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RESEARCH ARTICLE

Getting edgy: implications of fragmented seagrass meadows for fish assemblages

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Abstract

Context Seagrasses are key marine habitats that are increasingly degraded globally due to anthropogenic disturbances and climate change, compromising the ecosystem services they provide. While seagrass loss is often patchy, the ecological consequences of meadow fragmentation on marine fauna remains unclear.

Objectives This study (1) quantified decadal change in seagrass habitat and fragmentation of the globally important meadows of the Shark Bay World Heritage Area following the 2011 marine heatwave (MHW); and (2) assessed how meadow structure and fragmentation influence fish assemblages.

Methods We integrated in situ seagrass data with seascape metrics derived from habitat maps generated from satellite imagery to characterize temporal changes in meadow structure. Seagrass data and seascape metrics were related to fish abundance, diversity and productivity using fish data collected from trawls and unbaited remote underwater video (URUV).

Results A temporal lag in dense seagrass loss (1382 Ha) occurred approximately six years post-MHW; with an increase in sparse patches, indicating fragmentation. Greater cover of seagrass at the local meadow scale (~50 m^2) positively influenced the abundance, biomass and net productivity of small-bodied fishes collected in trawls. The high structural complexity of *Amphibolis antarctica* dominated meadows benefitted small-bodied fishes. URUVs recorded more large-bodied, mobile fishes near channels, possibly reflecting the importance of these areas facilitating habitat connectivity of adult fishes.

Conclusions Canopy-forming seagrass habitat are important for fish communities, and MHWs may

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impact small-bodied fishes via reductions in seagrass cover. These findings support management approaches that prioritise the conservation of patch connectivity and high seagrass cover in shallow coastal systems.

Keywords Seascape ecology · Fragmentation · Marine heatwave · Habitat loss · *Amphibolis antarctica* · *Posidonia australis*

Introduction

Climate change is driving profound shifts in the quality and quantity of foundation habitats, contributing to global reductions of biodiversity (Hanski 2011; Horváth et al. 2019). Both press and pulse pressures are contributing to changes in landscape structure, the degradation of ecologically important habitats, including reductions in structural complexity that can have lasting impacts on ecosystem function (Ellison et al. 2005; Hoegh-Guldberg and Bruno 2010; Holyoak and Heath 2016; Liu et al. 2018; Fischer et al. 2021; McCoy et al. 2022). Specifically, reduced biodiversity of faunal communities has been linked with loss of habitats such as temperate forests, riparian vegetation and saline ponds (Hanski 2011; Horváth et al. 2019). Marine foundation species that exist near their thermal biogeographical limits are especially vulnerable to impacts associated with elevated temperatures and large-scale stochastic climatic events (Mantyka-pringle et al. 2012; Thomson et al. 2015; Skirving et al. 2019). While our knowledge on the effects of warming on individual foundational species is growing (McClanahan et al. 2020; Nguyen et al. 2021), the flow-on effects from habitat loss, and the resulting fragmentation of habitat-forming species on faunal diversity, abundance and productivity remains comparatively limited.

Fragmentation, the process of breaking apart habitats into smaller, patchier, more isolated fragments (Fahrig 2003), can reduce the quantity and quality of habitat available for taxa (Horváth et al. 2019) with negative effects on biodiversity and ecosystem functioning (Liu et al. 2018). For example, fragmentation of saline pond habitat over 60 years led to reduced local and regional faunal diversity and the extinction of 22 species (Horváth et al. 2019). The effects of habitat fragmentation on faunal communities in terrestrial landscapes, such as grasslands, tropical and boreal forests, have been well-studied (Harrison and Bruna 1999; Fletcher Jr 2005; Murray et al. 2017; Taubert et al. 2018), and this approach is increasingly used to explore similar relationships within the seascape (Fahrig 2003; Pittman 2017). Various landscape ecology approaches have been applied in marine ecosystems, demonstrating that the spatial configuration and composition of seascapes influences the abundance, diversity, and assemblage composition of marine organisms (Grober-Dunsmore et al. 2009; Boström et al. 2011). A global review by Olds et al., (2016) further demonstrated that higher levels of seascape connectivity within marine reserves are associated with enhanced conservation outcomes and reserve performance.

Seagrass meadows are globally extensive coastal ecosystems that underpin fundamental ecological processes (Waycott et al. 2009; Unsworth et al. 2018). Meadows offer protection from predators, act as nursery grounds, provide trophic subsidies, and serve as foraging habitats for fishes across various life stages (Heck et al. 2003; Horinouchi 2007; Hyndes et al. 2018). Indeed, seagrass meadows support the productivity of 20% of the world's top 25 fisheries (based on tonnes landed, (SOFIA 2016). In particular, the slow-growing seagrass species (e.g. *Posidonia* spp., and *Amphibolis* spp.,) harbour high levels of epiphytic algal growth and abundant epifaunal communities offering fish plentiful food and shelter (Jernakoff and Nielsen 1998). Yet despite their importance, seagrass meadows are among the most threatened ecosystems globally due to pressures associated with climate change and anthropogenic activities (Dunic et al. 2021). Large-scale loss of seagrass has been linked with negative impacts on associated fauna (Kendrick et al. 2019). For example, seagrass loss in the North Atlantic resulted in the collapse of fisheries, reduced waterfowl populations and the extinction of a marine gastropod (Carlton et al. 1999; Orth et al. 2006). Reductions in seagrass cover following a disturbance is typically uneven, increasing the patchiness of meadows and fragmentation of the seascape (Strydom et al. 2020). Whilst reductions in seagrass habitat are known to detrimentally impact seagrass-associated fauna, the effects of seagrass meadow fragmentation remain complex.

Seagrass fragmentation can lead to reduced availability of foraging and refuge habitats, have negative effects on predator–prey relationships, and impede

fauna movement rates among patches (Irlandi et al. 1995; Hovel and Regan 2008; Williams et al. 2016). The magnitude of the effect of seagrass fragmentation on fish can depend on traits such as feeding guild, preferred microhabitat, life-history stage, predation style, and home-range size (Hyndes et al. 2018). For example, juvenile fishes are generally reliant upon complex habitat such as seagrass or macroalgae as they offer refuge from predators and increased quantity and quality of food resources, which can facilitate higher growth and survival rates compared to unstructured habitats (Kimirei et al. 2013; Grol et al. 2014). Moreover, fishes exhibit strong, but variable responses to seagrass edges. Indeed, patch edge effects are arguably complicated with responses varying among fish species, meadow patch size, and with time from fragmentation events (Connolly and Hindell 2006; Macreadie et al. 2009). Generally, benthic fishes respond more positively than benthopelagic fishes to edge effects likely due to the increased positive density response of their prey (i.e. epifaunal invertebrates) (Yarnall et al. 2022). For example, strong positive effects of increased patch edge were documented for pipefish, weedfish and gobies in *Zostera* meadows, whereas semi pelagic garfish and transient weed whiting were negatively affected (Smith et al. 2008). In addition, edge specialists like pipefish may benefit rapidly from fragmentation, while generalist and interior specialists may take longer (Macreadie et al. 2009).

Research suggests that patterns in faunal abundance and diversity are shaped by both within-patch (e.g. seagrass shoot density or cover), and seascape-scale factors (e.g., proximity to other habitats or configuration of patches) (Hovel and Lipcius 2001; Horinouchi 2007). Although, there are inconsistencies in the relationships between seascape metrics and species responses (Vega Fernández et al. 2005), the nature of these relationships often depends on spatial scale (Boström et al. 2011). For example, positive relationships occur between seagrass density and the abundance of small (resident and transient) fish within individual seagrass meadows (Bloomfield and Gillanders 2005), but this relationship may not apply at larger spatial scales. Bell & Westoby (1986) showed that sparse meadows may harbour higher fish densities than dense meadows. Local-scale seagrass patch area may also predict diversity in some locations (Boström et al. 2011), but patch size alone did not always account for variation in faunal abundance (Bell et al. 2001). When faunal abundance varies with patch size, these results often indicate the presence of an edge effect (Bell et al. 2001; Healey & Hovel 2004). Therefore, a multi-scale approach is essential when attempting to assess predictors of fish community structure in seascapes (van Lier et al. 2018; Moustaka et al. 2024a, b).

The unprecedented marine heatwave (MHW) of 2011 in the eastern Indian Ocean led to the loss of approximately 1000 km^2 of foundation seagrass habitat across the Shark Bay World Heritage Area (13,000 km^2) in Western Australia; the largest decline of dense seagrass habitats globally (Strydom et al. 2020). This MHW-induced seagrass loss impacted commercial fisheries (e.g. blue swimmer crabs, scallops) and iconic species such as green turtles, pied cormorants and sea snakes (Kendrick et al. 2019). However, the impacts on marine fauna were assessed in relation to overall seagrass loss, and the impacts of habitat fragmentation on seagrass-associated fish communities remain unknown. Here we use spatial pattern analysis to describe temporal changes of within patch and seascape-scale seagrass habitat quality (Strydom et al. 2020). We used metrics of seascape structure and patch dynamics to describe seagrass fragmentation and assessed the influence of these metrics on the composition of fish communities. Specifically we 1) temporally quantified seagrass seascape metrics pre- and post- MHW in the Shark Bay World Heritage Area, and 2) determined which meadow characteristics best predicted aspects of fish community structure. In doing so, we have offered novel insights into the effects of seagrass fragmentation on fish communities and discuss implications for management.

Methods

Study region

Monkey Mia is located within the Shark Bay Marine Reserves and World Heritage Area (Fig. S1), 800 km north of Perth, Western Australia (25°47′26′′S, 113°43′12′′E). This region is renowned for its remarkable marine biodiversity, and globally significant

seagrass meadows that support fauna such as dugongs, sea turtles, tiger sharks, and economically important fisheries (Preen et al. 1997; Heithaus et al. 2012; Christensen and Jackson 2014; Caputi et al. 2016). The coastline of Monkey Mia is lined with shallow seagrass meadows and deep sand channels; dominated by slow-growing temperate seagrasses *Posidonia australis* and *Amphibolis antarctica*, which have large canopies (i.e. mean canopy heights of 35 cm to 55 cm respectively based on values measured across sites in this study). These canopies are comparatively larger and denser than those of the smaller species (*Cymodocea angustata*, *Cymodocea serrulata, Halodule uninervis,* and *Halophila ovalis*) present in Shark Bay (Walker et al. 1988). Temperate seagrasses generally have persistent life-history traits, whereas the fast-growing tropical seagrasses are usually colonizing and ephemeral in nature. Furthermore, *P. australis* blade-like leaves grow from fury sheaths emerging from the sediment (Kuo and McComb 1989) and *A. antarctica* meadows provide a distinct architecture of a dense leafy canopy growing above a forest of erect stems. Seagrass loss in this region of Shark Bay was extensive following the MHW (Strydom et al. 2020), making it an ideal area to investigate fragmentation of seagrass habitats and how this may affect fish assemblages.

Mapping seagrass extent

Satellite imagery-derived habitat maps were used to provide assessments of spatial and temporal change in seagrass extent and density (sparse: 5–40% cover and dense: > 40% cover) at the seascape scale (Strydom et al. 2020). Total seagrass extent was defined as total seagrass area (Ha) within the Monkey Mia study site boundary and was mapped for years 2010, 2013, 2016 and 2020 by classifying 2 m resolution World View 2 (WV2) imagery (Digital Globe) tasked capture on 07/05/2010 and 03/06/2013. Sentinel 2 10 m resolution multispectral satellite imagery was classified for 12/10/2016, 24/06/2019 and 06/09/2020 (European Space Agency). Imagery dates reflect winter and spring months which often provide clear imagery free of wind effects and turbidity thus avoiding interference with image classification. These years were selected due availability of clear imagery and ground-truthing data, as well as spanning a period before and after the 2011 MHW. Classification, water correction, ground truthing, and validation processes (see Table S5 and S6) were conducted as described in Strydom et al. (2020), with the exception of WV2 imagery channel areas. These were removed from processing for 2010 and 2013 as ground-truthing indicated these channel areas were dominated by sand, not seagrass, and depth compromised a clean classification of seagrass in the adjacent areas. A bathymetry model was utilised for all years of classification (Patterson 2012). In preparation for fragmentation analysis, the 2010 and 2013 seagrass extent and density raster classifications were cleaned to fill holes and speckle using focal statistics and a 5×5 cell (10 m) majority filter from Spatial Analysis ArcGIS (ESRI 2017). The 2010 and 2013 raster products where then resampled to 10 m and products for all years were converted to vector format for spatial fragmentation analysis.

Seascape metrics to characterise temporal change in seagrass meadows

Applying seascape metrics to remotely sensed habitat classifications for each year allows the assessment of spatial and temporal change in meadow configuration (Clemente et al. 2023). Multiple metrics for evaluating spatial patterns were selected based on previous seagrass studies that have used such metrics to quantify changes in seascape habitat shape, configuration, and density (reviewed by Boström, 2006). The spatial metrics commonly used throughout the literature are cell, patch, class, and landscape (McGarigal 2012). The cell being the smallest level of resolution (e.g., pixel in a raster benthic map), the patch is the finest grouping of cells such as a polygon, a class is a group of patches within the same type (several polygons of dense seagrass) and landscape (or seascape) is a combination of all classes within the mapped area of focus. Note that during the analyses in this study patch level metrics were calculated using Rook's case (i.e., four directions of cell adjacencies considered neighbours). The landscapemetrics package (version 1.55, Hesselbarth 2019) was used to calculate metrics perimeter (m; PERIM), area (Ha; AREA), perimeter to area ratio (PARA), class area (Ha), number of patches and total edge (km) on each seagrass extent shapefile for 2010, 2013, 2016 and 2020 (see Table S1). Additional metrics such as landscape shape index, largest patch index, landscape division, gyrate and patch isolation were explored in the seascape (based on Sleeman et al.

2005; some presented in Supplement, Fig. S4). However, to prevent redundant measurements of similar spatial attributes not all of these indices were used in further analyses. Justification for inclusion in the analysis is provided in Table S1.

Seascape metrics calculated for 2019 to inform fish site selection

To investigate the influence of seagrass meadow characteristics and seascape metrics on fish communities, a seagrass habitat map was classified for sparse and dense categories using a 2019 image to identify a range of appropriate seagrass patches to conduct fish surveys. To characterise patch dynamics in the seascape, the following values were calculated: Euclidean distance from each seagrass patch to land (m), nearest neighbouring patch (type, distance and angle), and patch shape complexity using the shape complexity index tool in ArcGIS (ESRI 2017). Additionally, distance to nearest channel (m) was measured from the patch centroid using the distance tool in QGIS (2020). Patches had 50 m and 500 m buffers overlaid from each patch centroid. These radii were selected based on likely home range estimates of both large- and small- bodied fish communities (Green et al. 2000; Nash et al. 2015; van Lier et al. 2018). Metrics consistent with other seascape ecology studies with an ecologically meaningful approach for migrating fishes (e.g., Pittman and McAlpine 2003; Berkström et al. 2013) were calculated within each buffer zone: PERIM, AREA, and PARA. Based on these characteristics 20 sampling patches were selected as they captured a gradient across these attributes within which fish communities could be assessed.

Fish surveys and analyses

A combination of trawling and stationary video methods were used to detect the mobile above-canopy (supra-frond) fish assemblage and within-canopy (inter-frond) fish species respectively. While remote underwater stereo-video systems are a common non-extractive method for assessing fish length, relative abundance, and biomass (Schramm et al. 2020) they have a limited ability to detect cryptobenthic species (Watson et al. 2010; Whitmarsh et al. 2017). As such, the two methods employed here are complimentary and capture a holistic view of fish community structure, both above and within seagrass meadows (French et al. 2021) (Fig. 1). To quantify fish assemblages in seagrass patches with varying characteristics, one unbaited remote stereo-underwater video (URUV) deployment and one beam trawl were conducted per seagrass site (n = 20, Fig. S1). Both methods were used in the same patch on the same day with the URUV deployment preceding the trawls and all samples were collected over 3 days in September 2020.

Trawl surveys

One trawl was cast in a straight line over 50 m through the centre of the seagrass patch using a beam trawl frame (1.1 m wide and 0.5 m high) with smooth sled shoes and a roller-bar that flattened seagrass leaves while the sled moved forward thus minimising damage to seagrass. Attached to the trawl frame was a net (2.5 mm mesh size) and a tapered cod-end (1.0 mm mesh size) in which fish were funnelled (Hyndes et al. 2003; French et al. 2021). Fishes were removed from the cod end and euthanized immediately using an ice slurry (Blessing et al. 2010). All fishes were later identified to species level and standard length (SL; mm), total length (TL; mm), and wet weight (g) recorded. Total biomass of each trawl was calculated as the summed weight of individuals in the trawl per site.

URUV surveys

The above-canopy component of the fish assemblage was captured by deploying one unbaited remote stereo-underwater video (URUV) system with an empty bait bag for a 30-min soak time at each site following standard methods (Langlois et al. 2018). While baited remote underwater video systems (stereo-BRUV) are also useful for determining abundance and size of fishes (Langlois et al. 2020), the bait plume attracts fish from other habitats (i.e., sand or other seagrass patches) making it difficult to relate the fish assemblage to the seagrass patch characteristics (Taylor et al. 2013; Galaiduk et al. 2017; Perry et al. 2018; Mallet et al. 2021). All sampling was conducted during daylight hours between 08:45 and 15:45 to avoid crepuscular periods (Langlois et al. 2020). The stereo-video footage from the URUV drops were analysed using EventMeasure (SeaGIS Pty Ltd). All fish within the field of view were counted, identified to the

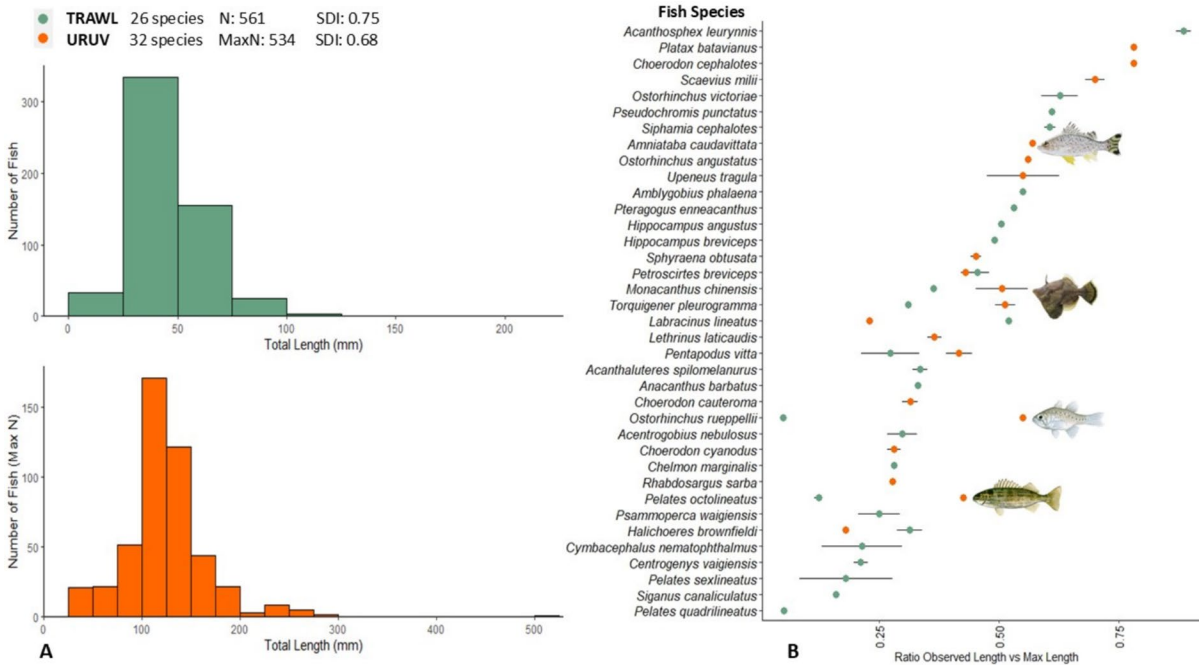


Fig. 1 **A** Length frequency histograms for both fish communities, note SDI values are Simpson's Diversity Index (SDI). **B** Maturity of fish collected by trawl or observed on URUV, as indicted by observed length divided by maximum possible length, (referred to as OL:ML). Values are mean OL:ML ± SE per fish species. Instances with both trawl (teal) and URUV (orange) points indicates OL:ML values for that species using that method. Fish icons represent that most abundant taxa: *Amniataba caudavittata, Monacanthus chinensis, Ostorhinchus rueppellii,* and *Pelates octolineatus* in order from top to bottom

highest possible taxonomic resolution, and their fork and total length measured, where possible. Abundance was quantified using MaxN, the maximum number of individual fish per species present in a single video frame (Langlois et al. 2020). MaxN is a conservative estimate of relative abundance that is accepted as the standard metric because it avoids duplicate counting of individual fish. In instances where fish could not be measured but species identification was possible, the median length of the species (calculated based on individuals of that species at that site) was used as a proxy. In order to directly compare fish lengths between URUV and trawl methods, length-length conversions were obtained from FishBase to convert URUV fork length to total length (mm) before plotting length frequency (Fig. 1). Fish biomass was calculated by using length to weight ratios obtained from FishBase (Froese and Pauly 2022) to calculate the weight of individuals.

Fish assemblage metrics

Total fish abundance, biomass, net productivity, average taxonomic distinctness, mean total length, observed length/maximum length (OL:ML), species richness, and Simpson's Diversity index were calculated separately for trawl and URUV data collected at the site level.

As diversity is an important consideration for conservation management and can be sensitive to changes in habitat composition (Graham et al. 2003; Warwick & Clarke 1998), we used a combination of metrics (average taxonomic distinctness, species richness, and Simpson's Diversity index) to capture different aspects of biodiversity (Ellingsen et al. 2005) using the vegan package (version 2.7–1) and R language for statistical computing (Oksanen et al. 2020). Taxonomic distinctness was measured because it captures phenotypic differences and functional richness (i.e. the degree to which species are related) (Warwick and Clarke 1998). Additionally,

we included species richness (irrespective of abundance) and the Simpson's Diversity index, the latter of which considers number of species present relative to abundance.

Basic parameters of fish population dynamics are strongly related to maximum length (Froese and Binohlan 2000). To approximate the life history stage of fish the variable OL:ML was quantified by dividing observed measured total length (OL) by maximum total length (ML). Whilst standing biomass of fish is an intuitive concept and robust indicator of population and community condition, quantifying fish productivity provides additional information on a process relevant to fisheries yields and trophodynamics (Rogers et al. 2014; Robinson et al. 2019; Morais and Bellwood 2020). Moreover, biomass and productivity may be decoupled, particularly where biomass of fishes is depleted (Morais et al. 2020). Net productivity of fish assemblages was estimated from trawl and URUV data following the methods of Morais & Bellwood (2020) and using the rfishprod package (version 0.0.3) in R. This method utilises a trait-based approach that incorporates information on the diet, position (where position is analogous to the term 'reef position' in Morais et al. 2018), and maximum reported length for each species, as well as the mean sea surface temperature (SST) of the study region, to estimate K_{max} (the growth coefficient at a theoretical maximum size) (Morais and Bellwood 2018). Trait information for each species (or a congeneric species) was obtained from FishBase (Froese and Pauly 2022). Some juvenile fish recorded on URUVs could not be identified beyond Family and were therefore excluded from biomass and productivity estimates (4% of total fish were excluded). The mean satellite-derived SST for the study location was calculated for the month in which surveys were conducted (September 2020) using data obtained from the NOAA ERDDAP server (dataset ID: jplMURSST41; (Chin et al. 2017). To convert lengths to daily somatic biomass increase, each fish was first placed within its respective growth curve and its daily growth in length estimated following the von Bertalanffy growth function (Von Bertalanffy 1949):

$$L_{t+1} = \left(L_{max}1 - exp\left(-K_{max} \times t\right)\right)$$

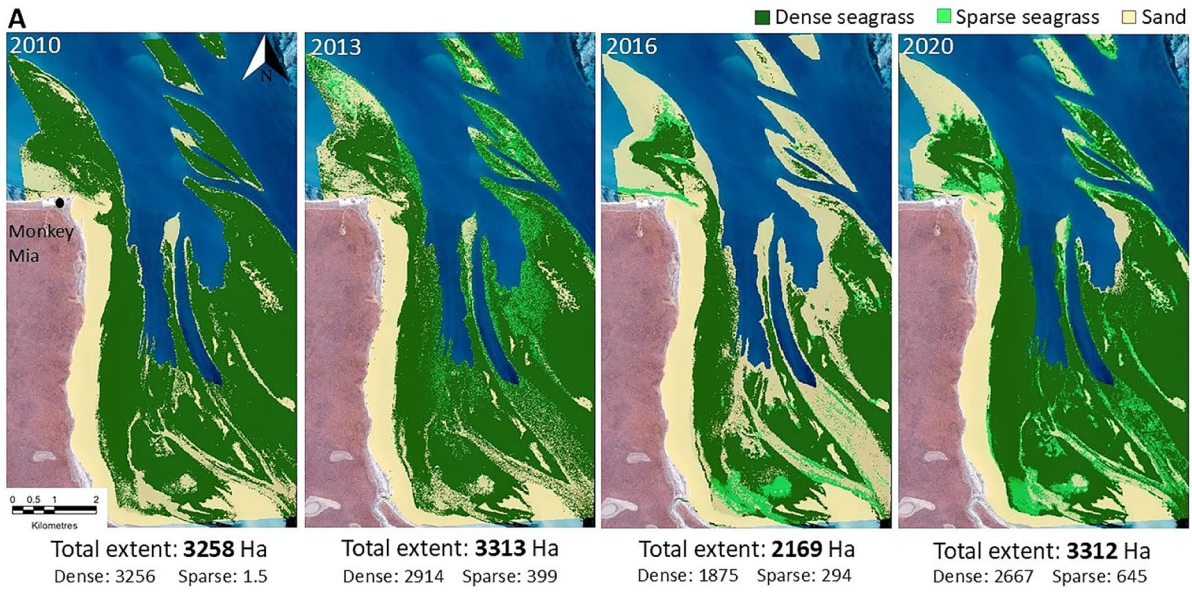
where L is the total length of the fish (cm) and t is the estimated age of the fish (days), simulated as being derived from otolith increment analysis (Morais and Bellwood 2020). Estimated length increases are converted to somatic mass using species-specific length–weight relationships obtained from FishBase (Froese and Pauly 2022). The probability of natural mortality was subsequently estimated for each fish using the Lorenzen size-based mortality risk function (Lorenzen et al. 2022). As natural mortality of fishes is stochastic and probabilistic in nature, this process was bootstrapped 1000 times and net total productivity was calculated as the average summed somatic growth after one day of all surviving fish at each site (Morais and Bellwood 2020). We note that fishing mortality was not considered in productivity estimates and therefore, mortality may be underestimated for targeted fish in the dataset.

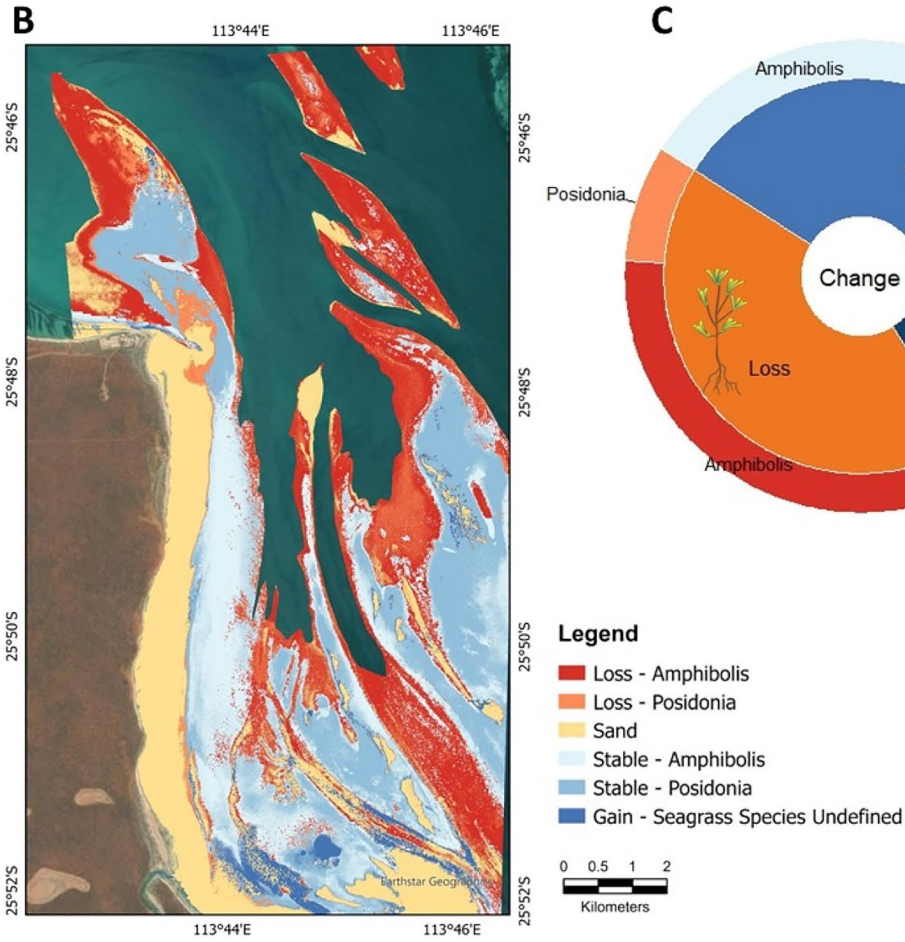
Seagrass meadow characteristics

The species composition and structural complexity of seagrass meadows are known to influence the abundance and diversity of fish assemblages (Heck et al. 2003; Bloomfield and Gillanders 2005; Hyndes et al. 2018). Therefore, once URUV and trawl fish surveys were complete, within-patch seagrass characteristics were measured at each seagrass patch where fish surveys were conducted. Five random replicates of canopy height were measured in situ by holding a handful of seagrass shoots and measuring vertical height using a ruler from the base of the plant to the highest shoot (mm) (Short and Coles 2001). Percent cover (%) of the dominant seagrass species was assessed visually by a single experienced observer and recorded (predominantly *P. australis*, or *A. antarctica*). Site depth (m) was recorded using the boat sounder at the same time seagrass measurements were taken.

Data analyses

Relationships between environmental predictor variables and fish assemblage response variables were investigated using a full subsets approach (FSS) and generalised additive mixed models (GAMMs) (Fisher et al. 2018). Separate FSS GAMMs were conducted for each response variable and for each sampling method. For the fish community level analyses, the response variables were total fish biomass (g), total abundance, mean length (cm), OL:ML, species richness, Simpson's Diversity index, and average taxonomic distinctness calculated at the site level. The


A
Dense seagrass
Sparse seagrass
Sand
2010
2013
2016
2020
Monkey Mia
0 0.5 1 2
Kilometres
Total extent: 3258 Ha
Dense: 3256 Sparse: 1.5
Total extent: 3313 Ha
Dense: 2914 Sparse: 399
Total extent: 2169 Ha
Dense: 1875 Sparse: 294
Total extent: 3312 Ha
Dense: 2667 Sparse: 645


B
113°44'E
113°46'E
25°46'S
25°48'S
25°50'S
25°52'S
C
Amphibolis
Posidonia
Stable
Posidonia
Change
Loss
Gain
Amphibolis
Seagrass
Legend
Loss - Amphibolis
Loss - Posidonia
Sand
Stable - Amphibolis
Stable - Posidonia
Gain - Seagrass Species Undefined
0 0.5 1 2
Kilometers

◂**Fig. 2** **A** Change in seagrass extent (Ha) in 2010, 2013, 2016 and 2020. Three main habitats were classified: dense seagrass (> 40% cover), sparse seagrass (5–40% cover) and sand (< 5% seagrass cover). The blue represents deep water channels where benthos could not be mapped with confidence. **B** Change in seagrass extent categorised by loss, stable, and gain from 2010 to 2016 in the Monkey Mia region. Loss and stable estimates were mapped to dominant seagrass species (*A. antarctica* and *P. australis*) and **C** proportional change values extracted and displayed as a donut chart

suite of predictor variables included site depth (m), distance to channel (m), distance to land (m), mean seagrass height (cm) and cover (%), seagrass class (i.e., *Amphibolis antarctica* and *Posidonia australis*), and three seascape seagrass metrics: area (Ha), perimeter (m), perimeter to area ratio measured within the 50 m and 500 m buffer areas (Table S1). Prior to analysis, distributions of predictor and response variables were inspected and transformed as required. Response variables were not transformed as the use of an appropriate error distribution (i.e. Tweedie for biomass, abundance, productivity, mean length, taxonomic distinctness, OL:ML, Simpson's Diversity index variables and Poisson for species richness) accounted for the non-normal distribution of data. The number of predictors in each model was limited to ≤ 2 (with interactions among terms prohibited), and smoothed using cubic regression splines to prevent overfitting. Models with correlated predictors (> 0.28) were removed automatically following pairwise correlation tests to avoid potential issues stemming from multicollinearity (Fisher et al. 2018; Graham 2003). The best models were selected based on Akaike Information Criterion, corrected for small sample sizes (AICc) and model weights. Further, models < 2 delta AICc were considered to have similar explanatory power and further model selection was based on model weight, parsimony and variable importance. Model weights were then summed for each variable to determine variable importance (see Fig. S2) (Burnham et al. 2011). A second set of FSS GAMMs were conducted to assess the influence of the same aforementioned predictor variables on the abundance of prominent fish taxa at an increased resolution (i.e. genus level). The genera with sufficient replication across sites to model were *Halichoeres, Monacanthus, Ostorhinchus, Pelates* and *Petroscirtes* for the trawl dataset; for the URUV models *Choerodon* and *Sphyraena* were used (Table S4).

Data wrangling was conducted utilising Tidyverse packages (version 2.0.0, Wickham 2019), spatial buffers calculated in sf version 1.09 (Pebedma 2018), spatial pattern metrics using landscapemetrics (version 1.55, Hesselbarth 2019), modelling using FSSgam (version 1.11; Fisher et al. 2018) and mgcv packages (version 1.9; Wood 2017), and gratia for plotting (version 0.9.2; Simpson 2024), using R Language for Statistical Computing (version 4.3.2; R Core Team 2023).

Results

Spatial and temporal changes in seagrass extent

Between 2010 and 2020 the total seagrass extent at Monkey Mia increased by only 1% (43 Ha); however, the proportions of dense and sparse seagrass fluctuated substantially during the study period. For example, while there was an overall increase of 53 Ha in seagrass extent between 2010 and 2013, dense seagrass declined by 344 Ha and a concomitant increase in the proportion of sparse seagrass, due to the 2011 MHW event (Fig. 2A). Further seagrass loss (1143 Ha) occurred between 2013 and 2016, with some recovery by 2020, although dense seagrass extent remained lower than pre-MHW levels present in 2010. Notable areas of decline were the outer north-eastern banks and the edges of large meadows near channels (Fig. 2B). Mapping indicated that areas that remained stable between 2010 and 2016 were comprised of 28% *P. australis* and 23% *A. antarctica* (Fig. 2C). Conversely areas that lost seagrass were initially comprised of 35% *A. antarctica*, and 8% *P. australis*. As such, *A. antarctica* was the highest contributor to seagrass loss post-MHW, particularly around the edges of continuous meadows, and near deep channels, whilst *P. australis* cover remained comparatively stable.

Temporal changes in seagrass extent and patch configuration were associated with an increased number of sparse seagrass patches and total length of patch edges (Fig. 3E; F). The number of seagrass patches increased dramatically between 2010 and 2013, most notably sparse seagrass patches, which were rare in 2010, before peaking in 2013 and remaining high relative to dense patches in subsequent survey years (Fig. 3F), indicating a more fragmented state following the 2011 MHW. The area of sparse seagrass meadows increased from

representing < 1% in 2010 to representing 7% of the seascape in 2020 (Fig. 3D), equating to an overall increase of 641 Ha since 2010. Conversely, the patch area of dense seagrass patches were highly variable during each survey year and went from comprising 35% to 28% of the seascape, representing an overall decline of 598 Ha between 2010 and 2020 (Fig. 3A). This increased occurrence of small, sparse seagrass patches also led to a greater patch perimeter in 2013 (Fig. 3B) and was associated with an overall increase in total edge present in the seascape between 2010 and 2020 (Fig. 3E).

Fish community structure

Trawl and URUV surveys captured distinct components of the fish assemblage in Monkey Mia both in terms of species composition and body size. 561 individuals (26 species) and 534 individuals (32 species) were identified from trawls and URUVs respectively. Fish caught in trawls were generally shorter in length (Fig. 1A). Of the 8 species that occurred across both methods, mean fish length was smaller in trawls compared to URUVs (Fig. 4), although most of the fish collected by both trawl and URUV were less than half their maximum length as indicated by OL:ML mean value of 0.363 across all fish species and both methods (Fig. 1B). Across both methods, the most abundant taxa were *Monacanthus chinensis* (n = 249), *Pelates octolineatus* (n = 161) and *Ostorhinchus rueppellii* (n = 108).

The combination of sampling methods provided an overview of how fish assemblage differs with respect to body sizes of fishes and habitat preference, which may be due to ontogenetic shifts in habitat use and/or fishing pressure. For example, URUV samples indicated that *P. octolineatus* dominated fish assemblages in *A. antarctica* meadows, while smaller conspecifics collected using the trawl were equally common in *P. australis* meadows. Trawl samples revealed four species unique to *A. antarctica* meadows: *Anacanthus barbatus*, *Acanthosphex leurynnis*, *Chelmon marginalis,* and *Psammoperca waigiensis*, while URUVs recorded an additional three species *Amniataba caudavittata, Chiloscyllium punctatum*, and *Choerodon cephalotes* (Fig. 4). *Halichoeres brownfieldi, M. chinensis, P. octolineatus, O. rueppellii, Siphamia cephalotes, Petroscirtes*

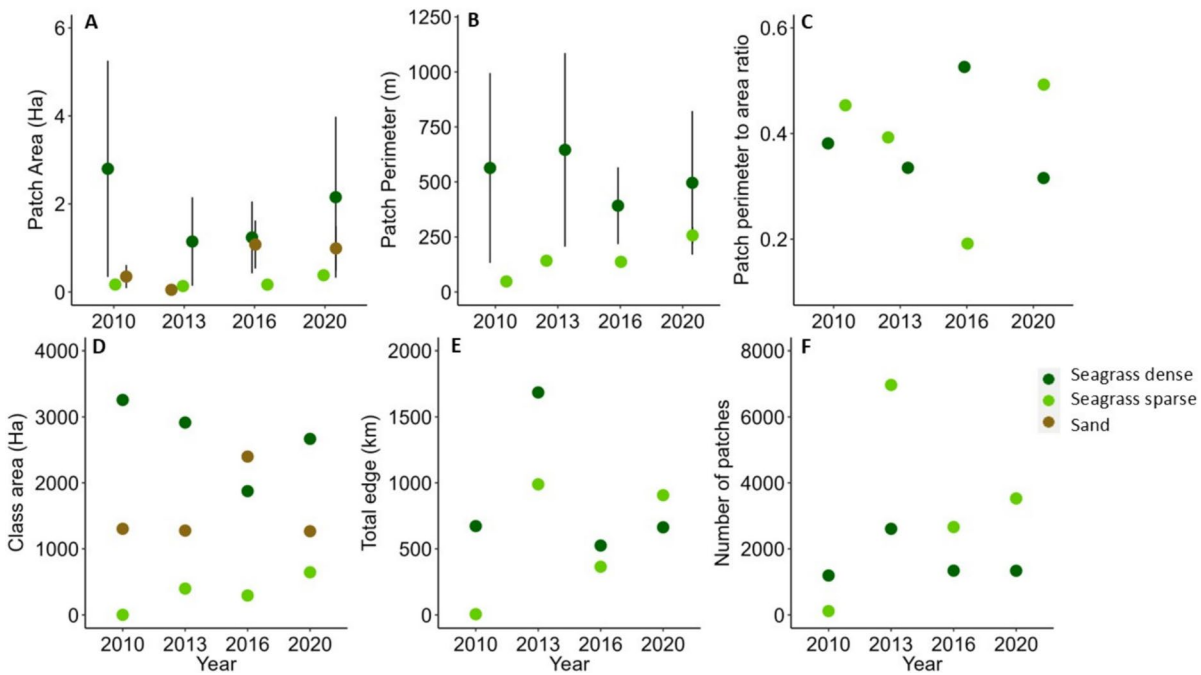


Fig. 3 Temporal change in spatial configuration metrics of seagrass at the patch and class level (A-F). Plots D, E and F do not have error bars because they are total values per year. Associated landscape scale graphs are located in the Supplement (Fig. S3)

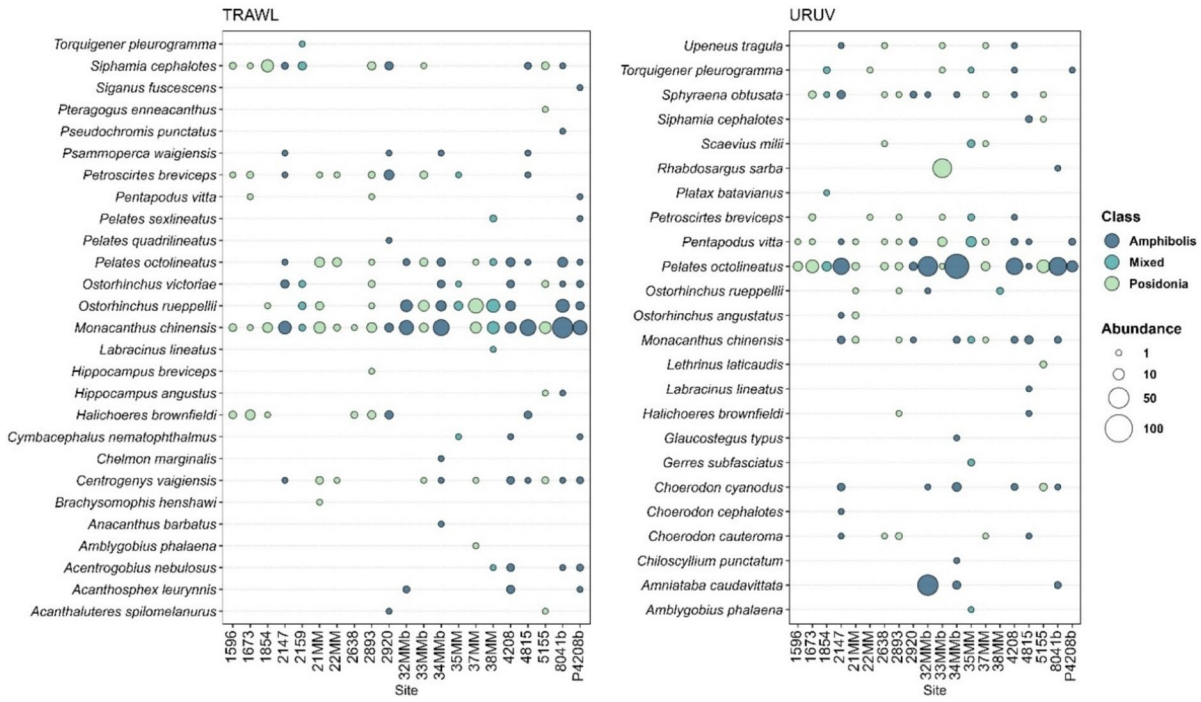


Fig. 4 Bubble plot indicating trawled fish abundance (total fish count per site) and URUV fish abundance (based on MaxN per site), coloured by majority seagrass class present at each site

breviceps, and Pentapodus vitta were ubiquitous across all seagrass meadow types and sampling methods (Fig. 4). Although higher abundance was captured for *M. chinensis* using trawls (19 of 20 sites) compared to only 10 sites using the URUV method. Three *Choerodon* species were exclusively sampled using the URUV method, whereas two *Hippocampus* species were only captured using trawls, indicating that each method captured different aspects of the fish community in terms of mobility and canopy utilization.

Influence of environmental metrics on fish assemblages

Trawled fish community

Spatial variation in total fish abundance, biomass, and net productivity of trawl collected samples were best explained by the amount of seagrass present at the patch scale (i.e. % cover field estimates and within 50 m Area). Higher seagrass cover and canopy height had a positive relationship with fish abundance, while the amount of seagrass perimeter at the 500 m scale was negatively correlated with abundance (Fig. 5). Biomass of trawled fishes also increased with both percent cover of seagrass and the area of seagrass within 50 m buffer, both of which were correlated (Fig. 5). Seagrass meadows dominated by *A. antarctica* harboured four times more fish biomass than *P. australis* meadows (mean biomass 187 ± 24 SE and 46 ± 13 SE, respectively). Taxonomic distinctness of fish assemblages was positively correlated with seagrass canopy height but was negatively related to patch perimeter to area ratio (PARA) at the 50 m scale. The null model was the best model for mean fish length, species richness, and diversity measures of the trawled fish, indicating that these metrics were not strongly related to any of the potential predictor variables (Table S3). The genera-focussed analyses indicated that the abundance of *Ostorhinchus* was positively influenced by the amount of seagrass area at the 50 m scale, and with increasing distance away from channels.

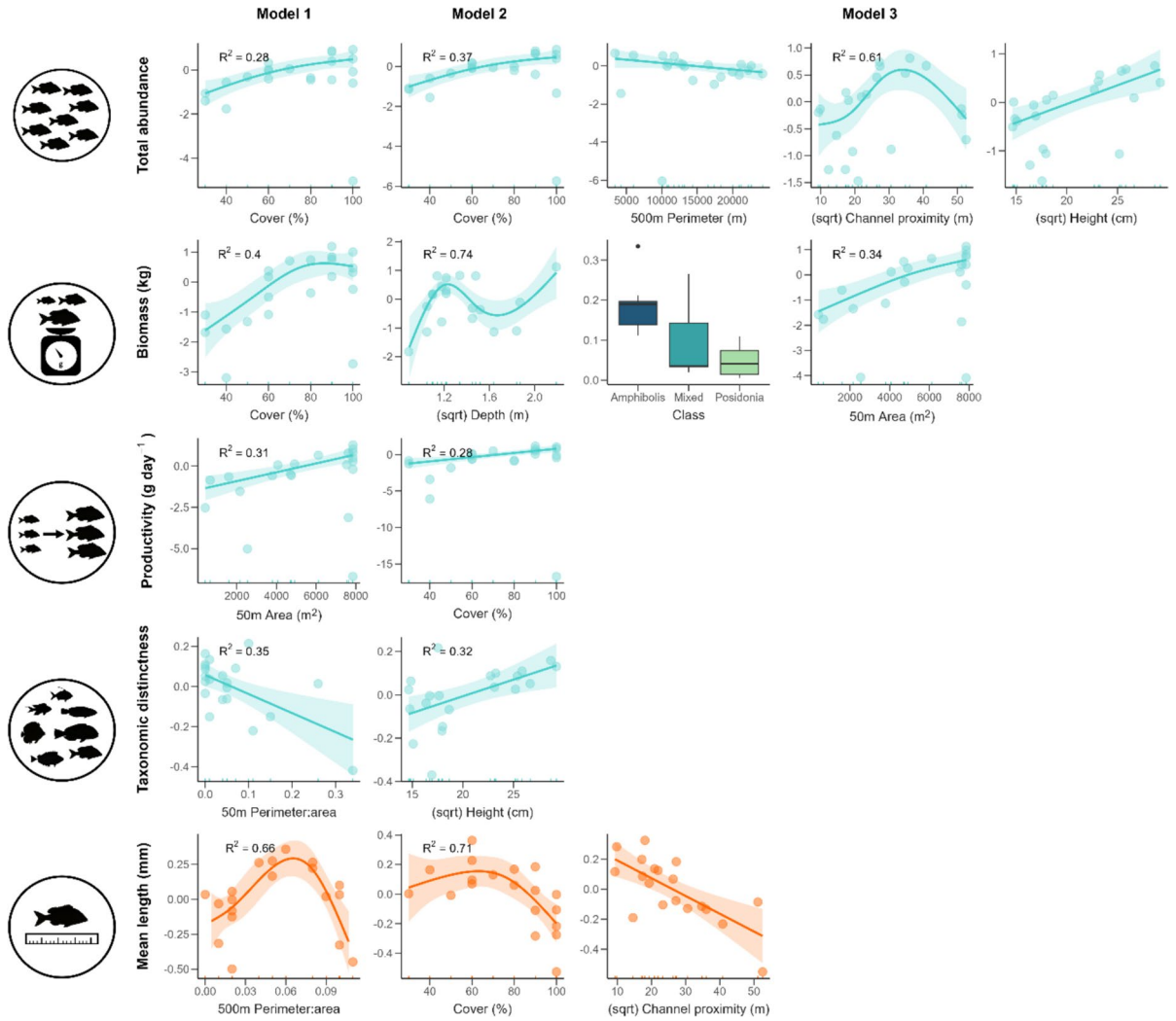


Fig. 5 Residual partial effect plots of trawled fish (teal plots) and URUV fish (orange plots) response variables relative to explanatory variables according to the best generalised additive models (AICc values for all models are displayed in Table S3)

Similarly, the abundance of *Pelates* increased with higher seagrass % cover, and with increasing distance away from channels (Table S4).

URUV fish community

The suite of predictor variables were generally poor predictors of fish community metrics (biomass, abundance, productivity, species richness and diversity) for communities sampled using URUVs (Table S3). The exception was mean fish length, which tended to be greater in URUV deployments close to channels, in meadows with ~ 40–80% seagrass cover, and peaked when the perimeter to area ratio at the 500 m scale was ~ 0.06 (Fig. 5). Interestingly, the larger-scale seascape metrics, such as patch perimeter to area ratio (PARA) measured at the 500 m scale and channel proximity, were better predictors of mean fish length for the URUV-derived community metrics, while metrics derived from trawl samples (characterised by predominantly small-bodied species) typically included variables that were measured in situ or within the 50 m buffer (Fig. 5). The genera-focussed analyses indicated increased abundance of the highly-mobile *Sphyraena* with increased perimeter edge and closer to channels.

Discussion

Loss of seagrass habitat after an acute MHW disturbance in 2011 was associated with a shift from dense to more sparse meadows at Monkey Mia in the globally significant Shark Bay World Heritage Area. This fragmentation of seagrass habitat increased the amount of meadow edge and total number of patches in the seascape. The full extent of seagrass decline was not evident until 2016 – suggesting an approximate six-year lag effect of overall habitat loss following the 2011 MHW. The receding seagrass extent at meadow edges and meadow thinning measured here reflects the different timescale of responses for *P. australis* and *A. antarctica*. Slow-growing seagrasses with persistent life history traits, such as *Posidonia,* can take years to respond to stressors (Kilminster et al. 2015), and decades to recover (O'Brien et al. 2018) which may be further inhibited by ongoing warming and recurrent MHWs (Marbà and Duarte 2009). Our mapping to seagrass species level illustrated that seagrass loss most evident at the edges of continuous meadows, and near deep channels, was mainly due to decline of *A. antarctica* between 2010 and 2013 (Fig. 2B). Moreover, our results show that *A. antarctica* was impacted earlier post-MHW (i.e., declined between 2010 and 2013), whilst *P. australis* cover initially remained relatively stable, before contributing to further seagrass loss in 2016. This finding highlights the vulnerability of *A. antarctica* to initial stochastic warming, such as MHW events, and the delayed response of *P. australis* (Kendrick et al. 2019; Said et al. 2025). Recovery in overall seagrass extent was apparent by 2020 in the Monkey Mia region. This higher proportion of sparse meadows might indicate a pathway via recolonisation of sparse meadows and recovery to dense meadows, or continued fragmentation of meadows remaining higher compared to before the MHW.

Habitat quality is important for fishes

The fragmentation of seagrass observed after the 2011 MHW has implications to the seagrass-associated fish community. The structural complexity of seagrass meadows typically support higher fish densities compared to adjacent unvegetated areas (Heck et al. 2003), but within-patch attributes can also influence the composition of seagrass-associated fauna (Boström 2006; Staveley et al. 2017; Bandeira et al. 2023). Here, we demonstrate that high seagrass cover and habitat area at the local-scale support higher biomass, abundance, and productivity of small-bodied fishes (i.e., species collected in trawl samples). While within-patch attributes are sometimes correlated (i.e. cover, shoot density, and canopy height) they remain independently important as each describes an aspect of complexity that contributes to the "3D structure" of seagrass habitats. Indeed, meadows with greater complexity (i.e., those with higher canopy height and cover) can provide increased shelter for fish and food availability via epiphytes/epifauna (Guidetti and Bussotti 2002; Gullström et al. 2008; Yeager et al. 2016, 2019). Generally, seascapes with higher seagrass area support higher consumer-resource encounter rates and are often considered hotspots for trophic transfer (Yarnall et al. 2024). In addition to total fish abundance, our results demonstrate that average taxonomic distinctness was positively correlated with seagrass canopy height. This infers fish assemblages with greater taxonomic diversity (phylogenetically), occur where a higher canopy provides more vertical niche habitats for various fish species. As such, our work, in conjunction with others, provides evidence that structurally complex seagrass meadows support great fish diversity and have high ecosystem service value; the thinning of meadows could lead to reduced fish abundance and diversity (McCloskey and Unsworth 2015).

The advantages offered by habitats with high structural complexity, cover, and canopy height may be size-dependent for fish. For the larger and more mobile fishes observed in our URUV surveys, mean fish length decreased as seagrass cover increased, concurring with evidence from trawl data that seagrass provides habitat for small-bodied fish. A possible explanation for the preponderance of smaller fish in the seagrass sub-canopy is that hunting by some predatory species becomes impeded in dense meadows (Horinouchi 2007). Overall abundance of high-mobility benthopelagic fish recorded on URUV may be unaffected by within-meadow characteristics, reflecting a lower reliance on seagrass, or due to foraging mode (i.e. microhabitat preferences), or an increased tolerance to small-scale changes in habitat by these fishes (Chen et al. 2022; Yarnall et al. 2024). While previous studies demonstrate relationships between seascape variables and fish metrics using URUV (e.g. Goodridge Gaines et al. 2022), we found few parameters that reliably predicted the typically larger

bodied, mobile species using this method. This may be because fragmentation has altered habitats at both small and larger scales, and that habitat needs to be considered across broader scales than measured here to fully detect seascape effects. The influence of habitat percent cover on these high-mobility fishes may also however depend upon life stage, with juveniles benefiting from reduced predation pressure in seagrass habitat (Horinouchi 2007). Our results also showed that larger fish were observed in meadows closer to channels, suggesting channels may serve as corridors connecting meadows or other habitats within the broader seascape for larger fishes. For example, the genera level modelling showed that *Sphyraena* (barracuda) abundance had a positive relationship with increased seagrass patch perimeter and closer to channels (Tabel S4) – likely reflecting a habitat preference in relation to hunting at the meadow edge. Other work demonstrated that larger fish including those belonging to the family Labridae occur in seagrass canopies as well as escarpments at the edge of channels and platform reefs in Shark Bay (Serrano et al. 2023). Mapping of the Monkey Mia area revealed that seagrass meadows are receding at their edges, resulting in increasing patch isolation and patches being further from channels for large fish.

Influence of increased patchiness and different seagrass species for fish assemblages

A key component of understanding fragmentation of habitat is detecting changes in edge to area ratios (Smith et al. 2008). The gradual receding of meadow edges and meadow-thinning 5 years post-MHW likely differentially impacted seagrass-associated fishes depending on their microhabitat preferences. For example, a threefold increase in perimeter to area (PARA) ratios led to species-specific positive edge effects for fishes preferentially utilising meadow edges in Phillip Bay, southeastern Australia (Macreadie et al. 2009). In our study, average taxonomic distinctness of trawl-collected fishes decreased as PARA increased (i.e. there was a decline in patch size and increase in perimeter edge). The corresponding decline in biodiversity—as measured using average taxonomic distinctness—suggested that some phylogenetically and functionally unique components of the assemblage were lost when this increase in PARA occurred. Interestingly, species richness and Simpsons Diversity index were unaffected as while the number of species was retained, these were likely similar phylogenetically. Therefore, a shift to smaller seagrass patches with more edges may then lead to negative edge effects for certain fish species, and fragmentation of meadows at the patch scale (50 m) may reduce phylogenetic diversity of the fish assemblage.

Fragmentation of seagrass meadows affects fish assemblages, but loss of seagrass habitat dominated by particular seagrass species will also impact fish assemblages. While some fish species were associated with either *P. australis* or *A. antarctica* dominated seagrass meadows, most fishes were found across both seagrass species in this study. However, our modelling showed that trawled fish biomass was higher in *A. antarctica* compared to mixed or *P. australis* dominated meadows, although seagrass species did not influence fish abundance, suggesting bigger fish utilise *A. antarctica* meadows. Furthermore, *A. antarctica* dominated meadows represent ~50% of the sites sampled and held 63% of the total fish biomass, which was dominated by three invertebrate feeding species *M. chinensis* (algae-invertivore), *O. rueppellii* (invertebrate-carnivore), and *P. waigiensis* (benthic-invertivore). *Amphibolis antarctica* is known to harbour greater densities of ascidians, crustaceans, and polychaetes compared to *Posidonia* spp. leaves in Shark Bay (Wells et al. 1985), suggesting *A. antarctica* meadows provide greater food resources for invertivorous fishes. Similarly, the stems of *Amphibolis* allow for high diversity and biomass of epiphytic algae compared to many other seagrass genera, including *Posidonia* (Borowitzka et al. 2006), which provides an abundant food resource for omnivores such as *M. chinensis*. Hyndes et al. (2003) also found that trawled fish biomass was significantly higher in *Amphibolis* spp. compared to *Posidonia* spp. meadows, which they attributed to the relatively larger understory space beneath a leafy *Amphibolis* canopy compared to the compact, dense strap-like leaves of *Posidonia*. The decline in *A. antarctica* habitat following the 2011 MHW (Kendrick et al. 2019) may have had a detrimental impact on larger bodied fish that preferentially use this habitat.

Broad implications of habitat quality change

The decline of foundation species that support biodiverse ecosystems can significantly disrupt habitat complexity and the species that depend on them

(Ellison et al. 2005). This study demonstrates that seagrass loss—measured in terms of reduced cover and canopy height—negatively affects the abundance, biomass, and productivity of small-bodied fish. Additionally, increased patchiness—as indicated by PARA—can have detrimental effects on the phylogenetic diversity of seagrass fish assemblages. The productivity of small-bodied fishes plays a key role in energy transfer to higher trophic levels through trophic relay and may contribute to nutrient transfer across the seascape into adjacent habitats (Hyndes et al. 2014). Therefore, loss and fragmentation of seagrass habitats will likely have flow-on effects throughout the coastal food web.

As 99% of the fish measured in this study were well below their maximum size, suggesting that these seagrass meadows serve as critical habitat for juvenile and sub-adult fish (Williams et al. 2016; Hyndes et al. 2018). Although seagrass extent may recover to pre-disturbance levels, habitat quality for fish may remain compromised due to changes in density, fragmentation, and dominance of different seagrass species. These changes can affect both the abundance and diversity of fish assemblages—key indicators of ecological condition in monitoring programs (Whitfield and Elliott 2002; Stuart-Smith et al. 2017; Holmes et al. 2019; French et al. 2021). Biodiversity loss undermines ecological redundancy and resilience to future disturbances, while shifts in abundance and biomass may alter ecological processes such as predation (Duffy et al. 2016).

In the context of conservation and management, detecting changes in habitat quality using a seascape mapping approach can inform the conservation prioritisation of seagrass habitats to maximise benefits for fish communities (e.g. high seagrass cover and proximity to channels). Seascape metrics derived from remotely sensed habitat maps can reveal temporal changes in seagrass habitats, including both degradation and recovery pathways, and can be used to support evidence-based management decisions. This work and that of Macreadie et al. (2009) suggest that decisions regarding the management of seagrass habitat should consider that the effects of fragmentation on fish may take several months or even years to become apparent. Insights into dynamics of patch types, habitat gaps, areas of high seagrass cover, vulnerable habitats, connectivity, and proximity to local disturbances may for example be used to identify where restoration is most likely to be successful. While maintaining high-cover seagrass meadows is important for enhancing local ecosystem resilience (Abadie et al. 2018), a thorough understanding of local seascape dynamics is important for implementing conservation and restoration actions with confidence. Olds et al. (2016) highlighted that increased seascape connectivity has been linked to greater productivity and biodiversity within protected area. Here, we provide an example of research that provides stronger linkages between seascape ecology and marine spatial planning that are likely to improve conservation outcomes.

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Author contributions Authors Simone Strydom, Shaun Wilson, and Glenn Hyndes contributed to the study conception and design. Material preparation, data collection and analysis were performed by Simone Strydom, Shaun Wilson, Kathy Murray and Molly Moustaka. The first draft of the manuscript was written by Simone Strydom and all authors commented on previous versions of the manuscript. All authors read and approved the final manuscript.

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Data availability The datasets generated and/or analysed during the current study are available from the corresponding author on reasonable request.

Declarations

Competing interests All authors have no relevant financial or non-financial interests to disclose.

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