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Seagrass *Posidonia* escarpments support high diversity and biomass of rocky reef fishes

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Abstract

Although seagrass meadows form a relatively homogenous habitat, escarpments, which form three-dimensional structures and originate from the erosion of seagrass peat, can provide important habitat for reef fishes. Here, we compare fish assemblages and habitat structural complexity among seagrass *Posidonia australis* escarpments and canopies, as well as limestone reef habitats, to understand the role of seagrass escarpments as reef fish habitat in Shark Bay, Western Australia. The total number of fish species, fish biomass, and top predator biomass were significantly higher in seagrass escarpments and reef habitats than in seagrass canopies due to lower habitat structural complexity and thus becoming suitable habitats for predators and prey in the latter. Both seagrass escarpment and reef habitats host similar assemblages of top predators and carnivorous fishes, such as *Epinephelus coioides*, *Microcanthus strigatus*, and *Choerodon schoenleinii*, that were absent in seagrass canopies. Seagrass escarpments provide an alternative habitat for reef fishes comparable to rocky reefs, which are limited in Shark Bay. Caves and ledges within the escarpments support 13.4 Mg of fish and 3.6 Mg of top predator species of commercial interest within the Shark Bay World Heritage Site. Additional research is needed to further understand the ecological importance of seagrass escarpments in enhancing fish biomass and biodiversity, as reproduction grounds or refuge from predators, and to investigate the role of meadow edges in ecosystem function.

KEYWORDS
Australia, biodiversity, biomass, escarpment, fish ecology, *Posidonia*, seagrass ecosystem service

INTRODUCTION

Seagrass meadows provide key ecological services, including nutrient cycling, organic carbon production and sequestration, sediment stabilization and coastal protection, enhanced biodiversity, cultural heritage preservation, nursery habitat for fishes, and nutrient supply to other coastal ecosystems (Barbier et al., 2011;

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Fourqurean et al., 2012; Heck et al., 2003; Hyndes et al., 2014; Krause-Jensen et al., 2019; Orth et al., 2006). These services are related to the high productivity and canopy structure of seagrasses, which dissipate wave energy and create structurally complex habitats (Duffy, 2006; Gacia & Duarte, 2001; Mazarrasa et al., 2015). The accumulation of organic-rich deposits beneath seagrass meadows is of great importance in marine biogeochemical cycles, revealing one of the largest organic carbon sinks worldwide (Mateo et al., 1997; Serrano et al., 2016). The role of seagrasses in buffering the impacts of rising sea level and wave action, and as carbon dioxide filters and sinks is likely important in the context of climate change mitigation and adaptation (Duarte et al., 2013). However, seagrass meadows are declining worldwide and conservation actions are required to protect and maintain the many ecosystem services seagrass meadows provide (Unsworth et al., 2018).

Seagrass canopy structure and primary production are generally considered as primary factors that influence fish diversity and productivity (Heck et al., 2003; Heithaus, 2004; Hyndes et al., 2018). Many juvenile fishes, including economically important species, spend their early life stages in seagrass meadows where they find refuge from predation and food, prior to migrating into other habitats such as reefs (Campbell et al., 2011; Dorenbosch et al., 2005). Indeed, differences in the structural complexity of seagrass vegetation (e.g., density, plant morphology, and algae inhabiting within the meadows) can influence the abundance and diversity of fishes, including size of predator and prey fish populations (Heck & Orth, 1980). However, the size of fishes increases proportionally to the volume of holes available within the habitat (Friedlander & Parrish, 1998). Therefore, the presence of crevices and caves in reefs creates greater three-dimensional (3D) structure (i.e., structural complexity) that is more closely aligned with predator body size compared with seagrass canopies, which in turn strongly enhances diversity and biomass of fishes (Connell & Jones, 1991; Garcıa-Charton et al., 2004). However, seagrasses can also form a heterogeneous and complex seascape resulting from the accumulation of peat-like deposits formed by plant remains (i.e., sheaths, rhizomes, and roots), which raises the seafloor (Bonhomme et al., 2015; Kendrick et al., 2005).

The erosion of seagrass meadows (e.g., by wave action, tidal/current flow, or dredging activities) can result in the exposure of peat, and the formation of escarpments in which large reef fishes have been observed (Serrano et al., 2017). The intertwined plant remains within the sediment matrix consolidate the sandy substrate and hold the 3D substrate together, maintaining a semirigid structure holding channels, ledges, and caves that serve as habitat for many reef fishes. Seagrass escarpments are known to form in the shallow highly productive *Posidonia oceanica* meadows in the Mediterranean Sea, *P. australis* meadows in the Indian Ocean (Figure 1), and in *Thalassia testudinum* meadows in the Caribbean Sea (Patriquin, 1975; Serrano et al., 2017; Wanless, 1981). The thickness of the peat escarpments can reach up to 3 m in height and their length can vary from a few to hundreds of meters (Serrano et al., 2016). Previous studies showed a positive correlation between 3D rocky reef structure and fish density, which is most likely related to the higher availability of food and/or shelters in highly structured and complex habitats (Thiriet et al., 2014; Verweij et al., 2006).

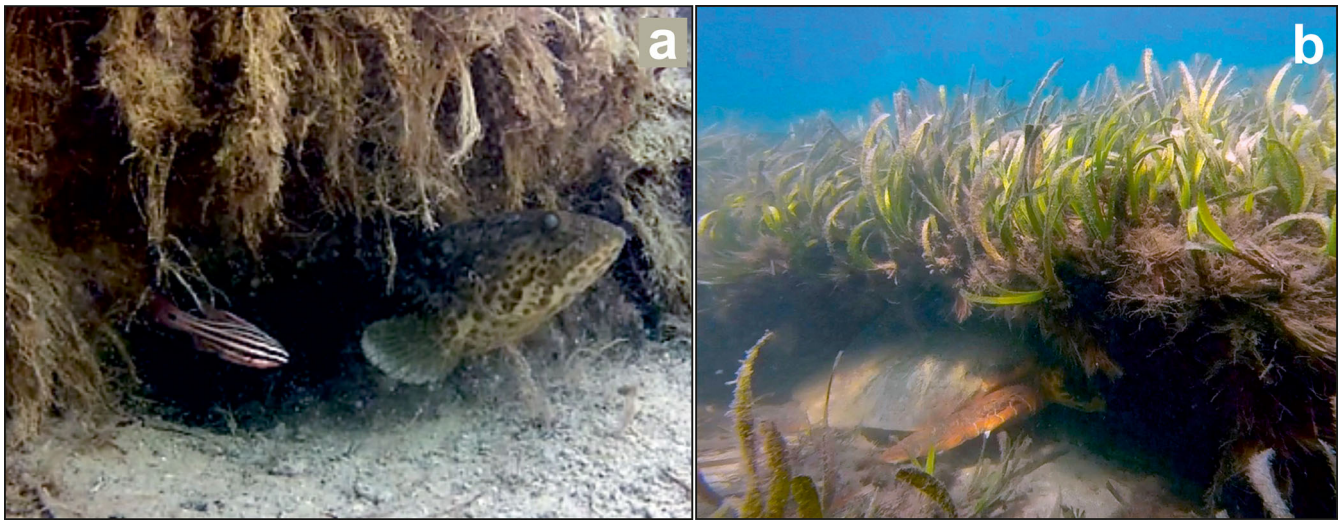

FIGURE 1 Reef fish and turtles inhabiting caves and ledges within *Posidonia australis* seagrass escarpments in Shark Bay (Indian Ocean, Western Australia). (a) The top predator fish *Epinephelus coioides* and the carnivore fish *Ostorhinchus victoriae* finding shelter in a cave at the base of the escarpment. (b) *Caretta caretta* sea turtle hiding underneath a ledge. Photo credit: Oscar Serrano.

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However, little is known about the natural history and the ecological importance of seagrass escarpments, including their role as habitat for reef fishes (Serrano, 2020).

Here, we aim to determine whether seagrass escarpments provide a similar habitat for reef fishes to that of rocky reefs. For the first time, we test this hypothesis empirically by examining the fish assemblages in *P. australis* meadows (canopies and escarpments) and reefs in Shark Bay, a World Heritage Area on the west coast of Australia. Seagrasses have contributed significantly to the evolution of Shark Bay, modifying the physical, chemical, and biological environment, as well as the geomorphology that has led to the development of major marine features including extensive sand banks and seagrass escarpments (Bufarale & Collins, 2015). We show for the first time that seagrass *Posidonia* escarpments provide 3D habitat enhancing reef fish biodiversity and biomass and discuss the natural history and ecological importance of these seagrass escarpments. In addition, we highlight future research directions to further understand the ecological importance of this newly described reef-like habitat, while contributing new evidence supporting the need to conserve seagrass meadows.

MATERIALS AND METHODS

Study site

This study was conducted in Shark Bay, located ~800 km north of Perth on the west coast of Australia (25° S–113° E; Figure 2). Shark Bay, a UNESCO World Heritage Site, is a vast, subtropical ecosystem on the eastern boundary of the Indian Ocean that hosts extensive populations of seagrasses, sharks, fishes, turtles, dolphins, and dugongs (Heithaus et al., 2007). Shark Bay is characterized by shallow water (<20 m), relatively deep and broad channels, sand banks, and sheltered embayments occupied by seagrass meadows (Bufarale & Collins, 2015). It contains one of the largest (4300 km^2) and most diverse seagrass areas worldwide (Arias-Ortiz et al., 2018; Walker et al., 1988). Around 12 seagrass species are found in Shark Bay, which have shaped its geomorphology over the last ~8000 years (Bufarale & Collins, 2015). The two main foundation seagrass species that form extensive canopies belong to the genera *Posidonia* and *Amphibolis* (Lavery et al., 2013), with the former characterized by thick peat beneath their canopies that have accumulated soil thickness ranging from 4 to 6 m over the last 4000 years (Arias-Ortiz et al., 2018). Despite the limestone geology of the region and the occasional presence of rocky shores along Shark Bay, there is a scarcity of submerged reefs.

Fish surveys

We conducted fish surveys using SCUBA in April 2017 between Peron Peninsula and Faure Island, and in Big Lagoon at Shark Bay (Figure 2; Appendix S1: Table S1). Three different habitats were surveyed within 11 study sites: *P. australis* seagrass canopies ranging from 15 to 40 cm in height ($n = 4$), *P. australis* escarpments ranging from 15 to 220 cm in height and inclination ranging from 60 to 100° ($n = 4$), and reefs ranging from 5 to 120 cm in height ($n = 3$). Although previous research showed that the edge effect in seagrass meadows adjacent to sand can increase fish abundance, in particular predator fish (Smith et al., 2012; Yarnall et al., 2021), we did not survey seagrass meadows edges without escarpments because our previous qualitative data did not show any presence of reef fish. The inclination of reefs was not measured. Water depth among study sites ranged between 1 and 3 m. Five 25-m transects were deployed at each study site. All fish data were collected by a single observer (i.e., EB) using standard underwater visual census technique (e.g., Sala et al., 2012). At each survey site, the diver swam at a constant speed (~10 min transect^{-1}) and identified, counted, and sized (to the nearest centimeter) all fishes within 1.5 m of either side of a randomly positioned 25-m line-transect (75 m^2) and throughout the 1–3 m depth from the sea bottom to the water surface. In seagrass escarpments, the transect was deployed at the base of the escarpment, and fishes within 3 m of the sandy substrate adjacent to the escarpment were surveyed. All fish surveys were conducted between >3 h after sunrise and <3 h before sunset, and during rising and high tide to minimize the effects of tide or time of day on fish behavior and fish counts (Castellanos-Galindo et al., 2010; Kruse et al., 2016). During field surveys, multiple meadows formed by *Posidonia* spp., *Amphibolis* spp., and other ephemeral and small seagrass species (e.g., genera *Halophila*, *Halodule*, and *Syringodium*) were also explored for the presence of escarpments.

The biomass of individual fishes (wet mass) was estimated from length–mass relationships from FishBase (Froese & Pauly, 2011), using the allometric conversion: $M = a \times (\mathrm{TL}^b)$, where parameters a and b are species-specific constants; TL is total length in centimeters; and M is mass in grams. For our analysis, we assigned each fish taxon to one of five trophic groups based on diet found in the literature: top predators, carnivores, herbivores, detritivores, and planktivores (Froese & Pauly, 2011; Appendix S1: Table S2). Total fish species (number of species per square meter), fish density (number of individual fishes per square meter), total fish biomass (in grams per

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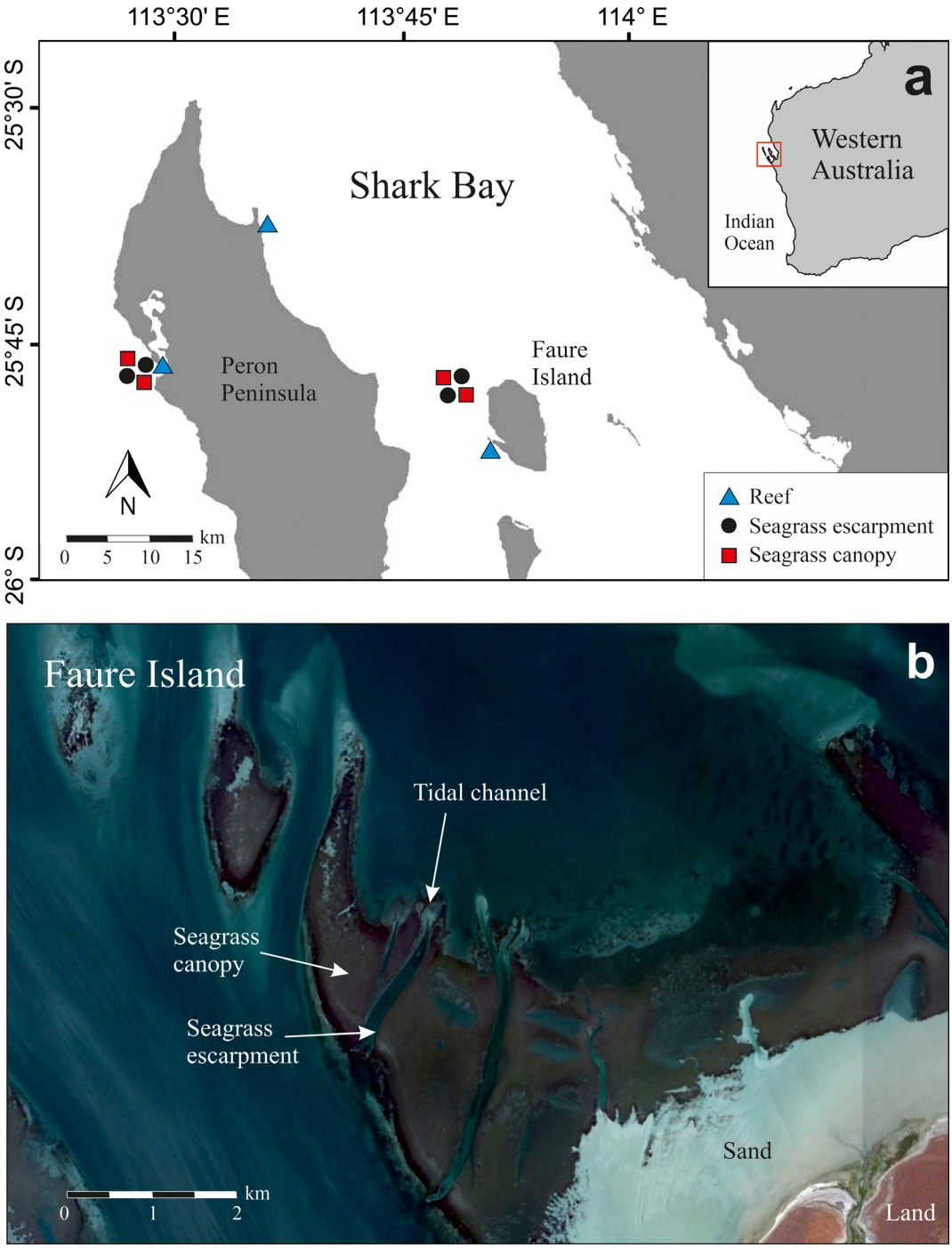

FIGURE 2 Study sites. (a) Map of Shark Bay in Western Australia showing the location of the 11 study sites where fish surveys were conducted across three habitat types (reefs, seagrass escarpments, and seagrass canopies). (b) Aerial photograph from northwestern Faure Island in Shark Bay showing seagrass canopies and the presence of tidal channels eroding the meadows, which led to the formation of seagrass escarpments.

square meter), and the percentage of total fish biomass of each trophic group were calculated for each transect. The fish size structure (in percentage) was categorized in 11 fish length size classes (in 5-cm intervals from 0 to >50 cm) to visualize the structure of the size–frequency distributions.

Structural complexity among habitats

At each study site, we examined the benthic structural complexity along the same transects where fish surveys were completed. At each transect, the SCUBA divers measured the dimensions (width, height, and length) of

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all visible caves and ledges with an entrance >20 cm in maximum diameter. The volume (V) of each cave was estimated using the formula of a cylinder ($V = \pi \times r^2 \times l$; where r is radius and l is length), and the volume of ledges using the formula of a rectangular prism ($V = w \times h \times l$; where w is width, h is height, and l is length). The height of reefs and seagrass escarpments, and the leaf height in seagrass canopies, was also measured at every 5-m intervals along each transect. The structural complexity of the habitats was estimated using the surface rugosity (i.e., the ratio of the 3D surface area to the projected planar area; Friedman et al., 2012; Equation 1). The projected planar area was estimated as the sum of the transect area (in square meters) plus the area of the vertical structure (in square meters). The total 3D area was calculated as the sum of the area of the transect, the area of the vertical structure, and the area of caves and ledges.

$$\text{Surface rugosity} = \left(\frac{\text{3D surface area}}{\text{Projected planar area}}\right) - 1 \times 100. \tag{1}$$

Seagrass canopies did not constitute a rigid 3D structure (i.e., lack of caves and ledges with an entrance >20 cm in maximum diameter), and therefore it was not possible to estimate surface rugosity using the ratio of the 3D surface area to the projected planar area. We acknowledge the semirigid structure of seagrass canopies creating habitat for fishes (Heck & Orth, 1980), but we did not survey enough data (e.g., shoot density and % cover) to properly estimate structural complexity in the seagrass canopies studied. Nevertheless, structural complexity of reefs and escarpments was on a different scale compared with seagrass canopies, and our study focused on examining adult fish assemblages rather than looking at recruitment and juvenile habitat.

Statistical analyses

Data for total fish species, total fish density, total fish biomass, and the biomass of each trophic group (top predator, carnivore, herbivore, detritivore, and planktivore) were standardized to square meters. Univariate permutational multivariate analysis of variance (PERMANOVA), which allows heteroscedasticity of samples and non-normality of the residuals, was used to test for significant differences among the three distinct habitats studied in the fish variables above as well as cave density, cave volume, habitat height, and structural complexity. The experimental design consisted of a one-factor design with habitat considered as a fixed factor. Data were square root transformed to down-weigh dominant groups, and a resemblance matrix for each variable was computed using Euclidean distance. A PERMANOVA was completed using the sum of squares type III (partial) with 9999 permutations of residuals under a reduced model method, and pair-wise comparisons were conducted on the significant factor habitat. The statistical design was completed using Primer-E PERMANOVA statistical software (Anderson et al., 2008).

Pearson correlation analyses were run to assess relationships between habitat structural complexity and fish variables (total fish species, fish density, total fish biomass, top predator biomass, and carnivore biomass). To determine the main fish species driving differences in fish biomass among habitats, a principal coordinates analysis (PCoA) was computed using Primer v6, and statistical differences were analyzed using a multivariate approach in Primer-E/PERMANOVA (Anderson et al., 2008). Species composition data were fourth root transformed to down-weigh the influence of highly abundant species. The Bray–Curtis similarity matrix was used as the best fit for biological assemblage data.

RESULTS

A total of 3373 individual fishes belonging to 41 species from 28 families were enumerated across 55 transects with a total of 1375 linear m at the 11 study sites in Shark Bay (Appendix S1: Table S2). The fish density per transect in reef habitats (mean ± SE; 1.45 ± 0.16 fish m^{-2}; 1634 individuals in total) was twofold higher than that observed in seagrass escarpments (0.75 ± 0.18 fish m^{-2}; 1028 individuals in total) and threefold higher than in seagrass canopies (0.47 ± 0.12 fish m^{-2}; 711 individuals in total). Of the total fishes identified, 167 were classified as top predators, 2149 as carnivores, 291 as herbivores, 51 as detritivores, and 715 as planktivores (Appendix S1: Table S2). The distribution of fish sizes was positively skewed toward the 5–15 cm size classes with a leptokurtic distribution in all habitats.

Habitat structural complexity

A total of 429 caves and ledges were counted within transects in reef ($n = 324$) and seagrass escarpment ($n = 105$) habitats, while they were absent in seagrass canopies. All structural characteristics differed significantly among habitats (Appendix S1: Table S3). Cave density was significantly higher in reefs than in seagrass escarpments (Appendix S1: Table S4; 0.86 and 0.28 caves m^{-2}, respectively). Reefs had significantly lower cave volume

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(0.06 ± 0.01 m^3) compared with seagrass escarpments (0.17 ± 0.04 m^3). Habitat height was also significantly lower in reefs (33 ± 2.4 cm) compared with seagrass escarpments (101 ± 4.5 cm). Seagrass canopy height ranged from 15 to 40 cm at our study sites. The structural complexity of the habitat was higher in reefs than in seagrass escarpments (Appendix S1: Table S4; $153 \pm 15\%$ and $88 \pm 24\%$, respectively).

Fish assemblages among habitats and their structural complexity

Overall, there was a significant habitat effect for all the variables studied ($p < 0.05$), except for carnivore, herbivore, and detritivore biomasses ($p > 0.05$; Appendix S1: Tables S3 and S4). Total fish species, total fish density and biomass, and top predator biomass were significantly higher in reefs and seagrass escarpments than in seagrass canopies (Figure 3). The total number of fish species was up to threefold higher in reefs and seagrass escarpments (0.17 ± 0.01 and 0.15 ± 0.01 individuals m^{-2}, respectively) than in seagrass canopies (0.05 ± 0.01 individuals m^{-2}; Figure 3). Total fish biomass was twofold higher in reefs (127 ± 22 g m^{-2}) than in seagrass escarpments (67 ± 34 g m^{-2}), and fivefold higher than in seagrass canopies (25 ± 21 g m^{-2}; Figure 3).

Top predator fish biomass was not significantly different between reefs and seagrass escarpments (35 ± 13 and 18 ± 5 g m^{-2}, respectively), whereas top predators were scarce in seagrass canopies (0.4 ± 0.2 g m^{-2}; Figure 3). Similarities between seagrass escarpments and canopies were found for fish density (0.75 ± 0.18 and 0.47 ± 0.12 individuals m^{-2}, respectively) and carnivore fish biomass (48 ± 35 and 23 ± 21 g m^{-2}), which were significantly lower than in reef habitats (1.45 ± 0.16 individuals m^{-2} and 88 ± 14 g m^{-2}; $p < 0.05$). Carnivores represented $69 \pm 4\%$ of total fish biomass in reefs, $72 \pm 6\%$ in seagrass escarpments, and $58 \pm 5\%$ in seagrass canopies, while top predators contributed $27 \pm 5\%$, $26 \pm 6\%$, and $10 \pm 5\%$ respectively, to the total fish biomass. Herbivore, detritivore, and planktivore biomasses represented <3% of the total fish biomass in reef and seagrass escarpment habitats, whereas herbivore and planktivore biomasses contributed 19% and 13% to total fish biomass in seagrass canopies (Figure 3).

The size–frequency distribution of fish individuals was similar across the three habitats, with 61% of fishes in the size class 5–15 cm in reef habitats, 62% in seagrass escarpments, and 92% in seagrass canopies (Figure 4). The percentage of fishes >15 cm was higher in reef habitats (28%) than in seagrass escarpments (8%) and seagrass canopies (4%). In all habitats, the distribution of fish sizes was positively skewed toward the 5–15 cm size classes with a leptokurtic distribution. Habitat structural complexity in reef habitats was positively correlated ($p < 0.05$) with total fish species ($R^2 = 0.56$) and fish density ($R^2 = 0.21$; Figure 5). Similarly, habitat structural complexity in seagrass escarpments was positively correlated with total fish species ($R^2 = 0.19$) and fish density ($R^2 = 0.31$).

Multivariate analyses

The first two principal components of the PCoA explained 46.5% of the total variance (Figure 6). The first principal component (PCoA1), which explained 32.5% of the variance, differentiated the biomass of fish species found in seagrass canopies from those found in reefs and seagrass escarpments. The second principal component (PCoA2) explained 14% of the variance and mainly differentiated seagrass escarpments from reef. The fish species that contributed >50% of the variance to this pattern were *Acentrogobius nebulosus*, *Epinephelus coiodes*, *Choerodon schoenleinii*, *Microcanthus strigatus*, and *Abudefduf bengalensis*. *Epinephelus coiodes* had higher biomass in reefs and seagrass escarpments than in seagrass canopies, while the biomass of *A. nebulosus* was greater in seagrass escarpments than in reefs. In comparison, *C. schoenleinii*, *M. strigatus*, and *A. bengalensis* tended to have greater biomass in reefs than in seagrass canopies and escarpments.

DISCUSSION

The structural complexity of seagrass canopies typically enhances fish biodiversity relative to other soft-sediment habitats (Heck et al., 2003; Hyndes et al., 2018), but the relatively flat habitat formed by the canopy is not suitable for reef fish species. Here, we show that seagrass from the genus *Posidonia* can provide additional habitat complexity owing to the presence of caves and ledges along erosional escarpments found at the edges of the meadows. Although visual survey methods have limitations, their relative ability to discern differences in fish assemblages among the habitat types surveyed provides useful comparisons. The results obtained showed that fish biomass was three times higher in the escarpments compared with the canopy, and the species composition was more similar to that observed in reefs than in seagrass canopies. Although the structural complexity of the reefs studied was higher than that of seagrass escarpments, we demonstrate that *P. australis* escarpments resemble reef habitats in terms of total fish species and top predator biomass. Both seagrass escarpments and reef habitats host similar assemblages of top predators and

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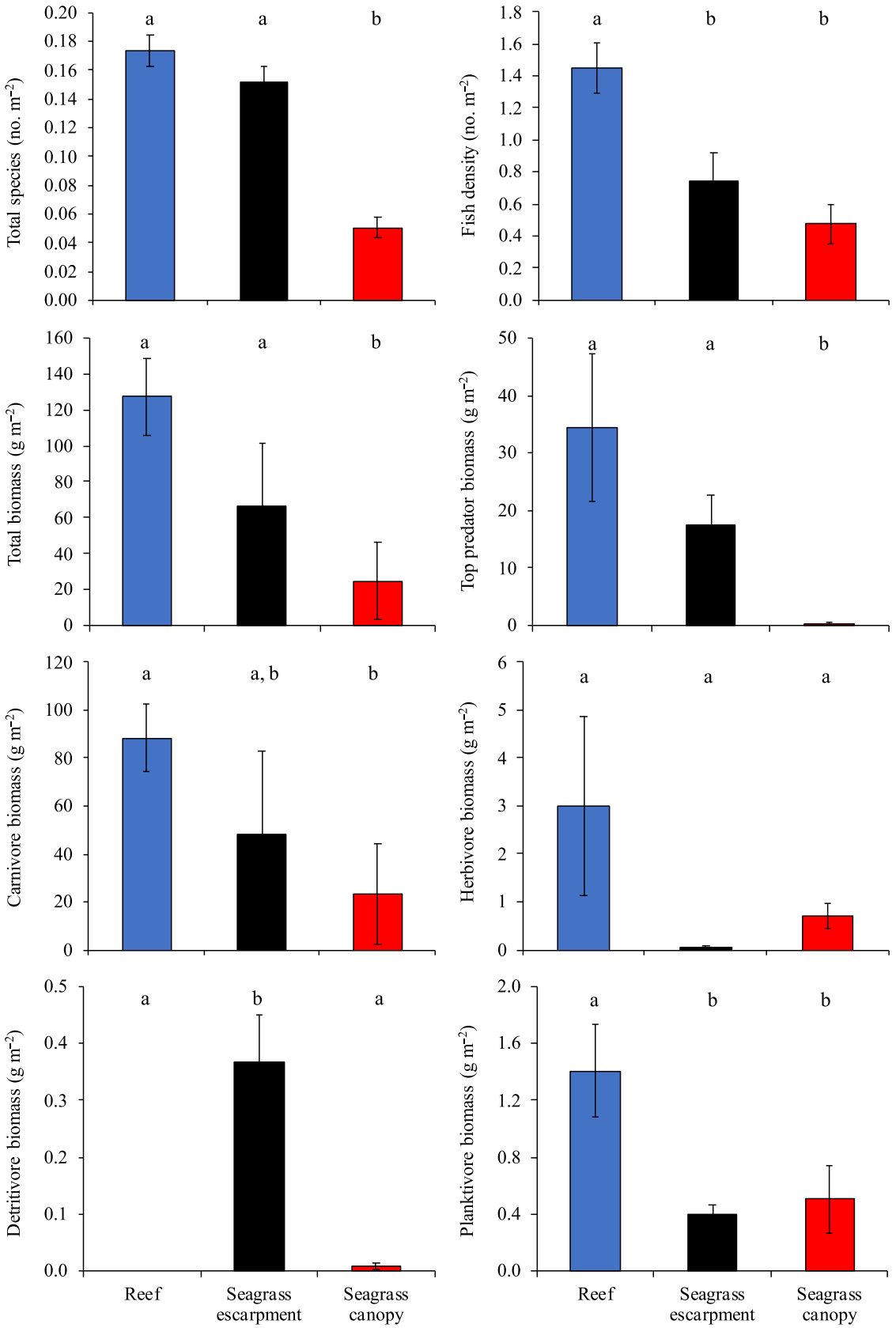

FIGURE 3 Total fish species, fish density, total fish biomass, top predator biomass, carnivore biomass, herbivore biomass, detritivore biomass, and planktivore biomass (mean ± SE) at three habitat types in Shark Bay. Different letters indicate significant differences ($p > 0.05$).

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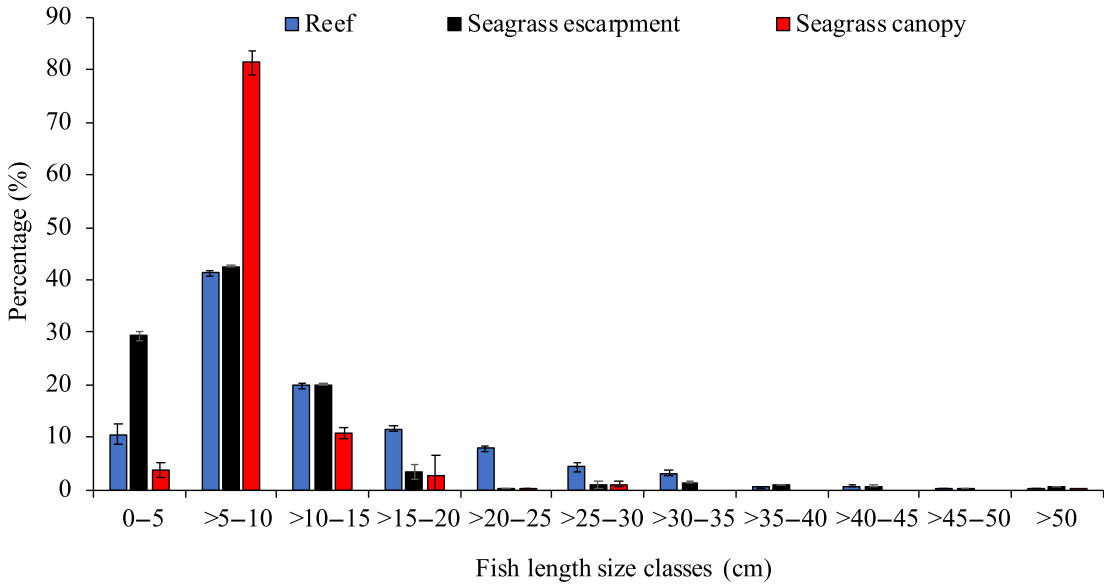

FIGURE 4 Size–frequency distribution (in percentage) of fish length size classes (in 5-cm intervals from 0 to >50 cm) across all fish species surveyed in reefs, seagrass escarpments, and seagrass canopies.

carnivore fish species such as *Epinephelus coioides*, *Lutjanus russellii*, *C. schoenleinii*, *M. strigatus*, *Abudefduf bengalensis*, and *Labracinus lineatus* that were scarce or absent in seagrass canopies, which supports the hypothesis that seagrass escarpments provide habitat for reef fishes. The presence of a 3D habitat within seagrass meadows provides another level of habitat complexity across the seascape and is particularly important in areas with limited reef habitat, such as in Shark Bay where it likely enhances fish biodiversity and biomass compared with homogeneous seagrass canopies, and connectivity among reef habitats.

Natural history of seagrass escarpments

Our surveys showed that escarpments suitable for reef-associated fishes are only found along the edges of some *P. australis* meadows, whereas meadows formed by *Amphibolis* spp. (*A. griffithii* and *A. antarctica*) or other ephemeral and small species do not form escarpments (e.g., genera *Halophila*, *Halodule*, and *Syringodium*) probably due to their limited rhizosphere. The height and length of the escarpments within Shark Bay were highly variable, ranging from 48 to 161 cm (100 ± 9 cm) and from a few meters to >1000 m, respectively. Indeed, the degree of inclination of the escarpments observed ranged from 60 to 140°, with a predominance of inclined escarpments formed by dead *P. australis* matter but covered by ephemeral seagrass species such as *Halophila* and *Cymodocea*. Escarpments with inclinations >100° were excluded from this survey because typically caves and ledges are not found and thereby constitute habitats with low structural complexity. It was observed that escarpment structural complexity, including the presence of overhangs from the edge of the escarpments and fallen portions of seagrass peat in front of the escarpment, provides additional structural complexity that attracts larger fish abundance and biodiversity.

The origin (biological and/or geological) of caves along the base, middle, and top edge of the escarpments remains unknown, but it seems plausible that fishes deliberately dig or burrow holes, as previously shown in other soft substrates (Mueller, 2015). In particular, at Big Lagoon, we observed a 1.5-m^3 cave with four tubular entrances and exits crossing several meters of seagrass peat, including one at the top of the escarpment within the living *P. australis* meadow. To the best of our knowledge, physical processes cannot result in the formation of these structures, and the presence of large and abundant *E. coioides* in the cave moving in and out suggests that fishes created these specific features that can simultaneously provide habitats for both subadult and adult predator and prey species.

Further studies are required to improve our understanding of the natural history of seagrass escarpments, such as reporting their distribution, size, and dimension elsewhere including genera other than *Posidonia* (e.g., *Thalassia*), and characterizing their mechanisms of formation and evolution. In addition, understanding the ecological importance of seagrass escarpments in enhancing fish biomass and biodiversity, as reproduction grounds, predator avoidance refuge or feeding areas, and acting as corridors enhancing connectivity among

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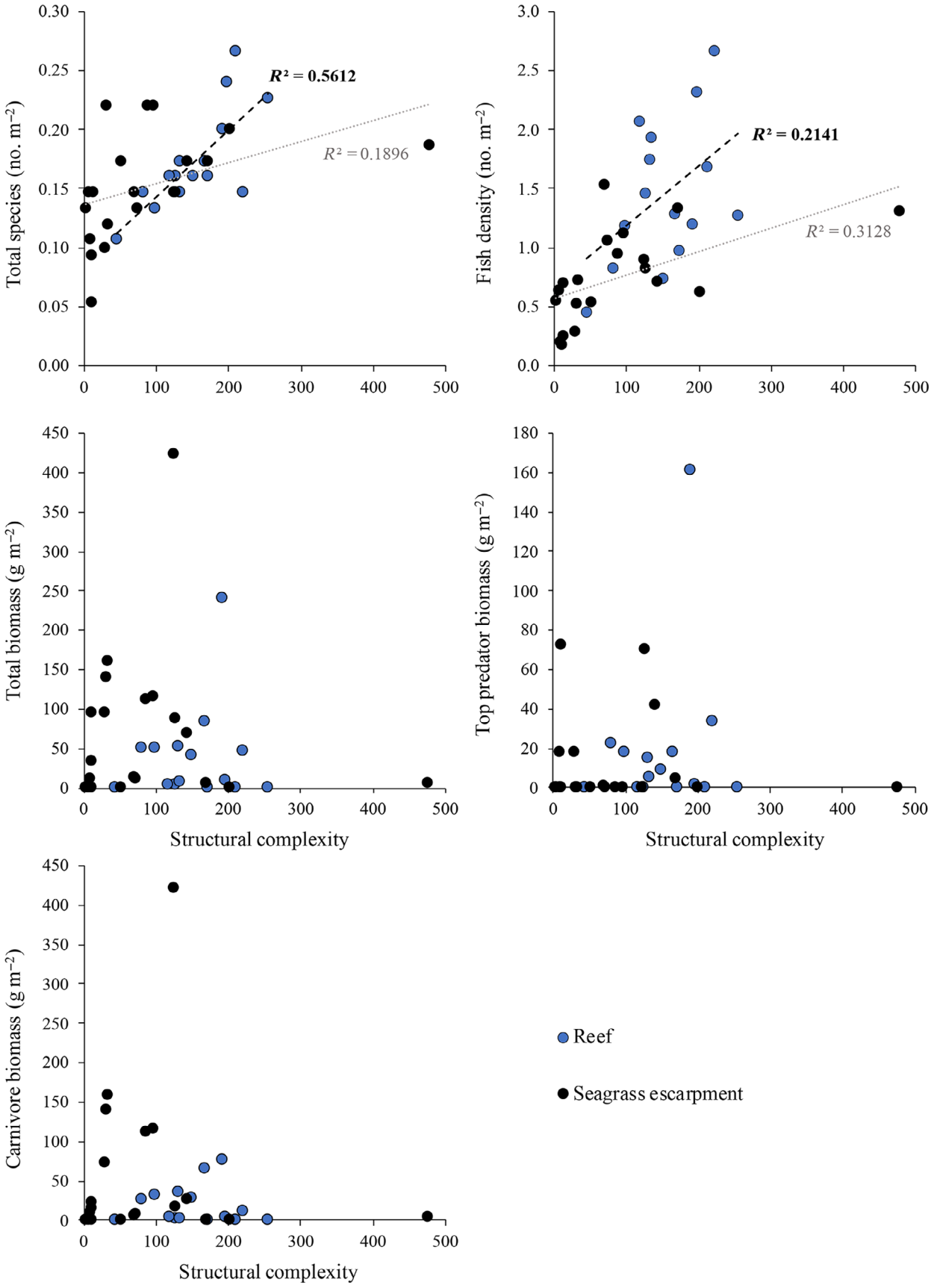

FIGURE 5 Relationships between habitat structural complexity and total species, total fish density, total fish biomass, top predator fish biomass, and carnivore fish biomass in reef (blue) and seagrass escarpment (black) habitats. Significant Pearson correlations ($p < 0.05$; R^2) are indicated with dotted lines for reef habitats and with dashed lines for seagrass escarpments.

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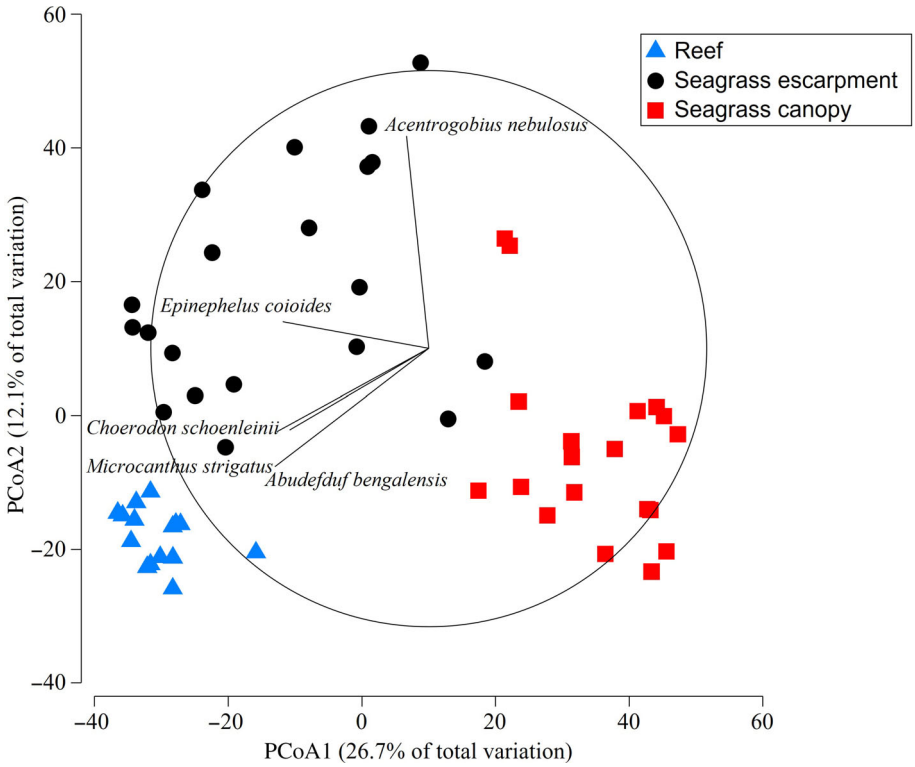

FIGURE 6 Principal coordinates analysis (PCoA) of fish biomass at reef, seagrass escarpment, and seagrass canopy habitats. Pearson correlation vectors overlaid to display fish species that contributed to >50% correlation.

isolated reefs should be further explored. The latter is particularly relevant within Shark Bay, owing to the scarcity of reefs but abundant seagrass meadows across vast areas within Faure and Wooramel banks (Bufarale & Collins, 2015).

Differences in fish assemblages among habitats

Our results revealed remarkable similarities in the total number of fish species, total fish biomass, and top predator biomass between reef and seagrass escarpment habitats, which can be related to resemblances in their structural complexity. Although seagrasses can offer shelter and food for a variety of fish species (Gullström et al., 2008; Thiriet et al., 2014; Verweij et al., 2006), the presence of top predators within seagrass canopies is rare. In agreement with previous studies showing strong relationships between structural complexity and reef fish communities (Darling et al., 2017; Friedlander & Parrish, 1998), the presence of ledges and caves up to 0.8 and 2.2 m^3 in both reef and seagrass escarpment habitats, respectively, provides habitat for large reef fishes. Both seagrass escarpments and reef habitats host similar assemblages of top predators and carnivore fish species such as *E. coioides*, *M. strigatus*, *C. schoenleinii*, and *Abudefduf bengalensis* that were absent or scarce in seagrass canopies. Caves are likely to constitute permanent dwellings for groupers and snappers, since they were shown to either inhabit caves or reside near the reef during the day. In addition, significant relationships between structural complexity and total species and fish density in seagrass escarpments support the hypothesis of increasing fish abundance with increasing habitat complexity (Figure 5). However, the lack of significant correlations between structural complexity and fish biomass in seagrass escarpments or reefs points to high variability in escarpment and reef geomorphologies and fish assemblages across the sites surveyed.

The large total fish density and biomass as well as carnivore biomass in reefs compared with seagrass escarpments could also be explained by the overall higher structural complexity of reef habitats (0.86 caves m^{-2}) compared with seagrass escarpments (0.28 caves m^{-2}) that can provide more shelter to relatively bigger fishes (Figure 4). The presence of *A. nebulosus* within and at the base of seagrass escarpments, thriving in fine sand to muddy substrate intertwined with seagrass matter, differentiated fish assemblages from the other habitats. Conversely, the relatively high abundance of the large-sized *C. cyanodus* inhabiting reef habitats resulted in higher carnivore biomass in reef compared with seagrass escarpments (Figure 5). The primary drivers of

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differences in fish biomass between reef and seagrass escarpments were linked to the more complex habitat in the former providing more suitable habitat for *O. rueppellii*, *E. coioides*, *C. marginalis*, *C. schoenleinii*, *M. strigatus*, and *A. bengalensis*, whereas *Acanthopagrus latus*, *Acanthurus grammoptilus*, *Cheilodactylus gibbosus*, *C. cyanodus*, *Gymnothorax undulatus*, *Lutjanus carponotatus*, *Pagrus auratus*, *Scarus ghobban*, and *Thalassoma lunare* were only found in reef habitats (Appendix S1: Table S2). The absence of these species in both seagrass canopies and escarpments could also be linked to the more diverse and complex reef habitats (Komyakova et al., 2013). The size of fishes in seagrass canopies (ranging mainly from 0 to 20 cm) linked to carnivore, herbivore, and planktivore trophic groups resulted in overall smaller fish biomass and density compared with seagrass escarpments and reefs, whereas the lack of reef-type habitat resulted in a relatively lower total number of species (Figures 3 and 4). The primary drivers of differences in fish biomass between seagrass canopies and escarpments were linked to the less complex habitat in the former providing a more suitable habitat for planktivore (i.e., *Atherinomorus endrachtensis*, *Hyporhamphus quoyi*) and herbivore (i.e., *Pelates octolineatus*) fishes that were only found in seagrass canopies. Overall, seagrass escarpments contribute to the complexity of seascape elements and the availability of alternative habitats within relatively homogenous seagrass meadows (Máñez-Crespo et al., 2022; Zubak Čižmek et al., 2021), impacting the fish structure. Further studies should examine fish assemblages across seasons and for cryptic species to test our conclusions.

Preliminary estimates of the dimensions of seagrass escarpments in Shark Bay's inner embayment using Google Earth imagery (~200 linear km long and 1 m in average height; 200,000 m^2 in area) suggest that seagrass escarpments in the bay support 13.4 Mg of fishes and 3.6 Mg of top predator species of commercial interest. Further surveys are required to verify the total fish stocks supported by seagrass escarpments at Shark Bay, in part to promote seagrass conservation strategies owing to the recent loss of 1000 km^2 of seagrass during a marine heat wave in 2010/2011 and associated impacts on marine fauna (Arias-Ortiz et al., 2018; Nowicki et al., 2017), as well as the predicted poleward retraction of *Posidonia* spp. over the next century due to ocean warming (Hyndes et al., 2017).

This study shows that seagrass escarpments are a novel and understudied ecosystem that can sustain fish biodiversity and biomass resembling rocky reef habitats, which adds to the growing knowledge around seagrass ecology, reinforcing the importance of the ecosystem services they provide, including sustained biodiversity and fisheries, and the need for further conservation and restoration actions. This is particularly relevant for the World Heritage-listed Shark Bay, where a marine heat wave decimated 25% of total seagrass extent (equivalent to 1000 km^2; Arias-Ortiz et al., 2018), and seagrass escarpments appear to supplement or support populations of reef fish species due to the scarcity of reef across the bay.

AUTHOR CONTRIBUTIONS

Oscar Serrano and Enric Ballesteros conceived the idea and designed the study. Oscar Serrano, Karina Inostroza, Caitlin Rae, Glenn A. Hyndes, and Enric Ballesteros performed the fieldwork. Enric Ballesteros conducted the fish surveys. Oscar Serrano, Karina Inostroza, Alan M. Friedlander, and Eduard Serrano analyzed the data. Oscar Serrano and Karina Inostroza led the writing of the manuscript. All authors contributed substantially to the drafts and gave final approval for publication.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

Data (Serrano et al., 2023) are available from Digital. CSIC: https://doi.org/10.20350/digitalCSIC/15298.

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