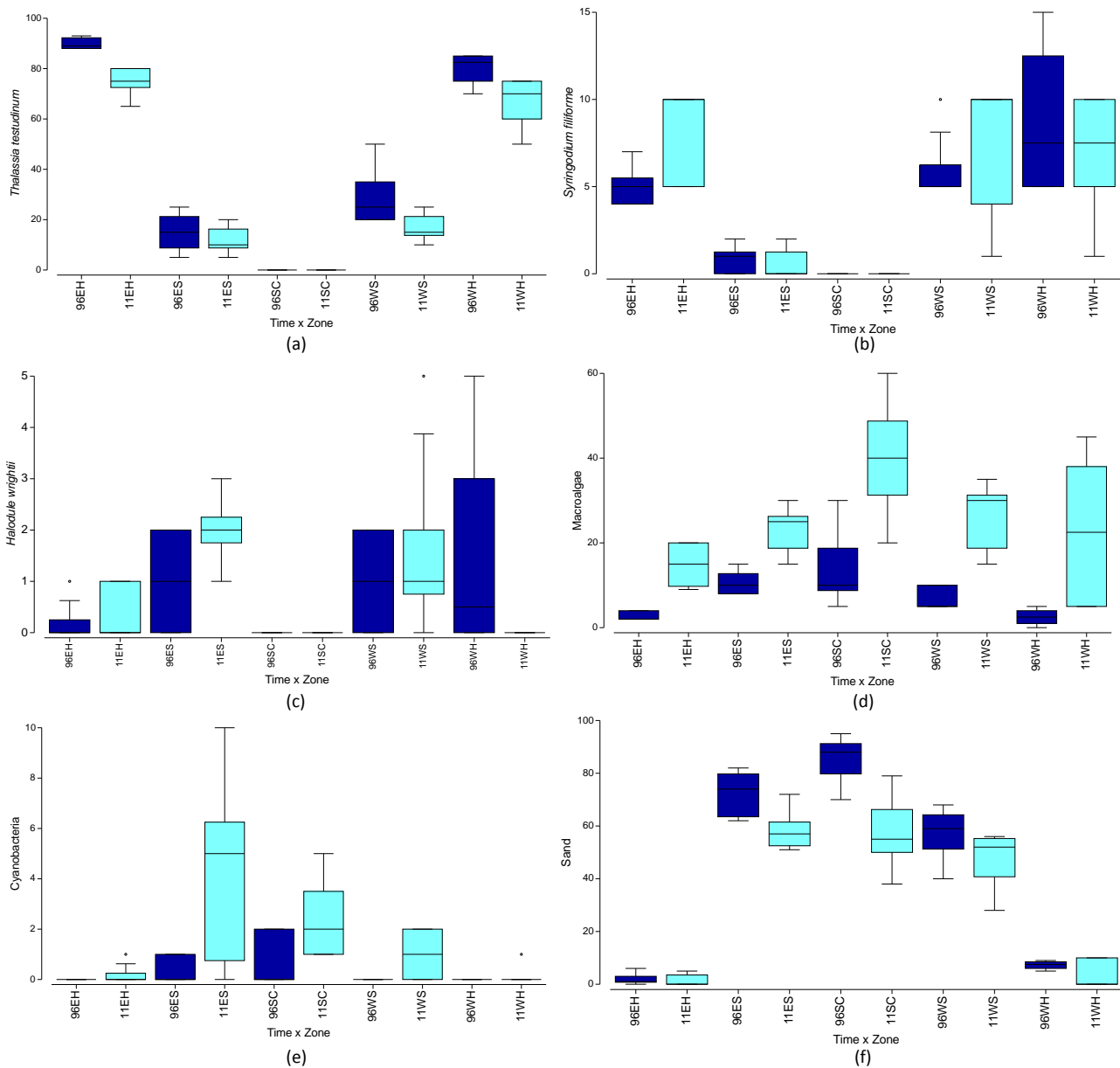
#### 3.1. Spatio-Temporal Patterns in Benthic Community Structure

There were significant spatio-temporal fluctuations in seagrass benthic community structure in time ( $p = 0.0421$ ), among zones ( $p < 0.0001$ ), and a significant time  $\times$  zone interaction ( $p < 0.0001$ ) (Table 1). Pairwise tests indicated significant spatio-temporal differences among all time  $\times$  zone combinations. *Thalassia testudinum* cover declined at EH zone from 90% in 1996 to 75% in 2011, and at WH zone from 80% to 67% (Figure 3(a)). Similarly, *T. testudinum* declined in ES from 15% to 12%, and from 29% to 17% in WS. No detectable percent cover of *T. testudinum* was documented at the scoured channel, but sporadic juvenile shoots were observed. Temporal variation in *T. testudinum* was significant ( $p = 0.0097$ ). Spatial patterns were also highly significant ( $p < 0.0001$ ), but there were no time  $\times$  zone interaction effects (Table 1).

**Table 1.** Two-way crossed permutational analysis of variance (PERMANOVA) of seagrass benthic community components.

Variable	2-way crossed PERMANOVA summary		
	Time	Zone	Time $\times$ Zone
Community structure	Pseudo-F = 3.99 <b><math>p = 0.0421</math></b> (ECV = 8.74)	Pseudo-F = 50.29 <b><math>p &lt; 0.0001</math></b> (ECV = 25.79)	Pseudo-F = 37.06 <b><math>p &lt; 0.0001</math></b> (ECV = 25.33)
<i>Thalassia testudinum</i>	Pseudo-F = 7.24 <b><math>p = 0.0097</math></b> (ECV = 0.75)	Pseudo-F = 774.8 <b><math>p &lt; 0.0001</math></b> (ECV = 13.24)	Pseudo-F = 1.01 $p = 0.4219$ (ECV = 0.05)
<i>Syringodium filiforme</i>	Pseudo-F = 0.17 $p = 0.6982$ (ECV = -0.75)	Pseudo-F = 52.12 <b><math>p &lt; 0.0001</math></b> (ECV = 9.24)	Pseudo-F = 0.44 $p = 0.7844$ (ECV = -1.37)
<i>Halodule wrightii</i>	Pseudo-F = 0.23 $p = 0.6325$ (ECV = -1.05)	Pseudo-F = 7.31 <b><math>p = 0.0002</math></b> (ECV = 4.76)	Pseudo-F = 2.11 $p = 0.0916$ (ECV = 2.83)
Macroalgae	Pseudo-F = 50.72 <b><math>p &lt; 0.0001</math></b> (ECV = 4.76)	Pseudo-F = 7.02 <b><math>p = 0.0002</math></b> (ECV = 2.62)	Pseudo-F = 1.89 $p = 0.1031$ (ECV = 1.43)
Cyanobacteria	Pseudo-F = 14.92 <b><math>p = 0.0004</math></b> (ECV = 4.50)	Pseudo-F = 6.17 <b><math>p = 0.0003</math></b> (ECV = 4.33)	Pseudo-F = 0.97 $p = 0.4373$ (ECV = -0.50)
Sand	Pseudo-F = 7.84 <b><math>p = 0.0071</math></b> (ECV = 2.99)	Pseudo-F = 33.82 <b><math>p = 0.0002</math></b> (ECV = 10.37)	Pseudo-F = 2.04 $p = 0.1103$ (ECV = 2.61)

Note: ECV =  $\sqrt{\cdot}$ -transformed estimates of components of variation; Degrees of freedom: Time (1, 48), Zone (4, 45), Time  $\times$  Zone (4, 45).



**Figure 3.** Summary of spatio-temporal variation in seagrass benthic community components percentage cover: (a) *Thalassia testudinum*; (b) *Syringodium filiforme*; (c) *Halodule wrightii*; (d) Macroalgae; (e) Cyanobacteria; and (f) Sand (open substrate). Navy blue = 1996; Light blue = 2011. For zone acronyms refer to **Figure 1**.

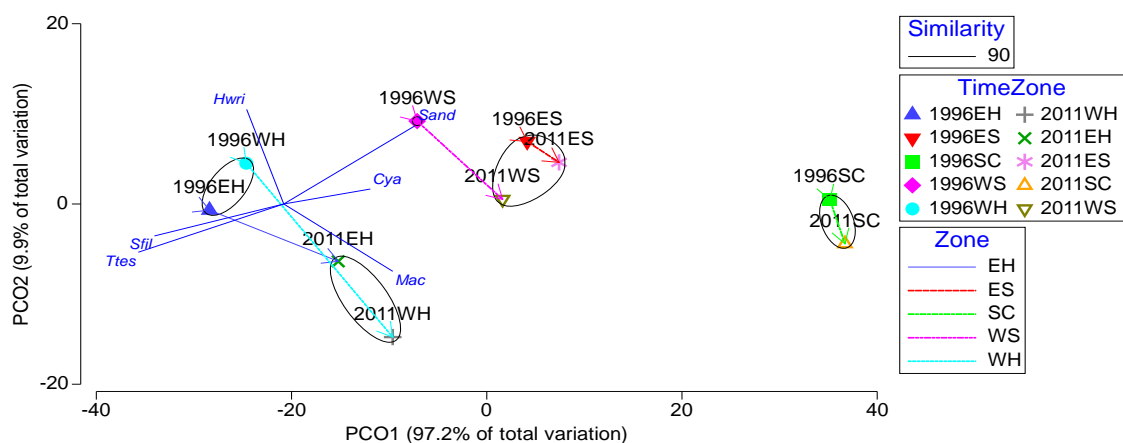
*Syringodium filiforme* cover increased at EH zone from 5% in 1996 to 8% in 2011, but slightly declined at WH zone from 8.8% to 6.8% (**Figure 3(b)**). Similarly, *S. filiforme* slightly declined in ES from 0.8% to 0.6% but increased from 6% to 7.2% in WS. No *S. filiforme* was documented on the scoured channel. Spatial variation among zones was highly significant ( $p < 0.0001$ ), but there was no significant temporal variation, neither time  $\times$  zone interaction effects (**Table 1**). *Halodule wrightii* cover slightly declined at EH zone from 0.2% in 1996 to 0% in 2011, and at WH zone from 1.5% to 0.4% (**Figure 3(c)**). There was no temporal variation in ES, with 1% during both sampling events, but a slight loss from 2%

to 1.6% was observed in WS. No *H. wrightii* was documented on the scoured channel. Spatial variation among zones was highly significant ( $p = 0.0002$ ), but there was no significant temporal variation, neither time  $\times$  zone interaction effects (Table 1).

Macroalgal cover, mostly brown algae *Dictyota* spp., increased at EH zone from 2.8% in 1996 to 14.8% in 2011, a 4.3-fold increase, and from 2.5% to 23% at WH, an 8.2-fold increase (Figure 3(d)). Macroalgae also increased in ES from 10.6% to 23%, a 1.2-fold increase, and from 7% to 26% in WS, a 2.7-fold increase. Macroalgae increased from 14% to 40% at the scoured channel, a 1.9-fold increase. Temporal increase in macroalgae was highly significant ( $p < 0.0001$ ). Spatial patterns were also highly significant ( $p = 0.0002$ ), but there were no time  $\times$  zone interaction effects (Table 1). Cyanobacteria were absent at EH and WH during 1996 but cover increased in 2011 to 0.2% at EH and to 0.17% in WH (Figure 3(e)). Cyanobacteria also increased in ES from 0.4% to 4.2%, a 9.5-fold increase. It was absent at WS during 1996, and cover was 1% in 2011. Cyanobacteria increased from 0.8% to 2.4% at the scoured channel, a 2-fold increase. Temporal increase in cyanobacteria was highly significant ( $p = 0.0004$ ). Spatial patterns were also highly significant ( $p = 0.0002$ ), but there were no time  $\times$  zone interaction effects (Table 1).

Open sand substrate cover slightly declined at EH from 2% in 1996 to 1.6% in 2011, and from 7.3% to 3.3% at WH (Figure 3(f)). Sand declined in ES from 72.2% to 58.2%, and from 57% to 47.2% in WS. Sand also declined from 85.2 to 57.6% at the scoured channel, mostly as a result from macroalgal colonization of open substrate. Temporal decline in open sand substrate was highly significant ( $p = 0.0071$ ). Spatial patterns were also highly significant ( $p = 0.0002$ ), but there were no time  $\times$  zone interaction effects (Table 1).

There was a significant modification in the trajectory of benthic seagrass community structure across all the surveyed zones, but particularly at WH, followed by EH, WS, and then ES, and SC (Figure 4). Zones EH and WH clustered



**Figure 4.** Principal coordinates ordination (PCO) analysis of the spatio-temporal variation in benthic seagrass community structure trajectory between 1996 and 2011. For zone acronyms refer to Figure 1.



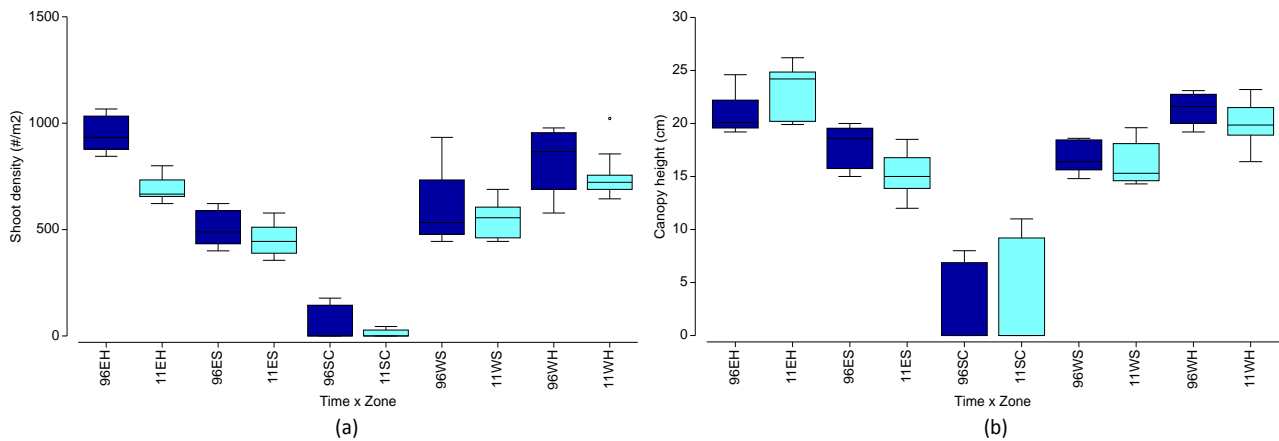
apart in 1996 from EH and WH in 2011. Most of this variation was explained by the higher percent cover of *T. testudinum*, *S. filiforme*, and *H. wrightii* during 1996, and the combination of declining seagrass cover and increased macroalgal cover (mostly *Dictyota* spp.) during 2011. Zone WS constituted an independent cluster in 1996, largely dominated by low seagrass cover and a high cover of open sand bottom. However, in 2011 WS clustered with ES due to increased cover by macroalgae and cyanobacteria. SC zone in 1996 and 2011 clustered together due to dominance by open sand substrate. However, there was also a trend of increased macroalgae and cyanobacteria. The combination of long-term seagrass cover loss and the colonization of open sand substrates by macroalgae and cyanobacteria were the predominant trajectory and were spatially correlated to the proximity of surveyed areas to the shallow scoured navigation channel to Mata de la Gata Island.

SIMPER test showed that *T. testudinum* was the dominant component at EH (48% contribution) and WH (47% contribution), while sand was the dominant component at ES (37%), WS (31%), and SC (54%). *Thalassia testudinum* explained the observed difference in seagrass assemblage dominance in 50% of the potential comparisons of surveyed zones, mostly due to its dominance on healthy zones. Sand explained 40% of the spatial variation among zones, particularly, due to its dominance at SC, ES, and WS. *Syringodium filiforme* explained most of the observed differences between ES and WS. Sand (34%), followed by *T. testudinum* (27%), explained most of the benthic assemblages across all zones combined in 1996, while increasing macroalgae (mostly *Dictyota* spp.) (29%) and declining *T. testudinum* (28%) explained most of the benthic assemblages in 2011. Increased macroalgae (27%) and cyanobacteria (21%), and declining sand (21%) explained most of the observed temporal variation in seagrass assemblages between 1996 and 2011.

### 3.2. *Thalassia testudinum* Shoot Density and Canopy Height

*Thalassia testudinum* shoot density slightly declined at EH from 951 shoots/m<sup>2</sup> in 1996 to 693 shoots/m<sup>2</sup> in 2011, and from 822 to 759 shoots/m<sup>2</sup> at WH (Figure 5(a)). Shoot density also showed a slight decline at ES from 507 to 453 shoots/m<sup>2</sup>, and from 613 to 547 shoots/m<sup>2</sup> in WS. Sporadic juvenile shoots were observed at the SC and declined from 62 to 13 shoots/m<sup>2</sup>. Spatial variation in *T. testudinum* shoot density were highly significant ( $p < 0.0001$ ), but there was no significant temporal variation, neither time  $\times$  zone interaction effects (Table 2).

*Thalassia testudinum* canopy height at EH averaged 21 cm in 1996 and 23 cm in 2011, and shifted from 21.4 cm in 1996 to 20 cm in 2011 at WH (Figure 5(b)). Canopy height showed a slight decline at ES from 17.8 to 15.2 cm, and from 16.8 to 16.3 cm in WS. Canopy height on sporadic shoots on the vessel disturbed channel at SC averaged 2.9 cm in 1996 and 3.9 cm in 2011, showing high consistency. Spatial variation in *T. testudinum* canopy height were highly significant ( $p < 0.0001$ ), but there was no significant temporal variation, neither time  $\times$  zone interaction effects (Table 2).



**Figure 5.** Spatio-temporal variation in *Thalassia testudinum*: (a) Shoot density (#/m<sup>2</sup>); and (b) Canopy height (cm). Navy blue = 1996; Aquamarine = 2011. For zone acronyms refer to **Figure 1**.

**Table 2.** Two-way crossed permutational analysis of variance (PERMANOVA) of *Thalassia testudinum* shoot density and canopy height.

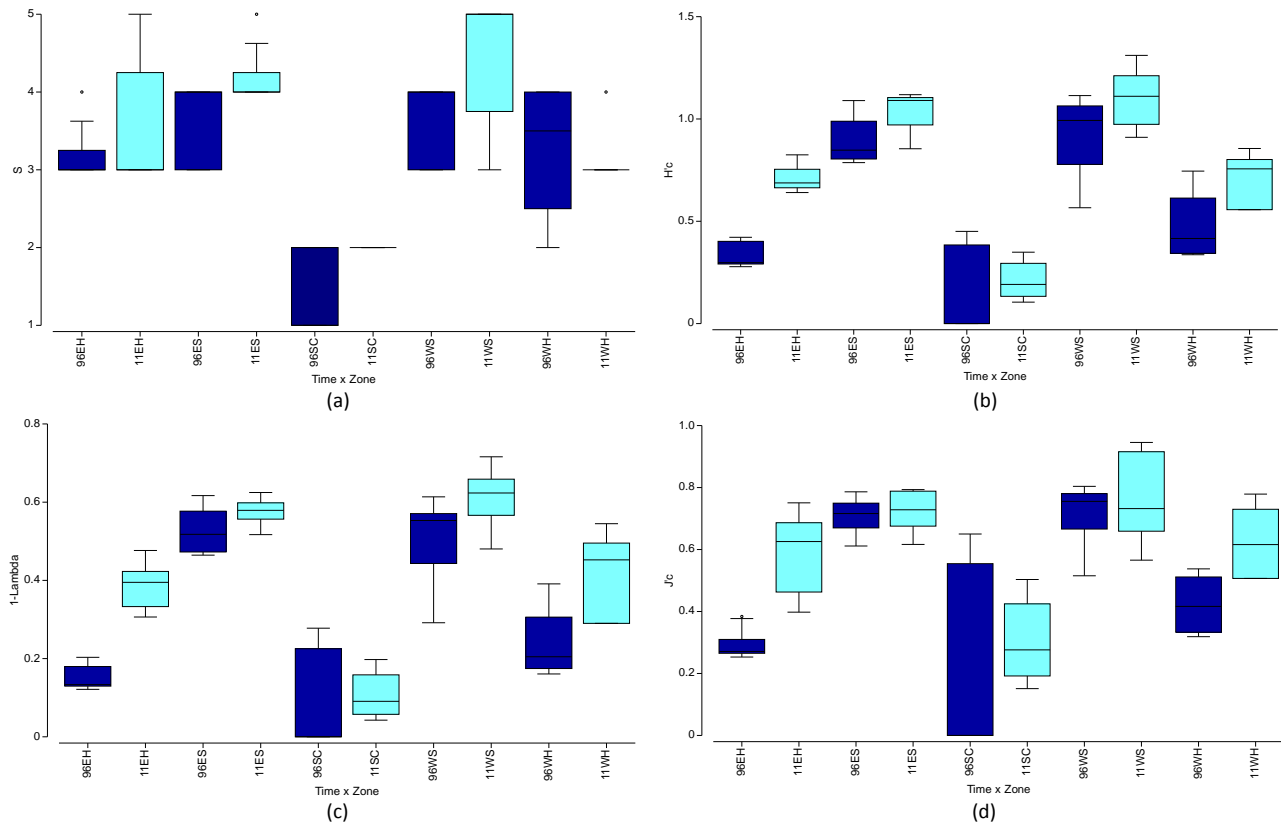
Variable	2-way crossed PERMANOVA summary		
	Time	Zone	Time × Zone
<i>T. testudinum</i> shoot density (#/m <sup>2</sup> )	Pseudo-F = 0.56 <i>p</i> = 0.4876 (ECV = -2.66)	Pseudo-F = 22.71 <b><i>p</i> &lt; 0.0001</b> (ECV = 29.68)	Pseudo-F = 0.25 <i>p</i> = 0.9548 (ECV = -7.81)
<i>T. testudinum</i> canopy height (cm)	Pseudo-F = 0.005 <i>p</i> = 0.9750 (ECV = -2.94)	Pseudo-F = 19.38 <b><i>p</i> &lt; 0.0001</b> (ECV = 19.95)	Pseudo-F = 0.06 <i>p</i> = 0.9977 (ECV = -6.38)

Note: ECV =  $\sqrt{}$ -transformed estimates of components of variation; Degrees of freedom: Time (1, 48), Zone (4, 45), Time × Zone (4, 45).

### 3.3. Spatio-Temporal Patterns in Seagrass Benthic Assemblage Diversity

Seagrass benthic assemblages showed significant spatio-temporal fluctuations because of chronic stress associated with recreational navigation and with the widespread colonization of macroalgae on open bottom gaps. Seagrass species richness at EH increased from 3.2 in 1996 to 3.6 in 2011, but slightly declined at WH from 3.25 to 3.17 (**Figure 6(a)**). Species richness increased from 3.6 to 4.2 at ES, from 3.6 to 4.4 at WS, and from 1.4 to 2.0 at SC. Temporal increase in species richness was significant (*p* = 0.0126) (**Table 3**). The spatial variation was highly significant (*p* < 0.0001), with a pattern showing higher species richness on areas of moderate navigational disturbance (ES, WS), in comparison to areas of lower disturbance and seagrass dominance (EH, WH), and areas of chronic severe navigation disturbance (SC). There were no significant time × zone interaction effects.

Shannon’s species diversity index ( $H'_c$ ) at EH increased from 0.3377 in 1996 to 0.7109 in 2011, and from 0.4784 to 0.7139 at WH (**Figure 6(b)**).  $H'_c$  increased from 0.8980 to 1.0346 at ES, from 0.9138 to 1.1010 at WS, and from 0.1626 to



**Figure 6.** Spatio-temporal variation in seagrass benthic assemblage diversity indices: (a) Species richness ( $S$ ); (b) Shannon's species diversity index ( $H'_c$ ); (c) Simpson's species diversity index ( $1 - \lambda$ ); and (d) Pielou's species evenness index ( $J'_c$ ); C Navy blue = 1996; Aquamarine = 2011. For zone acronyms refer to **Figure 1**.

**Table 3.** Two-way crossed permutational analysis of variance (PERMANOVA) of seagrass benthic assemblage diversity.

Variable	2-way crossed PERMANOVA summary		
	Time	Zone	Time $\times$ Zone
Species richness ( $S$ )	Pseudo-F = 7.01 <b><math>p = 0.0126</math></b> (ECV = 0.30)	Pseudo-F = 22.47 <b><math>p &lt; 0.0001</math></b> (ECV = 0.90)	Pseudo-F = 0.73 $p = 0.5777$ (ECV = -0.14)
$H'_c$ – Shannon's species diversity index	Pseudo-F = 22.13 <b><math>p &lt; 0.0001</math></b> (ECV = 0.14)	Pseudo-F = 53.14 <b><math>p &lt; 0.0001</math></b> (ECV = 0.34)	Pseudo-F = 1.67 $p = 0.1830$ (ECV = 0.05)
$1 - \lambda$ – Simpson's species diversity index	Pseudo-F = 21.34 <b><math>p = 0.0002</math></b> (ECV = 0.08)	Pseudo-F = 48.03 <b><math>p &lt; 0.0001</math></b> (ECV = 0.19)	Pseudo-F = 2.65 <b><math>p = 0.0494</math></b> (ECV = 0.05)
$J'_c$ – Pielou's species evenness index	Pseudo-F = 2.73 $p = 0.1168$ (ECV = 0.03)	Pseudo-F = 18.70 <b><math>p &lt; 0.0001</math></b> (ECV = 0.14)	Pseudo-F = 7.36 <b><math>p = 0.0005</math></b> (ECV = 0.12)

Note: ECV =  $\sqrt{}$ -transformed estimates of components of variation; Degrees of freedom: Time (1, 48), Zone (4, 45), Time  $\times$  Zone (4, 45).

0.2127 at SC. Both, the temporal increase in  $H'_c$  and the observed spatial variation were highly significant ( $p < 0.0001$ ) (**Table 3**). There were no significant time

× zone interaction effects. Observed patterns suggest increased  $H'_c$  with moderate navigation disturbance, and lower values under severe, chronic navigation disturbance.

Simpson's species diversity index ( $1 - \lambda$ ) at EH increased from 0.1524 in 1996 to 0.3849 in 2011, and from 0.2403 to 0.4209 at WH (**Figure 6(c)**).  $1 - \lambda$  increased from 0.5276 to 0.5760 at ES, from 0.5018 to 0.6109 at WS, and from 0.0971 to 0.1077 at SC. Both, the temporal increase in  $1 - \lambda$  ( $p = 0.0002$ ) and the observed spatial variation ( $p < 0.0001$ ) were highly significant (**Table 3**). There was also a significant time × zone interaction effect ( $p = 0.0494$ ). Observed patterns also suggest increased  $1 - \lambda$  with moderate navigation disturbance, and lower values under severe, chronic navigation disturbance.

Pielou's evenness index ( $J'_c$ ) at EH increased from 0.2924 in 1996 to 0.5847 in 2011, and from 0.4223 to 0.6257 at WH (**Figure 6(d)**).  $J'_c$  increased from 0.7081 to 0.7240 at ES, and from 0.7126 to 0.7678 at WS, but declined from 0.5863 to 0.3069 at SC due to high macroalgal colonization during 2011. However, temporal variation in  $J'_c$  was not significant, though spatial variation ( $p < 0.0001$ ) was highly significant (**Table 3**). There were no significant time × zone interaction effects.

### 3.4. Spatio-Temporal Patterns in Seagrass Demersal Faunal Assemblages

Seagrass demersal faunal community structure showed a highly significant temporal variation between years 1996 and 2011 ( $p = 0.0133$ ), spatial variation among zones ( $p < 0.0001$ ), and a highly significant time × zone interaction effect ( $p < 0.0001$ ) (**Table 4**). This interaction was the most significant factor explaining observed variation in benthic invertebrate community structure. Scleractinian coral density showed a significant spatial decline with increasing proximity to SC ( $p = 0.0030$ ), but no temporal or interaction effects (**Figure 7, Table 4**). Other cnidarians showed significant temporal ( $p = 0.0073$ ) and spatial decline ( $p < 0.0001$ ) with increasing boating disturbance, but no significant interactions. Echinoids showed a highly significant temporal ( $p < 0.0001$ ) and spatial decline ( $p < 0.0001$ ), and a significant time × zone interaction ( $p = 0.0032$ ). There was also a significant temporal ( $p = 0.0031$ ) and spatial decline ( $p < 0.0001$ ) in ophiuroids, and a marginally significant time × zone interaction ( $p = 0.0569$ ). Holothuroids exhibited a highly significant temporal ( $p < 0.0001$ ) and spatial decline ( $p < 0.0001$ ), and a significant time × zone interaction ( $p < 0.0001$ ).

Gastropods displayed a significant temporal increase ( $p = 0.0133$ ) and significantly higher densities with increasing proximity to SC ( $p < 0.0001$ ), and a significant time × zone interaction ( $p = 0.0002$ ) (**Figure 7, Table 4**). Bivalves showed a significant spatial increase in density with increasing proximity to SC ( $p < 0.0001$ ), but no temporal or interaction effects. Polyplacophorans showed a significant spatial increase in density with increasing proximity to SC ( $p < 0.0001$ ), but no temporal effects. Time × zone interaction was also significant ( $p = 0.0010$ ). Polychaetes presented a significant temporal increase ( $p = 0.0423$ ) and

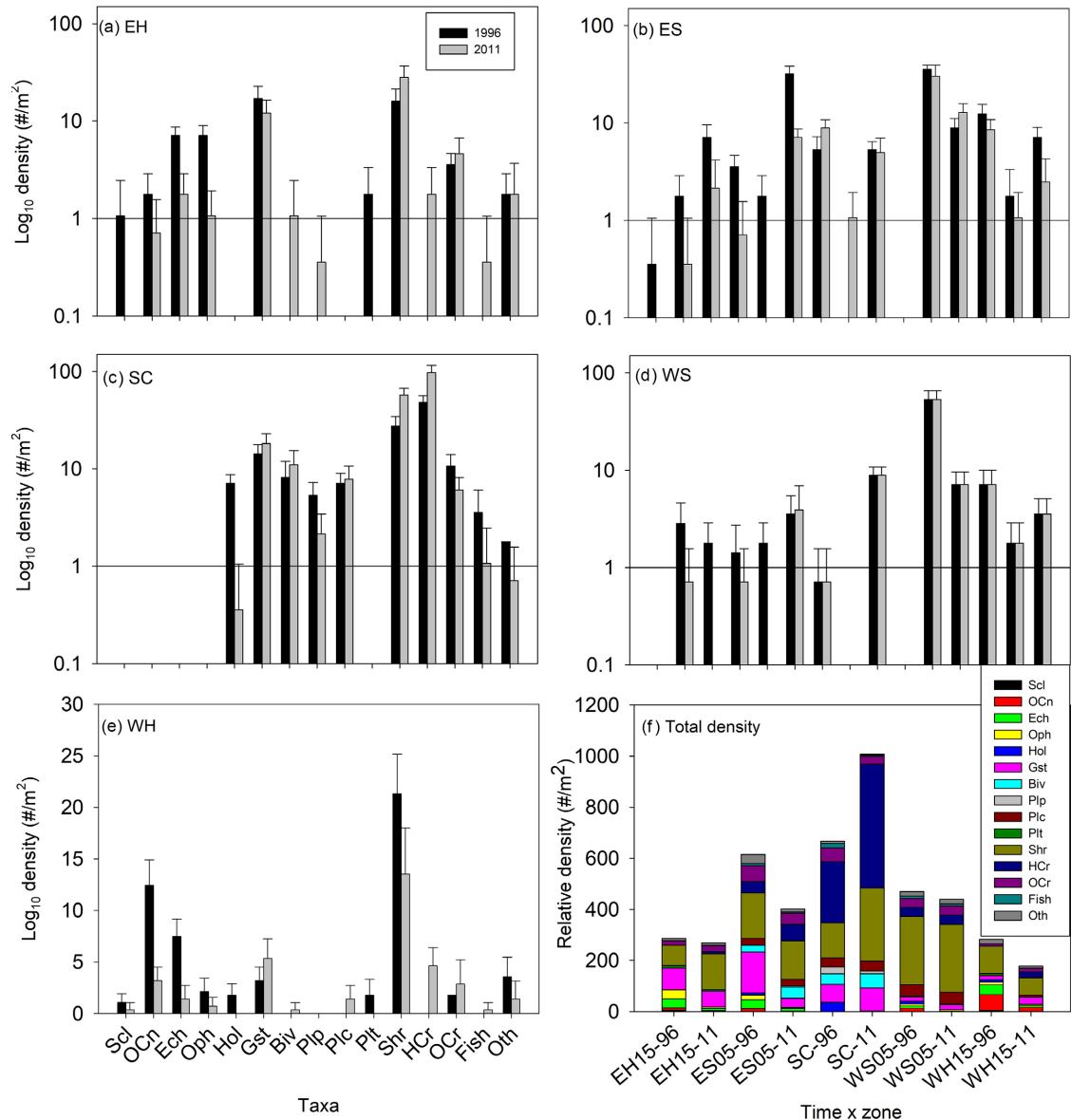
**Table 4.** Two-way crossed permutational analysis of variance (PERMANOVA) of sea-grass demersal faunal assemblages.

Variable	2-way crossed PERMANOVA summary		
	Time	Zone	Time × Zone
Community structure	Pseudo-F = 4.61 <b><i>p</i> = 0.0133</b> (ECV = 9.56)	Pseudo-F = 24.61 <b><i>p</i> &lt; 0.0001</b> (ECV = 23.42)	Pseudo-F = 18.09 <b><i>p</i> &lt; 0.0001</b> (ECV = 23.69)
Scleractinians (Scl)	Pseudo-F = 1.75 <i>p</i> = 0.1879 (ECV = 2.37)	Pseudo-F = 5.31 <b><i>p</i> = 0.0030</b> (ECV = 8.99)	Pseudo-F = 0.81 <i>p</i> = 0.5265 (ECV = -2.65)
Other cnidarians (OCn)	Pseudo-F = 7.84 <b><i>p</i> = 0.0073</b> (ECV = 7.37)	Pseudo-F = 15.17 <b><i>p</i> &lt; 0.0001</b> (ECV = 16.77)	Pseudo-F = 1.40 <i>p</i> = 0.2524 (ECV = 3.99)
Echinoids (ECH)	Pseudo-F = 22.87 <b><i>p</i> &lt; 0.0001</b> (ECV = 11.74)	Pseudo-F = 34.79 <b><i>p</i> &lt; 0.0001</b> (ECV = 23.07)	Pseudo-F = 4.56 <b><i>p</i> = 0.0032</b> (ECV = 10.59)
Ophiuroids (Oph)	Pseudo-F = 9.69 <b><i>p</i> = 0.0031</b> (ECV = 10.05)	Pseudo-F = 8.86 <b><i>p</i> &lt; 0.0001</b> (ECV = 15.12)	Pseudo-F = 2.50 <i>p</i> = 0.0569 (ECV = 9.35)
Holothurians (Hol)	Pseudo-F = 36.02 <b><i>p</i> &lt; 0.0001</b> (ECV = 16.05)	Pseudo-F = 10.84 <b><i>p</i> &lt; 0.0001</b> (ECV = 13.25)	Pseudo-F = 6.88 <b><i>p</i> &lt; 0.0001</b> (ECV = 14.71)
Gastropods (Gst)	Pseudo-F = 4.74 <b><i>p</i> = 0.0133</b> (ECV = 3.93)	Pseudo-F = 21.74 <b><i>p</i> &lt; 0.0001</b> (ECV = 14.62)	Pseudo-F = 4.55 <b><i>p</i> = 0.0002</b> (ECV = 8.56)
Bivalves (Blv)	Pseudo-F = 2.31 <i>p</i> = 0.1247 (ECV = 3.07)	Pseudo-F = 42.86 <b><i>p</i> &lt; 0.0001</b> (ECV = 27.45)	Pseudo-F = 0.95 <i>p</i> = 0.4518 (ECV = -1.39)
Polyplacophorans (Plp)	Pseudo-F = 1.32 <i>p</i> = 0.2610 (ECV = 1.27)	Pseudo-F = 27.19 <b><i>p</i> &lt; 0.0001</b> (ECV = 18.18)	Pseudo-F = 4.53 <b><i>p</i> = 0.0010</b> (ECV = 9.44)
Polychaetes (Plc)	Pseudo-F = 3.76 <b><i>p</i> = 0.0423</b> (ECV = 2.95)	Pseudo-F = 98.94 <b><i>p</i> &lt; 0.0001</b> (ECV = 27.79)	Pseudo-F = 4.31 <b><i>p</i> = 0.0014</b> (ECV = 7.23)
Platyhelminthes (Plt)	Pseudo-F = 11.65 <b><i>p</i> = 0.0017</b> (ECV = 7.40)	Pseudo-F = 4.37 <b><i>p</i> = 0.0049</b> (ECV = 6.58)	Pseudo-F = 4.37 <b><i>p</i> = 0.0045</b> (ECV = 9.30)
Shrimps (Shr)	Pseudo-F = 2.51 <i>p</i> = 0.1099 (ECV = 1.54)	Pseudo-F = 23.54 <b><i>p</i> &lt; 0.0001</b> (ECV = 9.40)	Pseudo-F = 7.29 <b><i>p</i> &lt; 0.0001</b> (ECV = 7.02)
Hermit crabs (HCr)	Pseudo-F = 34.56 <b><i>p</i> &lt; 0.0001</b> (ECV = 11.20)	Pseudo-F = 99.04 <b><i>p</i> &lt; 0.0001</b> (ECV = 30.27)	Pseudo-F = 15.21 <b><i>p</i> &lt; 0.0001</b> (ECV = 16.30)
Other crabs (OCr)	Pseudo-F = 0.70 <i>p</i> = 0.4608 (ECV = -1.14)	Pseudo-F = 10.98 <b><i>p</i> &lt; 0.0001</b> (ECV = 10.37)	Pseudo-F = 1.02 <i>p</i> = 0.4049 (ECV = 0.61)

Continued

Demersal fish (Fish)	Pseudo-F = 0.20 $p = 0.6707$ (ECV = -3.43)	Pseudo-F = 5.49 $p = 0.0015$ (ECV = 12.83)	Pseudo-F = 1.03 $p = 0.4063$ (ECV = 1.55)
Other taxa (Oth)	Pseudo-F = 7.70 $p = 0.0081$ (ECV = 9.51)	Pseudo-F = 2.92 $p = 0.0296$ (ECV = 8.05)	Pseudo-F = 0.99 $p = 0.4249$ (ECV = -0.76)

Note: ECV =  $\sqrt{\lambda}$ -transformed estimates of components of variation; Degrees of freedom: Time (1, 48), Zone (4, 45), Time  $\times$  Zone (4, 45).

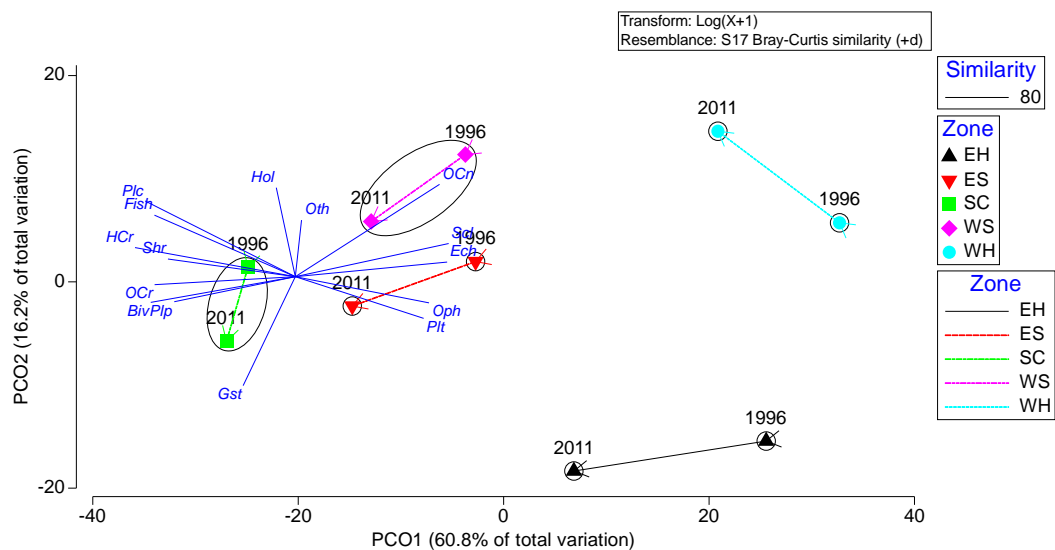


**Figure 7.** Spatio-temporal variation in density of benthic community assemblages: (a) EH; (b) ES; (c) SC; (d) WS; (e) WH; and (f) Relative density of all taxa. Scl = scleractinian corals; OCn = other cnidarians; Ech = echinoids; Oph = ophiuroids; Hol = holothurians; Gst = gastropods; Biv = bivalves; Plp = polyplacophorans; Plc = polychaetes; Plt = platyhelminths; Shr = shrimps; HCr = hermit crabs; OCr = other crabs; Fish = demersal fishes; Oth = other taxa. For zone acronyms refer to **Figure 1**.

significantly higher densities with increasing proximity to SC ( $p < 0.0001$ ), and a significant time  $\times$  zone interaction ( $p = 0.0014$ ). Platyhelminthes exhibited a significant temporal decline ( $p = 0.0017$ ) and significantly higher densities with increasing distance from SC ( $p = 0.0049$ ), and a significant time  $\times$  zone interaction ( $p = 0.0045$ ).

Shrimps showed significantly higher densities at SC and WS ( $p < 0.0001$ ), but no significant temporal effects (Figure 7, Table 4). There was a significant time  $\times$  zone interaction ( $p < 0.0001$ ). Hermit crabs displayed a highly significant temporal increase ( $p < 0.0001$ ) and significantly higher densities with increasing proximity to SC ( $p < 0.0001$ ), and a significant time  $\times$  zone interaction ( $p < 0.0001$ ). Other crabs showed a significant increase in density with increased proximity to disturbed zones by recreational boating ( $p < 0.0001$ ). There were non-significant temporal and interaction effects. Demersal fish also showed a significant increase in density with increased proximity to disturbed zones by recreational boating ( $p = 0.0020$ ). Non-significant temporal and interaction effects were documented. Other taxa showed a significant temporal decline ( $p = 0.0081$ ) and a significant increase in zones exposed to recreational boating disturbance ( $p = 0.0296$ ). However, there were non-significant interaction effects.

PCO analysis of benthic faunal assemblage trajectories reflect a consistent spatio-temporal trend of change, with particularly significant temporal fluctuations in ES, EH and WH. Observed benthic faunal assemblage trajectory change in ES and EH was largely explained by declining scleractinian coral and echinoid density from 1996 to 2011, and by increasing density of ophiuroids and platyhelminthes in 2011 (Figure 8). Also, the decline in holothurians and in other taxa explained most of the observed variation at WH. Temporal variation at SC was mostly explained by increased density of gastropods, bivalves, polyplacophorans, and of other crabs. Interestingly, boating disturbance at the SC explained



**Figure 8.** Principal coordinates ordination (PCO) analysis of the spatio-temporal variation in benthic sea-grass faunal community structure trajectory between 1996 and 2011. For zone acronyms refer to Figure 1.

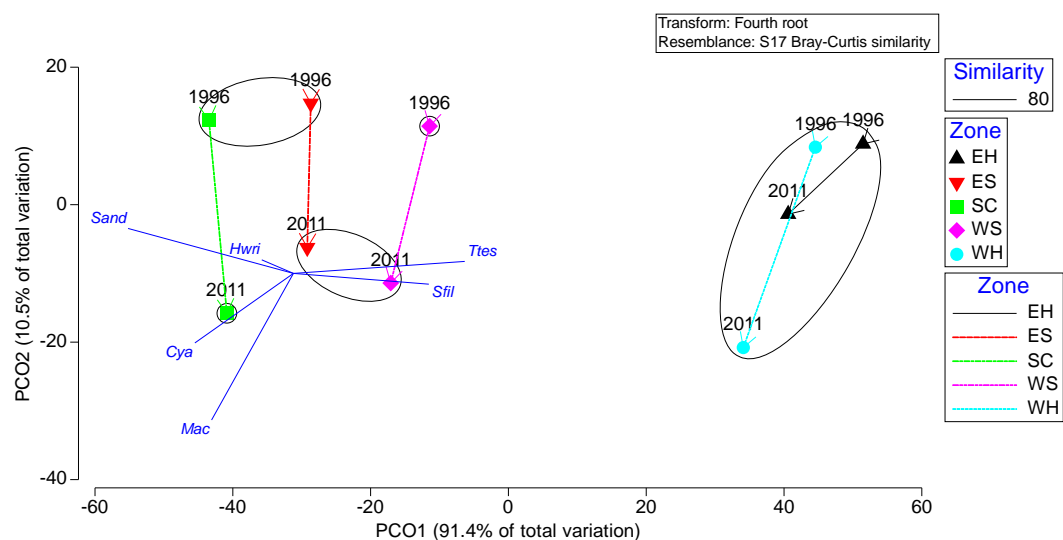
most of the observed spatial patterns of benthic faunal assemblages, with some taxa such as gastropods, bivalves, polyplacophorans, shrimps, hermit crabs, other crabs, polychaetes, and demersal fish being more abundant in comparison to healthy seagrasses with denser canopies.

Spatio-temporal fluctuation in seagrass benthic community structure was also a significant driver of spatio-temporal variation in benthic faunal assemblages. A PCO test showed that increased macroalgae, cyanobacteria and open sand substrate explained most of the observed spatio-temporal variation in faunal assemblages (Figure 9). Also, spatial variation in *T. testudinum* and *S. filiforme* explained observed clustering in EH and WH faunal assemblages, in comparison to other zones.

### 3.5. Spatio-Temporal Patterns in Seagrass Demersal Faunal Assemblage Biodiversity

A benthic invertebrates  $\beta$ -diversity test following a PERMDISP analysis showed highly significant spatio-temporal variation ( $F = 8.32$ ; d.f. = 9.40;  $p(\text{perm}) < 0.0001$ ). There were significant differences during 1996 in benthic invertebrates  $\beta$ -diversity between SC and EH ( $t = 5.01$ ,  $p = 0.0091$ ), WS ( $t = 5.10$ ,  $p = 0.0082$ ), and WH ( $t = 2.06$ ,  $p = 0.0071$ ). There was no significant difference between SC and ES during 1996 ( $t = 0.60$ ,  $p = 0.6466$ ). Differences between EH and ES were only marginally significant ( $t = 2.74$ ,  $p = 0.0569$ ), and non-significant between EH and WS ( $t = 0.39$ ,  $p = 0.6175$ ), and between EH and WH ( $t = 0.35$ ,  $p = 0.6975$ ). Differences were also significant between ES and WS ( $t = 2.98$ ,  $p = 0.0447$ ), but non-significant between ES and WH ( $t = 1.46$ ,  $p = 0.1902$ ), and between WS and WH ( $t = 0.59$ ,  $p = 0.5535$ ).

There were significant differences during 2011 in benthic invertebrates  $\beta$ -diversity between SC and EH ( $t = 5.06$ ,  $p = 0.0090$ ), ES ( $t = 2.63$ ,  $p = 0.0310$ ), WS ( $t$



**Figure 9.** Principal coordinates ordination (PCO) analysis of the spatio-temporal variation in benthic seagrass faunal community structure trajectory between 1996 and 2011 as a function of variation in seagrass assemblages. For zone acronyms refer to Figure 1.



= 4.00,  $p = 0.0142$ ), and WH ( $t = 3.30$ ,  $p = 0.0095$ ). Differences between EH and ES were also significant ( $t = 3.28$ ,  $p = 0.0166$ ), and WS ( $t = 3.24$ ,  $p = 0.0243$ ), and non-significant between EH and WH ( $t = 1.75$ ,  $p = 0.1620$ ). Differences were non-significant between ES and WS ( $t = 0.42$ ,  $p = 0.7048$ ), between ES and WH ( $t = 1.40$ ,  $p = 0.1799$ ), and between WS and WH ( $t = 1.23$ ,  $p = 0.2644$ ).

Within-zone temporal variation in benthic invertebrates  $\beta$ -diversity was significant within SC ( $t = 2.29$ ,  $p = 0.0080$ ), within EH ( $t = 3.52$ ,  $p = 0.0166$ ), only marginal within ES ( $t = 2.66$ ,  $p = 0.0556$ ), and non-significant within WS ( $t = 0.25$ ,  $p = 0.7556$ ), and within WH ( $t = 1.51$ ,  $p = 0.1435$ ). Observed patterns showed significant spatio-temporal variation in benthic invertebrates'  $\beta$ -diversity with increased impacts through time in recreational navigation.

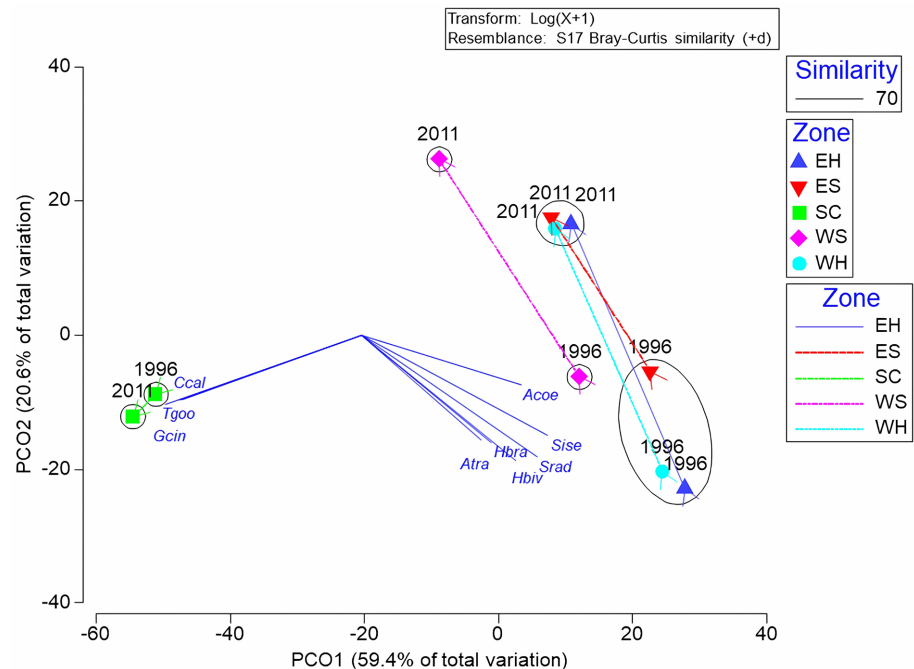
Taxa richness at EH averaged 7.6 taxa per count in 1996 and 6.8 in 2011, and 8.6 and 9.2, respectively at WH. It averaged 9.2 taxa per count in 1996 and 11.4 in 2011 at ES, and 10.2 and 7.8, respectively at WS. Taxa richness averaged 9.8 per count in 1996 and 7.8 in 2011 at SC.  $H'_n$  at EH averaged 2.0048 in 1996 and 1.8612 in 2011, and 2.1190 and 2.1932, respectively at WH. Taxa richness showed a significant decline between 1996 and 2011 ( $p = 0.0027$ ), as well as a significant spatial increase in areas subjected to recreational boating disturbance in relation to denser seagrass canopies ( $p = 0.0009$ ) (Table 5). There was also a highly significant time  $\times$  zone interaction ( $p < 0.0001$ ).

The 1996 mean  $H'_n$  at ES was 2.4010 and 2.1768 in 2011, and 2.2828 and 2.0092, respectively at WS.  $H'_n$  averaged 2.2532 in 1996 and 1.9904 in 2011 at SC.  $J'_n$  at EH averaged 0.9828 in 1996 and 0.9824 in 2011, and 0.9879 and 0.9917, respectively at WH.  $H'_n$  presented also significant decline between 1996 and 2011 ( $p = 0.0021$ ), as well as a significant spatial increase in areas subjected to recreational boating disturbance ( $p = 0.0014$ ) (Table 5). There was also a highly significant time  $\times$  zone interaction ( $p < 0.0001$ ). The 1996 mean  $J'_n$  at ES was 0.9883 and 0.9885 in 2011, and 0.9832 and 0.9804, respectively at WS.

**Table 5.** Two-way crossed permutational analysis of variance (PERMANOVA) of seagrass benthic faunal assemblage sdiversity.

Variable	2-way crossed PERMANOVA summary		
	Time	Zone	Time $\times$ Zone
Species/taxa richness ( $S$ )	Pseudo-F = 9.46 <b><math>p = 0.0027</math></b> (ECV = 1.84)	Pseudo-F = 5.60 <b><math>P = 0.0009</math></b> (ECV = 1.44)	Pseudo-F = 6.50 <b><math>p &lt; 0.0001</math></b> (ECV = 1.85)
$H'_c$ – Shannon's species diversity index	Pseudo-F = 10.10 <b><math>p = 0.0021</math></b> (ECV = 0.67)	Pseudo-F = 5.37 <b><math>p = 0.0014</math></b> (ECV = 0.69)	Pseudo-F = 6.53 <b><math>p &lt; 0.0001</math></b> (ECV = 0.90)
$J'_c$ – Pielou's species evenness index	Pseudo-F = 5.91 <b><math>p = 0.0227</math></b> (ECV = 0.03)	Pseudo-F = 6.24 <b><math>p = 0.0010</math></b> (ECV = 0.04)	Pseudo-F = 10.83 <b><math>p &lt; 0.0001</math></b> (ECV = 0.06)

Note: ECV =  $\sqrt{\lambda}$ -transformed estimates of components of variation; Degrees of freedom: Time (1, 48), Zone (4, 45), Time  $\times$  Zone (4, 45).



**Figure 10.** Principal coordinates ordination (PCO) analysis of the spatio-temporal variation in demersal fish community structure trajectory between 1996 and 2011. For zone acronyms refer to **Figure 1**.

$J'_n$  averaged 0.9877 in 1996 and 0.9748 in 2011 at SC.  $J'_n$  demonstrated a significant temporal decline ( $p = 0.0227$ ), as well as a significant spatial increase in areas subjected to recreational boating disturbance ( $p = 0.0010$ ) (**Table 5**). There was also a highly significant time  $\times$  zone interaction ( $p = 0.0001$ ).

Observed temporal trajectories in demersal fish community structure across the EH, ES, WH, and WS zones between 1996 and 2011 were mostly explained by declining numbers in *Sparisoma radians*, *Scarus iseri*, and *Halichoeres bivittatus*, and in a lesser degree by the declining abundance of *Hemiramphus brasiliensis*, *Acanthurus coeruleus*, and *A. tractus* (**Figure 10**). Changing trajectories within the SC was mostly explained by the increasing abundance of *Calamus calamus*, *Gerres cinereus*, and *Trachinotus goodei*. This solution explains 80% of the observed spatio-temporal variation in demersal fish assemblages.

## 4. Discussion

### 4.1. Spatio-Temporal Variation in Seagrass Benthic and Faunal Assemblages

Significant changes in the trajectory of seagrass community structure and in benthic faunal assemblages were documented between 1996 and 2011 at Mata de la Gata Island in La Parguera, Puerto Rico. Changes are presumed to be the long-term consequences of uncontrolled recreational navigation over shallow seagrass ecosystems. The most important findings evidenced: 1) a consistent spatial gradient, both in 1996 and in 2011, in the ecological conditions of seagrasses across the chronically disturbed SC zone, with generally increased percent sea-

grass cover, density and canopy height, and seagrass benthic assemblage biodiversity with increasing distance from the SC zone; 2) a temporal increase in recreational boating disturbance impacts on seagrass benthic community structure in the form of an expanded width of the SC zone, a decline in percent seagrass cover and density, and an increased macroalgal and cyanobacterial percent cover around the ES and WS channel edge zones, which led to a general phase shift in the overall seagrass benthic community structure; 3) an important shift in seagrass assemblage biodiversity evidenced by a significant temporal increase in  $S$ ,  $H'_c$ , and  $1 - \lambda$ , which may suggest a response to the long-term increase in recreational boating disturbance that followed the intermediate disturbance hypothesis; 4) a consistent spatial shift in benthic faunal community structure suggesting the long-term, chronic effect of recreational navigation disturbances on benthic seagrass communities, in turn adversely affecting the spatial distribution and survival of multiple benthic invertebrate taxa in relation to the SC zone; 5) an important temporal shift in benthic faunal assemblages, with a significant decline in cnidarians, echinoids, ophiuroids, holothurians, and gastropods, and an increase in polychaetes, platyhelminths, and hermit crabs, particularly in areas more exposed to boating disturbance and drifting macroalgal accumulation (e.g. SC, ES, WS); and 6) spatio-temporal variation in seagrass community structure that explained the observed spatio-temporal variation in benthic faunal community structure and its overall fish and invertebrate biodiversity.

This study evidenced the temporal consistency in seagrass community structure spatial gradients. Areas directly subjected to chronic, long-term impacts of recreational boating showed total or nearly total extirpation of seagrasses across a widened scoured channel (SC zone). During 1996, the SC was mostly dominated by open sand bottom, but dominance during 2011 shifted to drifting macroalgae, mostly brown weedy macroalga *Dictyota* spp., and cyanobacteria, which might have followed nutrient pulse events. Areas adjacent to SC were characterized by very low seagrass percent cover, shoot density, and lower canopies, while habitats farthest from the navigation disturbed areas (e.g. EH, WH) were characterized by higher percent seagrass cover, shoot density, canopy height, and dominance by *T. testudinum*. The observed pattern of disturbance showed a persistent, long-lasting major landscape-level fragmentation like that documented in previous studies [76] [77] [83]. These observations were also consistent with studies that documented increased cyanobacterial and macroalgal abundance over propeller-scoured bottoms [57] [84] [86].

There was also a persistent spatio-temporal variation pattern in seagrass benthic community biodiversity that suggested a classical intermediate disturbance hypothesis effect [95]. Observed diversity indices showed overall significantly higher values across areas subjected to moderate boating disturbance across the scoured channel edges (e.g. ES, WS). But diversity declined both in areas exposed to chronic, persistent navigation disturbance (SC), and in areas farthest from disturbance (e.g. EH, WH). This was explained by the higher frequency and/or severity of boating disturbances that resulted in the total or nearly total

extirpation of shallow seagrasses, and the dominance of sandy open substrates, drifting macroalgae and cyanobacteria in the SC bottom. On the opposite, EH and WH locations were dominated by seagrasses, mostly *T. testudinum*. Both conditions resulted in reduced diversity, but due to contrasting vessel disturbance conditions. Surveyed locations subjected to moderate disturbances were characterized by the coexistence of all benthic categories, which resulted in higher biodiversity. This study evidenced a significant temporal increase in biodiversity across all surveyed locations subjected to moderate and low boating disturbance, except that of the SC subjected to frequent and/or severe boating disturbance. This may suggest the persistence and possible increase in recreational navigation disturbances between 1996 and 2011 at Mata de la Gata Island.

Consistent with changes observed in seagrass benthic communities, benthic faunal community structure and  $\beta$ -diversity also showed significant spatio-temporal fluctuations. A major spatial gradient in faunal taxa abundance was observed both in 1996 and 2011 that followed a gradient of increasing distance from the highly disturbed SC. However, the increased expansion of the SC and the observed habitat homogenization trend across the SC edges (e.g. ES, WS) during 2011 reflected enhanced gradients in abundance and in  $\beta$ -diversity, both for benthic invertebrates and demersal fish assemblages. A significant temporal decline in the abundance of cnidarians, echinoids, ophiuroids, holothurians, and gastropods was documented, while an increase in polychaetes, platyhelminths, and hermit crabs, particularly in areas more exposed to boating disturbance (e.g. SC, ES, WS) was observed. Species with reduced abundances were typically those directly associated with healthy seagrass ecosystems, while those that showed increased abundance were those often associated with disturbed seagrass bottoms and open sandy substrate, which often feed upon accumulated decaying organic matter. Caribbean seagrass ecosystems support highly diverse benthic invertebrate communities [96], which are subjected to some levels of seasonal variability in abundance [97] but remain highly productive and supportive of multiple other ecosystems [98]. However, it is argued that observed spatio-temporal changes in seagrass benthic community structure in this study fostered an increased abundance in detritivore fauna.

Detritus in seagrass meadows can be an important food source for multiple species and is a critical pathway of nutrient and energy flow in interconnected tropical coastal ecosystems [98]. Some of the common detritivores found in seagrass habitats include certain species of crustaceans, mollusks, and polychaetes, which feed on decaying seagrass and macroalgae found in the sediment. Also, numerous species of crabs, snails, and shrimps feed on accumulated detrital material in seagrass meadows. These organisms play an important role in the ecosystem by contributing to breaking down decaying organic material and recycling nutrients back into the food web [7], contributing to the energetic connectivity with other adjacent ecosystems, such as coral reefs, mangroves, and estuaries. However, under moderate to severe, long-term disturbance regimes, such as chronic recreational boating and anchoring, shallow seagrass habitats are ex-

posed to severe mechanical impacts that can result in enhanced seagrass dislodgment and mortality, generating an increase in the production of decaying organic material, that in combination with factors such as natural seasonal variation in rainfall and runoff patterns, human-altered water quality, and climate change-related stress, may lead to enhanced macroalgal and cyanobacterial overgrowth. These combined factors may lead to enhanced local production of detritus, which may in turn foster enhanced conditions for the recruitment and survival of detritivore taxa as it was observed to occur between 1996 and 2011 in this study.

The implications of habitat alterations are critical for the long-term sustainability of seagrass fish assemblages. There is still poor knowledge of the impacts of habitat changes on seagrass fish communities due to human-driven factors, particularly recreational navigation. Observed alterations in benthic seagrass community structure were also reflected in fish assemblage spatio-temporal variation patterns. There was an overall decline in the abundance of juvenile scrapper herbivores such as *S. radians*, and *S. iseri*, in the generalist benthic invertivore *H. bivittatus*, in planktivore *H. brasiliensis*, and in browser herbivores *A. coeruleus*, and *A. tractus*. Observed changes in these groups may have resulted from altered habitat characteristics, which might have reduced their essential fish habitat and juvenile nursery role. There could have also been a possible water quality decline due to chronic sediment resuspension and possible pollution from vessels, though that was not addressed in this study.

The increased abundance of generalist invertivores such as *Calamus calamus*, *Gerres cinereus*, and *Trachinotus goodei* at the SC zone might be explained by the indirect effect exerted by the increased abundance of detritus feeder invertebrates. Fish biodiversity showed higher richness in areas farthest from boating disturbance, suggesting a persistent essential fish habitat and juvenile fish nursery role of healthy seagrasses, but an increased alteration of such ecological functions in locations chronically disturbed by recreational navigation might have led to the elimination of many species from disturbed zones. This finding supports the findings of previous studies across multiple biogeographic regions. Boating and navigation adversely affected fish recruitment in the Baltic Sea [99]. Habitat degradation resulted in losing the most attractive habitat physiotypes for fish, which failed to support basic fish ecological features [100], favoring an increase in less attractive ones, which can lead to potential changes in the nursery carrying capacity of disturbed habitats and in the functioning of the fish assemblages. Fish also showed lower abundance, diversity, and altered feeding behavior near recreational boat moorings [101]. Even harmful blooms of microalgae *Karenia brevis* have led to declines in fish diversity and abundance in seagrass habitats as a potential combined effect of water quality decline and habitat alteration [102]. The combined impact of long-term alterations in benthic habitat conditions and water quality might have played a key role in the observed changes in demersal fish fauna in this study.

## 4.2. Long-Term Consequences of Uncontrolled Recreational Navigation on Seagrass Ecosystem Functions and Services

Recreational navigation can have several long-term adverse impacts on seagrass ecosystems, including physical damage to the seagrass stands by propeller scouring, turbine scarring or anchoring, including breakage of seagrass canopy or rhizome and root dislodgment [76] [83]. There could also be increased sediment resuspension and deposition rates over adjacent seagrasses, and water turbidity, which can reduce light penetration and affect seagrass growth [103] [104] [105] [106]. In this study, vessels reaching Mata de la Gata Island created a major scoured channel due to the chronic mechanical disturbance to shallow seagrass habitats along the main waterway that can damage the plants by breaking, uprooting, or displacing them. Furthermore, seagrass gaps can trap drifting macroalgae and cyanobacteria, which can also affect seagrass recolonization ability through interference outcompetition mechanisms. Over a period of 15 years, this damage had long-term effects on the seagrass ecosystem that resulted in an increased width of the scoured channel and in a significant decline in seagrass percent cover, shoot density, and canopy height on adjacent bottoms. It also resulted in a significant alteration of benthic faunal assemblages, which may contribute to an overall reduction in ecosystem productivity.

Recurrent recreational boating can also result in increased anoxic sediment resuspension and in the subsequent sedimentation of adjacent remnant seagrasses. Sedimentation can cover the seagrass leaves, blocking sunlight, and reducing the photosynthesis process, which can lead to a long-term decline in seagrass growth and productivity [106]. An enhanced resuspension of anoxic sediments may also lead to increased concentrations of toxic  $H_2S$ , potentially affecting its associated benthic faunal assemblages [107]. Previous studies in Australia have shown that heavy recreational boating activities resulted in declining *Posidonia* stands due to significant sediment resuspension by propeller scarring, impacting the composition of faunal assemblages [108]. Resuspended sediment can also lead to increased water turbidity. Turbid water can result from the movement of boats and jet skis through shallow seagrass ecosystems, and from anchoring activities. Chronic turbidity can reduce light penetration, which can impact the growth and survival of seagrasses [49] [51] [52]. In the long term, such a combination of impacts can result in the physical fragmentation and disruption of seagrass meadows.

The scoured channel at Mata de la Gata Island is an example of how the chronic movement of boats through shallow seagrass meadows can create permanent channels of disrupted seagrass growth. Chronic mechanical disturbances can reduce seagrass' overall size and connectivity and can also affect the natural distribution and connectivity of its benthic faunal and fish assemblages. Such physical disruption can be further enhanced by recurrent anchor damage and trampling. Anchoring in seagrass meadows can cause physical damage to the plants and their surrounding habitat [74] [78] [108], and has long been a major

concern for the conservation of seagrasses and coral reefs [109]. Anchoring impacts, in combination with other forms of mechanical disturbances and pollution, have been deemed to promote the rapid loss of *Halodule wrightii* in Brazil, affecting benthic faunal assemblages [110].

Mechanical disturbances also promoted the rapid colonization by invasive sea vine *Halophila stipulacea* on Caribbean shallow coastal habitats [67] [71] [111] [112]. At the time of sampling, *H. stipulacea* was absent from the study location. There is no information available at present regarding this species' presence within La Parguera Natural Reserve. However, the species is largely distributed across other locations in Puerto Rico [67] [71].

It is argued that observed spatio-temporal alterations in benthic invertebrate and demersal fish assemblages in this study responded to physical changes and habitat homogenization trends documented on shallow seagrass meadows from chronic recreational navigation. Recreational navigation impacts can range from physical damage to individuals of certain species to habitat modification or destruction, and changes in water quality that affect the overall health of the ecosystem and may lead to the subsequent loss of biodiversity. Significant resuspension of hydrogen sulfide caused by recurrent anchoring over *Posidonia oceanica* was observed in France, altering the seascape of submerged aquatic vegetation stands and its associated faunal assemblages [113].

Physical damage caused by propellers, turbines and hulls of vessels can damage seagrass stands, causing loss of vegetation, changing the physical structure of the seafloor, and resulting in a significant habitat homogenization and in a reduced function as nursery ground and essential fish habitat. Anchoring is another critical form of direct mechanical disruption of submerged aquatic vegetation [59] [114] [115] [116]. The frequency of boat use has been directly correlated to the extent of physical damage to seagrasses [117]. This can impact the growth and reproduction of important ecosystem engineer taxa (seagrasses), its ecological functions and ecosystem services, including sustaining many of its associated benthic fauna that depend on seagrass spatial heterogeneity and health for survival. Such impacts have also resulted in the loss of *Posidonia oceanica* spatial extent in France, with a 9% decline in its carbon sequestration ability and a net loss of \$4.72 million euros  $y^{-1}$  [116].

Boating may also have a combination of direct and indirect impacts on demersal fish assemblages. Altered wave climate in shallow wave-protected areas due to high-speed boating and water turbidity due to sediment resuspension may influence fishes and their habitats, especially in submerged aquatic vegetation [114]. Finally, the role of recreational boats as vectors of aquatic invasive organisms is also a significant concern and has created major problems for the ecology of aquatic systems [114].

Another chronic impact of recreational navigation is the release of pollutants from boat exhaust, fuel leaks, liquid and solid wastes, and other sources, including heavy metals [118], that combined with anoxic sediment mechanical resus-

pension [119], increased turbidity, and with the potential resuspension of pollutants trapped in sediments, can negatively affect water quality on local scales and create conditions that are unsuitable for seagrass and its associated benthic fauna. Pollution risks arising from fuel spillage, exhaust emissions and antifouling paints all have detrimental effects on fish [114] and in other demersal fauna [119]. This aspect was not addressed in the present study but might be a potentially important factor affecting the observed changes in seagrass and benthic faunal assemblages.

Noise is another form of disturbance caused by boats that can also have impacts on benthic fauna. The sound generated by engines can influence the communication and behavior of certain species [114], particularly during larval stages, which may interfere with recruitment processes. The vibrations and noise caused by boats can disrupt the feeding and mating behaviors of marine life, which can impact the overall health and survival of populations of multiple species. Boat noise can have significant impacts on the behavior of coral reef- and seagrass-associated fish assemblages, which can ultimately impact the entire food web of the ecosystem [120]. Noise pollution can also have a detrimental impact on the behavior and survival of fish larvae on coral reefs and seagrasses by disrupting their natural acoustic environment. Noise can interfere with fish larvae's ability to detect and locate suitable habitats [121] [122] [123] [124], food sources, and potential mates. It can affect fish larval settlement success by as much as nearly 50% [125]. It can also disrupt their ability to communicate with each other, which can affect social behavior and survival, and can cause stress and physiological changes, which can impair their growth and development [121]-[126]. Although this study did not measure the impact of recreational navigation noise pollution, it cannot be ruled out as an important long-term driver of change in demersal fish assemblages at Mata de la Gata Island shallow seagrass habitats and measures should be taken to reduce the impact of noise pollution on this fragile habitat by regulating vessel numbers and traffic speed.

This study evidenced that although nature-based tourism activities involving recreational boating and anchoring operations on shallow tropical seagrass ecosystems might be deemed as having low environmental impacts, and to be within safe levels of acceptable change, over the long term, such disturbances can be locally significant, long-lasting, and may result in permanent alteration of benthic seagrass community structure and of demersal faunal assemblages. The case study of Mata de la Gata Island showcases that even the designation of a Natural Reserve is not enough to prevent such damage and that chronic lack of governance, commitment, enforcement, and political will by government institutions are instrumental for the conservation of paramount coastal resources.

The potential long-term implications of recreational navigation on seagrass habitats can have far-reaching ecological and socio-economic effects, making these habitats more vulnerable to other sources of anthropogenic stress, including climate change and sea level rise. Some of the long-term ecological and so-



cio-economic consequences include:

1) *Habitat fragmentation and loss*. Seagrasses are fundamental ecosystem engineer species and provide critical habitat for a diverse range of marine taxa. Their decline will lead to habitat fragmentation and loss, reducing the availability of shelter, nursery habitats, and foraging grounds of numerous species, as well as reducing its role as a soft bottom stabilizer, wave energy buffer, and as a CO<sub>2</sub> sinkhole.

2) *Biodiversity loss*. Seagrass habitats support high biodiversity, providing refuge for numerous species, including invertebrates, fish, and marine reptiles and mammals. Long-term seagrass decline may result in disrupting ecological interactions and functions, leading to a net loss in ecosystem resilience.

3) *Water quality degradation*. Seagrasses play a principal role in maintaining coastal water quality by dampening wave action, trapping sediments, and filtering sediments, nutrients and pollutants from the water column. Their decline can lead to a long-term increase in sediment resuspension, turbidity, nutrient enrichment, and pollution.

4) *Carbon sequestration*. Seagrasses are highly efficient carbon sinks, storing CO<sub>2</sub> and contributing to climate regulation. Under projected climate change, their decline can reduce this capacity, potentially exacerbating long-term climate change effects, in addition to losing other ecological functions.

5) *Coastal erosion*. Seagrass habitats stabilize coastlines by reducing wave energy and shoreline erosion. As seagrass loss weakens this protective function, coastlines will become more vulnerable to long-term erosion under projected sea level rise (SLR) and under projected increases in the recurrence of extreme weather events associated with climate change.

6) *Fisheries, livelihoods, and food security*. Seagrass habitats are vital nursery grounds for a myriad of commercially important fish and invertebrate species. Their long-term decline can lead to reduced fishery yields, impacting local economies, livelihoods, and food security for coastal communities.

7) *Tourism and recreation*. Seagrasses are usually wave-protected habitats that attract ecotourism and recreational activities like snorkeling, diving, kayaking, and swimming. Their degradation can negatively impact local tourism revenues, employment opportunities, and coastal community livelihoods.

8) *Storm protection*. Healthy seagrass meadows mitigate the impacts of storm surges by acting as natural buffers of wave energy. Their decline can increase risk to life, vulnerability to property damage and economic losses during storms. This risk may increase under projected storm frequency and/or severity associated with climate change.

9) *Cultural importance*. Seagrass ecosystems hold important cultural significance for many indigenous communities and local cultures. Their long-term loss can impact traditional practices and values.

10) *Climate change synergies*. Degraded seagrass ecosystems are less resilient to the impacts of climate change, such as SLR, ocean acidification and sea sur-

face temperature increase. The loss of ecosystem services provided by seagrasses can further compound the long-term negative effects of these stressors.

11) *Increased disease susceptibility*. Weakened and chronically degraded seagrass ecosystems are more susceptible to diseases, pathogens, and opportunist species, making them less able to resist and recover from potential outbreaks, which can be exacerbated by local anthropogenic stressors in combination with changing climate.

12) *Altered community dynamics*. The chronic loss of seagrasses can disrupt predator-prey relationships and can alter trophic interactions, potentially leading to biodiversity and functional imbalances, and to cascading effects on the entire ecosystems. In the long term, these can lead to a major loss in ecosystem persistence, functional redundancy, and resilience.

13) *Feedback loops*. The long-term degradation of seagrass meadows can also lead to positive feedback loops where reduced carbon sequestration, habitat loss, and altered nutrient dynamics may contribute to more severe climate impacts, by leading to further biodiversity loss, a net erosion in ecosystem functions, and to altered trophic states, exacerbating the degradation of these ecosystems.

These impacts can weaken seagrass habitats and make them less resilient to climate change-related stressors such as SLR, sea surface warming, and ocean acidification. Conservation and restoration efforts to promote seagrass recovery and resilience, sustainable boating practices, proper land use management practices, and marine spatial planning are essential to mitigate and/or prevent these impacts, and improve the seagrass ecosystem to withstand future challenges. Integrating seagrass protection into climate adaptation strategies is also critical for maintaining its ecological and socio-economic benefits.

Variations in seagrass benthic community structure, shoot density, and canopy height can have substantial effects on the overall ecological functioning of seagrass ecosystems, associated biodiversity and in net primary productivity. Any adverse impact to seagrass ecosystems that might affect any of these characteristics may impair its ecological benefits including:

1) *Canopy height*. Seagrasses canopy height directly affects primary production and carbon cycling. Tall canopies provide more photosynthetic surface area, leading to higher productivity. This, in turn, contributes to increased carbon sequestration and enhanced provision of organic matter to the food web, enhanced energy flows and ecological connectivity to adjacent ecosystems, and enhanced shelter for associated fauna.

2) *Shoot density*. High shoot density enhances primary production by increasing the total abundance of seagrass shoots available for photosynthesis. Dense seagrass stands are more efficient at capturing and storing carbon and can support a more extensive range of species due to increased habitat complexity. High shoot density also provides more habitat structure and refuge for a diverse array of species, including enhanced protection for juvenile fish and invertebrates from predators.

3) *Benthic community structure*. The composition of seagrass benthic-associated communities can vary under different ecological and environmental regimes. Different seagrass species host distinct benthic communities, with some species attracting more epiphytic algae, encrusting invertebrates, invertebrate egg masses, etc.

4) *Biodiversity and species composition*. Some seagrass species enhance microhabitat complexity, and niche diversity to support more diverse fish and invertebrate assemblages.

5) *Erosion control and sediment stabilization*. Higher shoot density results in enhanced wave dampening, sediment trapping ability and improved water quality. Tall seagrass canopies also help prevent erosion along coastlines, which is vital for protecting coastal ecosystems, infrastructure, and life.

6) *Nutrient cycling*. Variations in benthic communities can affect nutrient cycling within seagrass ecosystems. Different seagrass species and associated species may have varying functional roles in nutrient uptake and cycling, influencing nutrient dynamics across coastal systems.

7) *Water quality and filtration*. Besides seagrasses, some filter-feeding invertebrates can help improve water quality by removing suspended particles, and filtering out excess nutrients and contaminants.

8) *Fisheries support*. Higher shoot density can support more abundant and diverse fish populations by providing shelter and foraging opportunities for a wide range of species, including commercially valuable ones.

9) *Carbon storage and climate regulation*. Seagrass habitats with tall canopies store more carbon in their biomass and sediments, contributing to CO<sub>2</sub> sequestration.

In summary, variations in seagrass benthic community structure, shoot density, and canopy height directly affect important ecological functions and services. In the long term, these variations influence primary production, habitat provision, biodiversity, erosion control, nutrient cycling, water quality, fisheries support, and carbon storage. Understanding, managing, mitigating and/or restoring these variations are crucial for the conservation and sustainable use of seagrass ecosystems and the services they provide to other coastal ecosystems and human communities.

To prevent direct boating and anchoring disturbances on shallow seagrass habitats, the following critical best management practices (BMPs) should be considered:

1) *Designate navigation channels and waterways*. Boaters should always use designated channels and approaches to designated disembarking areas, which should be appropriately identified with illuminated and numbered buoys, and properly identified in nautical charts, when entering or leaving a waterway, or when accessing shallow-water piers in areas adjacent to seagrasses, coral reefs, and small keys. This can significantly minimize damage to seagrasses and other sensitive habitats.

2) *Avoid anchoring in seagrass meadows.* Anchoring can cause significant mechanical damage to seagrasses, particularly by larger yachts, sailboats, and cruise ships. Instead, the use of mooring buoys or designated anchoring areas over open sandy bottoms must be emphasized. Mooring systems have been shown to significantly reduce mechanical anchoring damage on seagrasses [127]. Similarly, mooring in adjacent mangrove trees should be strictly prohibited as a measure to protect critical essential fish habitats interconnected with seagrasses and coral reefs.

3) *Slow down in shallow seagrass habitats.* When boating in shallow seagrass areas, reducing vessel speed is critical to minimize the impact of boat wakes on seagrass stands and to adjacent mangrove areas. This will reduce sediment re-suspension and turbidity, as well as minimize physical disturbance to benthic faunal assemblages adapted to low-wave energy.

4) *Establish recreational vessel carrying capacity.* It is important to establish the carrying capacity or the limits of acceptable change of recreational use on shallow seagrass habitats to reduce any significant impact on submerged aquatic ecosystems [128].

5) *Avoid the construction of docking facilities over seagrass habitats.* Dock construction over seagrass habitats results in a significant loss of seagrass cover and biomass [87]. Docking facilities should be avoided on seagrasses, but under some circumstances, such facilities are necessary to concentrate recreational uses in some specific locations with appropriate management and regulations to avoid widespread uncontrolled impacts.

6) *Educate recreational navigators and tourism operators.* Education has been deemed critical to raising awareness and minimizing impacts [129] [130] and is key to preventing damage to shallow seagrasses and associated habitats. Boaters, anglers, tourism operators, and other resource users should be educated about the importance of shallow seagrasses, coral reefs, and mangroves, and the impact of their activities on these fragile ecosystems.

7) *Support seagrass conservation and restoration efforts.* Supporting conservation efforts to protect and restore seagrass habitats can help ensure their long-term health, the sustainability of their ecological functions and services, and their socio-economic and ecological resilience. This may include participating in citizen's science monitoring programs, restoration projects, supporting the creation of marine protected areas, and participating in continuous education programs and outreach activities. Fostering the integration of base communities, and critical stakeholders, such as fishers, tourism operators and non-governmental organizations should lead to enhanced stewardship and participatory co-management.

Research on the impacts of recreational navigation on seagrasses is ongoing and has become increasingly important in the context of increasing numbers of recreational vessels and of an enhanced widespread demand for coastal recreational opportunities and activities. However, there are still several important know-

ledge gaps and research needs that warrant further interdisciplinary investigation. Some of the most important gaps and needs include:

1) *Cumulative impacts assessment*. There is a need for comprehensive interdisciplinary studies that characterize and quantify cumulative impacts of recreational navigation, particularly on Western Atlantic/Caribbean seagrass ecosystems, in conjunction with other stressors, including pollution, coastal development, and climate change. Understanding how multiple stressors interact and compound their effects is paramount for effective conservation- and restoration-oriented management.

2) *Long-term monitoring*. Long-term ecological monitoring programs are essential to characterize and quantify the recovery potential of seagrass habitats following recreational navigation disturbances and the impacts of other stressors. Such studies can provide insights into the persistence of impacts, cascading effects over time, and the effectiveness of conservation and restoration efforts. It can also be an important opportunity for the development of citizens' science programs and the integration of community-based actors, non-governmental organizations, academia, etc. into management-oriented efforts.

3) *Ecosystem services valuation*. Research is needed to quantify the socio-economic and ecological value of seagrass ecosystems, including the diverse services they provide, particularly in the context of determining and mitigating potential losses associated with uncontrolled recreational abuse, and with impacts from other stressors. This information can help resource managers, policymakers and stakeholders understand the significance of seagrasses and the consequences of their long-term loss to prioritize future resource allocation, and conservation and restoration efforts.

4) *Boat-related BMPs*. More research is required to identify and promote BMPs for recreational boating to minimize impacts on seagrass habitats. This includes assessing the effectiveness of different mooring systems, management-driven anchoring practices, and navigational regulations aimed at reducing damage to seagrass meadows. Also, the effectiveness of marine protected area designation can be quantified in the context of boating/anchoring BMPs.

5) *Erosion mitigation*. Understanding the role of seagrasses in coastal erosion prevention and the potential for recreational navigation to exacerbate shoreline erosion and benthic habitat destabilization is vital. Research on how seagrass habitats can be strategically conserved and/or restored to protect vulnerable coastlines is also needed, with particular emphasis on urban coastal scenarios.

6) *Community dynamics*. Investigating the impacts of recreational navigation on the diversity and abundance of seagrass demersal invertebrate and fish assemblages is essential. This includes assessing how alterations in seagrass meadows' structural integrity, species composition, habitat fragmentation, and even how nuisance macroalgal blooms and invasive seagrasses, as well as altered soundscapes, affect the composition of associated demersal faunal assemblages and the cascading effects on ecosystem dynamics, ecological functions and servic-

es, and on ecosystem resilience to disturbance.

7) *Sustainable tourism practices*. Given the importance of seagrass habitats for ecotourism, recreational activities and community-based livelihoods, there is a need for research on sustainable tourism BMPs that can minimize disturbances, while allowing for responsible enjoyment of these ecosystems. The impacts of the implementation of such BMPs should be quantified in the context of changes in ecosystem indicators.

8) *Climate change interactions*. Research should also focus on understanding how recreational navigation impacts interact with climate change stressors, such as sea surface warming, ocean acidification and SLR, to affect seagrass persistence and resilience. This should include studying the potential for navigation-related stressors to exacerbate or ameliorate climate-induced impacts.

9) *Policy and management*. Research on the effectiveness of policies and management strategies aimed at reducing and mitigating the impacts of recreational navigation on seagrasses is also key. This should include assessing the enforcement and compliance with regulations, as well as the socio-economic implications of management decisions.

10) *Public awareness and education*. Quantifying the effectiveness of public awareness and education campaigns in reducing the ecological footprint of recreational navigation and anchoring and promoting responsible behavior around seagrass habitats is an important interdisciplinary research area and one of the most critical challenges for resource managers.

The interdisciplinary collaboration among multiple societal actors (e.g. natural, and social scientists, economists, conservation organizations, community-based leaders, fishers, the tourism industry, recreational boaters, resource managers, policymakers) is essential to address numerous knowledge gaps, community-based concerns, and to develop science-based strategies for the sustainable coexistence of recreational navigation and seagrass ecosystem conservation. Additionally, interdisciplinary research that integrates ecological, socio-economic, and cultural perspectives is valuable for holistic conservation efforts. Such integrated efforts are particularly important for SIDS, many of which significantly lack human, economic and technological resources, and many of which still suffer from critical colonial legacies, neo-colonial policies, environmental injustice, lack of equity, and suffer from increased vulnerability to climate change, SLR, and extreme weather events.

Damage to seagrass habitats described in this study is significant but can be slowed down or even reverted if recreational navigation and tourism activities at Mata de la Gata Island are appropriately managed through stronger governance and strict enforcement of a limit of acceptable change and by regulating the number of daily visitors to the island. This case study presents an excellent lesson-learning opportunity to promote the implementation of ecosystem-based management strategies to support the conservation and restoration of this impacted Natural Reserve. It can also become an important model for other small

tropical islands to manage their coastal resources. But it would be paramount to follow these recommendations to prevent boating and anchoring disturbances on seagrass habitats and ensure their long-term health and sustainability in the face of projected threats by SLR, ocean acidification and climate change.

### Acknowledgements

This project was possible thanks to the support of the Center for Applied Tropical Ecology and Conservation (CATEC) of the University of Puerto Rico (UPR), Río Piedras Campus during the 2011 sampling effort, and by the support of Sociedad Ambiente Marino (SAM). Guidance provided by Dr. Jeff Holmquist and by the Department of Marine Sciences, UPR, Mayagüez Campus, and by Dr. T. Mitchell Aide and by the Department of Biology of UPR, Río Piedras, was also important during the 1996 sampling effort. This publication is a contribution to the collaboration between CATEC and SAM.

### Conflicts of Interest

The author declares no conflicts of interest regarding the publication of this paper.

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