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Multi-decadal change in a tropical seagrass meadow reshapes juvenile fish assemblages

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ABSTRACT

Seagrass meadows are essential habitats that support diverse and abundant fish assemblages, yet they are increasingly threatened by disturbance from anthropogenic impacts and extreme climate events. This study quantified changes in fish assemblages associated with seagrass loss and recovery in a tropical estuarine system in Cairns Harbour, Australia, using a multi-decadal beam trawl dataset spanning pre-disturbance, disturbance, and recovery periods.

Seagrass loss from consecutive storms and floods was associated with substantial declines in fish abundance (~84%) and taxonomic richness (~73%), consistent with major habitat loss. Following disturbance, both abundance and richness recovered to levels comparable to pre-disturbance conditions, indicating recovery based on fish abundance and richness.

Despite this recovery, assemblage composition differed significantly among pre-disturbance, disturbance and recovery periods, indicating a restructured fish community, with shifts in functional composition and trophic structure rather than a return to pre-disturbance conditions. Indicator species analysis further highlighted this transition, some taxa were associated with disturbance conditions, while seagrass-associated species were absent or slower to recover.

These findings demonstrate that recovery following seagrass disturbance is characterised not by a simple return to pre-disturbance conditions, but by a reorganisation of fish assemblages across both taxonomic and functional dimensions. This highlights the importance of integrating abundance, composition and functional metrics when assessing ecosystem recovery in tropical seagrass habitats.

1. Introduction

Coastal ecosystems such as seagrass meadows support high levels of biodiversity and provide important habitat for a wide variety of marine organisms, including fish (Jackson et al., 2001; Hyndes et al., 2018; York et al., 2018; Lefcheck et al., 2019). These habitats function as important nursery, foraging, and spawning grounds, supporting fishes across different phases of their life cycle (French et al., 2021a). Some fish species occur as residents within seagrass meadows, while others use these habitats transiently or seasonally, often in connection with adjacent ecosystems such as mangroves or coral reefs (Unsworth et al., 2008; Honda et al., 2013; Henderson et al., 2017; Whitfield, 2017). Seagrass meadows play an essential role in maintaining biodiversity and ecosystem functioning, supporting key processes such as productivity and trophic interactions (Duffy, 2006; Colvin and Snelgrove, 2025; Duarte et al., 2025).

The structural complexity of seagrass meadows makes them particularly important habitats for juvenile fish (Beck et al., 2001). Dense vegetation provides refuge from predation and abundant food resources that enhance growth and survival during early life stages (Duffy, 2006;

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Colvin and Snelgrove, 2025; Duarte et al., 2025). Nursery habitats are generally defined as areas that support juveniles that make a disproportionate contribution to adult populations relative to juveniles from other habitats (Beck et al., 2001). As a result, many commercially and ecologically important species depend on seagrass habitats during these vulnerable life stages (Heck et al., 2003).

Global assessments have documented widespread seagrass losses due to a range of natural and anthropogenic stressors including coastal development, dredging, declining water quality, and extreme climate events (Waycott et al., 2009; Grech et al., 2012; Cullen-Unsworth and Unsworth, 2018; Turschwell et al., 2021). Loss or degradation of these habitats can alter fish assemblages, reduce biodiversity, and affect ecosystem services such as nursery function (Unsworth and Cullen, 2010; Nowicki et al., 2017; O'Brien et al., 2018; Orth et al., 2020). Therefore, understanding how fish communities respond to seagrass decline and recovery is essential for effective management and conservation of coastal fisheries (Duarte et al., 2025; Sievers et al., 2025).

While the impacts of seagrass loss on fish assemblages are well documented, less is known about how communities respond following habitat recovery (Orth et al., 2020; Hardison et al., 2023; Sievers et al., 2024). Recovery is often assumed to restore ecological function, yet biological responses may lag behind habitat recovery, vary among species, or result in persistent shifts in community composition (Heck et al., 2003; Pihl et al., 2006; Sobocinski et al., 2013; Castro-Fernández et al., 2025a,b). Such shifts can alter food-web structure and predator-prey interactions if disturbance favours different feeding groups or energy pathways (Byrnes et al., 2007; Estes et al., 2011). In some cases, disturbance can drive ecosystems into alternative stable states, where assemblages reorganise and fail to return to pre-disturbance conditions despite habitat recovery (Hempson et al., 2018; Stuart-Smith et al., 2021). Seagrass-associated fish communities may undergo regime shifts, with long-term implications for ecosystem function and resilience (Scheffer et al., 2001; Robertson et al., 2021; Turschwell et al., 2021). Determining whether fish assemblages recover in parallel with seagrass habitats, or transition to alternate states, is essential for assessing ecosystem resilience and the effectiveness of habitat recovery (McSkimming et al., 2016; Gagnon et al., 2023).

Long-term ecological datasets are invaluable for resolving these dynamics, yet multi-decadal records capturing both seagrass decline and recovery remain rare (Orth et al., 2020). Such datasets provide a unique opportunity to examine whether habitat recovery is accompanied by the return of ecological function or whether assemblages remain altered following disturbance (Cook et al., 2022). They also enable the detection of delayed or non-linear responses that may indicate altered states in community structure (Graham et al., 2015; Hempson et al., 2018; Garcia et al., 2025).

The Great Barrier Reef (GBR) region has experienced several major weather and climatic events that have caused widespread loss of seagrass meadows (Pollard and Greenway, 2013; McKenzie et al., 2014; Rasheed et al., 2014; McKenna et al., 2015). A strong La Niña event between 2009 and 2011 brought prolonged rainfall and flooding to north Queensland, causing widespread loss of coastal seagrass meadows (Rasheed et al., 2014). This decline was compounded by Tropical Cyclone Yasi, which resulted in an estimated 98% loss of intertidal seagrass in some areas (McKenzie et al. 2012, 2014; Rasheed et al., 2014).

Trinity Inlet, Cairns, north Queensland, is a dynamic tropical estuarine system where seagrass habitats have experienced periodic loss and recovery over the past three decades. The seagrass meadows in Trinity Inlet are estimated to support over 154 species of ecological, recreational and commercial importance (Blaber, 1980; Coles et al., 1993; Philpott et al., 2026) and have historically contributed substantially to local fisheries productivity, with prawn fisheries in Cairns Harbour valued at $1.24 million in 1993 (Watson et al., 1993). Following the 2009–2011 disturbances, seagrass recovery began from 2015 onwards, with recent annual monitoring indicating total seagrass area now exceeds the long-term average, although biomass remains variable (Reason et al., 2025).

Historical beam trawl samples collected before the later meadow-scale seagrass loss, during seagrass absence, and following recent recovery, combined with long-term seagrass monitoring, provide a rare opportunity to examine how seagrass-associated fish assemblages have responded to habitat loss and recovery in Trinity Inlet over the last 35 years. Because Ellie Point and Esplanade represent two long-term monitoring meadows that differ in their position within the estuary and local meadow characteristics, we also expected fish assemblage responses to vary between sites.

Specifically, we aimed to 1) quantify changes in catch abundance, defined as the number of individuals collected per standardised beam trawl sample, and taxonomic richness associated with seagrass disturbance and recovery, 2) examine shifts in taxonomic structure across disturbance phases and seasons, and 3) assess changes in the functional structure of fish assemblages to evaluate how ecological roles respond to habitat loss and recovery. We expected seagrass loss to reduce fish abundance and diversity and alter species composition, with fish abundance and diversity increasing as seagrass recovered. However, given potential ecological lags, we predicted that structural and functional assemblage composition may not have fully returned to pre-disturbance conditions.

2. Method

2.1. Study area

Cairns Harbour, in tropical north Queensland, is a shallow estuarine bay at the seaward end of Trinity Inlet. The system is fringed by extensive mangroves and connected to adjacent seagrass meadows, forming an integrated coastal habitat. Freshwater and sediment inputs are driven by discharge from the Barron River catchment and Trinity Inlet, with substantial runoff occurring during the wet season (December – March), when the average annual rainfall exceeds 2000 mm (BOM, 2025).

The study was conducted within an intertidal seagrass meadow dominated by *Zostera muelleri*, located on the western side of Cairns Harbour between the Cairns Marina and Ellie Point (Fig. 1). This meadow forms part of a long-term seagrass monitoring program established in 2001, assessing seagrass condition (Reason et al., 2025).

Samples were collected from two sites within this meadow: Ellie Point (16°53′05.8"S 145°46′30.4"E) and Esplanade (16°54′25.6"S 145°46′27.4"E) (Fig. 1). Temporal trends in seagrass condition were characterised using annual estimates of mean above-ground biomass (g DW m^{-2}) and total meadow area (ha) from 2001 to 2024, derived from long-term monitoring surveys (Reason et al., 2025) (Fig. 2). Seagrass biomass and meadow area showed substantial interannual variability, including a pronounced decline between 2009 and 2012, followed by a period of recovery from 2015 onwards.

Because annual monitoring did not begin until 2001, seagrass condition during earlier fish sampling years (1991 and 2000) was inferred from the closest available surveys and historical records. Aerial imagery with ground-truthing, followed by annual monitoring from 2001, indicates the *Zostera muelleri* meadow underwent minimal change to its distribution from at least the 1950s until 2010 (Pollard and Greenway,

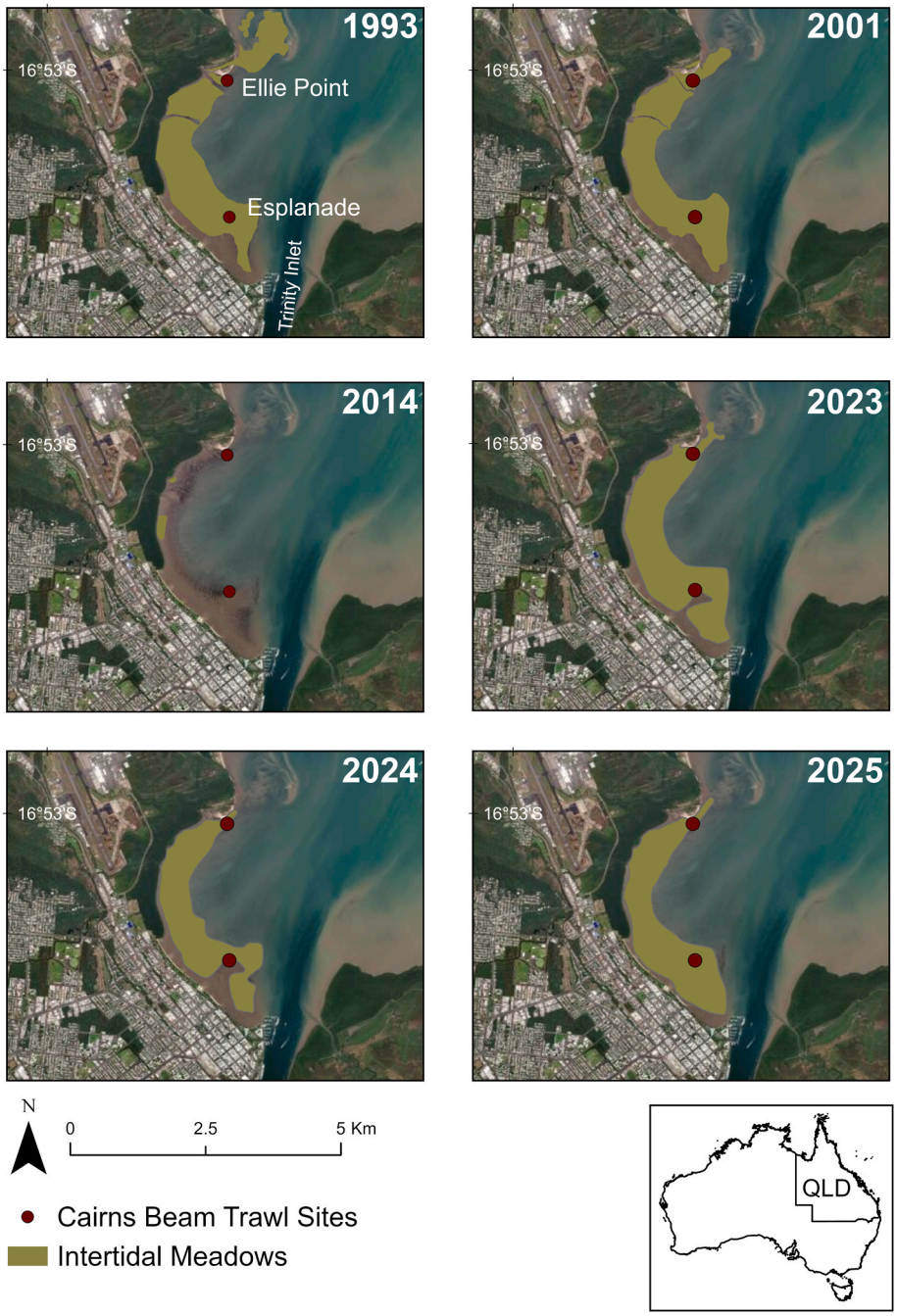

Fig. 1. Location of Ellie Point and Esplanade study sites (red dots) within the intertidal seagrass meadows, western Cairns Harbour, tropical north Queensland, Australia. Spatial extent of seagrass meadows is shown for selected years (1993, 2001, 2014, 2023–2025) to illustrate historical variability in meadow distribution. Data from Lee Long et al. (1996), Campbell et al. (2001), and Reason et al. (2025). (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

2013; McKenna et al., 2015). The closest seagrass monitoring survey to the 1991 fish sampling was conducted in 1993, which mapped the meadow extent (Fig. 1) and recorded 72.67 ± 5.39% percentage cover of *Zostera muelleri* (Lee Long et al., 1996). The closest available estimate to the 2000 sampling period was from the commencement of the long-term monitoring program in 2001 (Reason et al., 2025), when mean above-ground biomass was approximately 35.5 g DW m^{-2} (Campbell et al., 2001).

Although seagrass was present at the study sites throughout this period, meadow extent and density varied interannually. Flood-related reductions in meadow footprint were recorded in 2000, including losses offshore from the Ellie Point sampling site (Campbell et al., 2001). However, these changes differed from the later sustained meadow-scale decline observed between 2009 and 2012, which resulted in seagrass

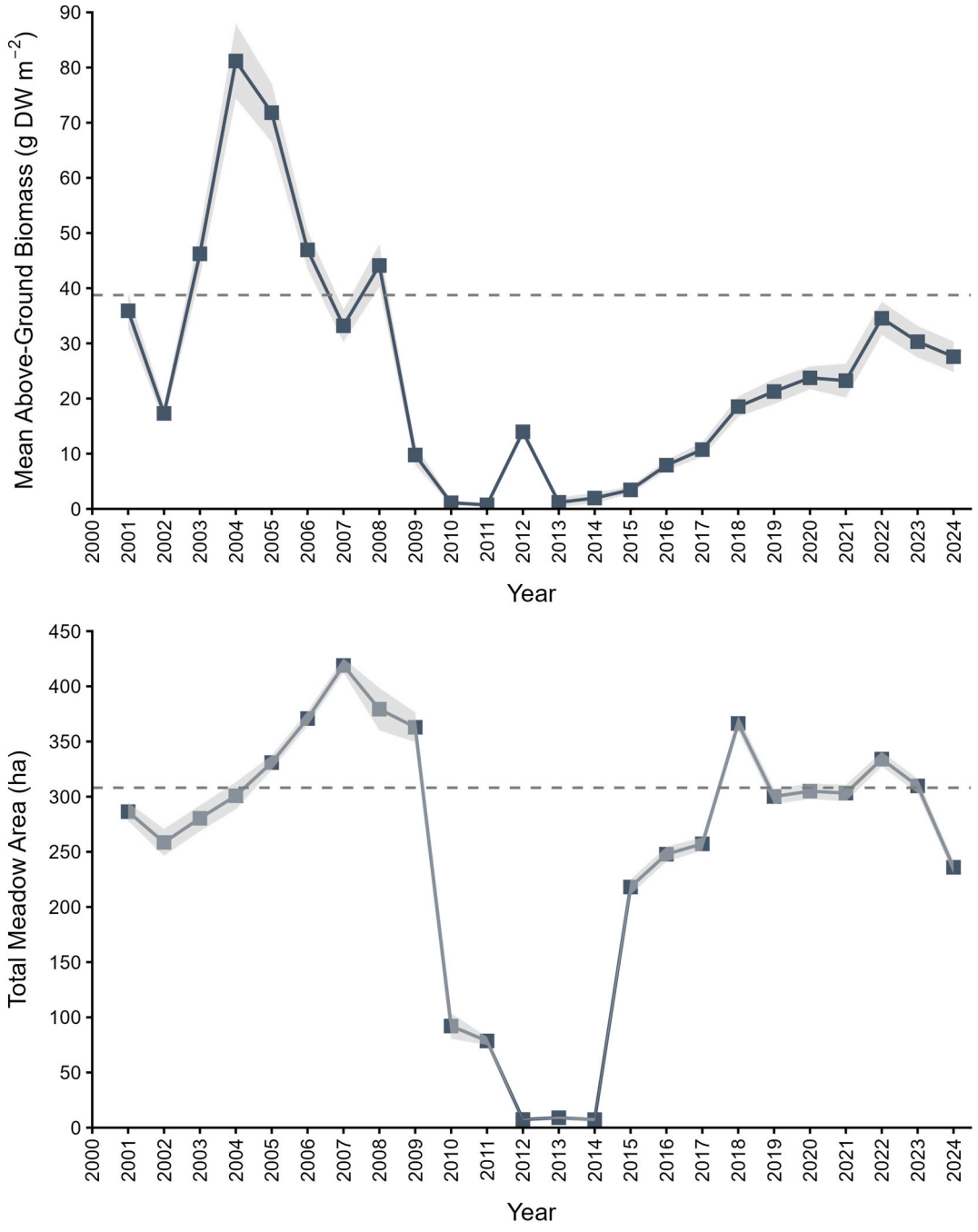

Fig. 2. Interannual variation in (a) mean above-ground biomass (g DW m^{-2}) and (b) total meadow area (ha) for the intertidal meadow encompassing the study sites in Cairns Harbour (2001-2024). Points represent annual means. In a), the shaded area indicates ± standard error, while in b) it represents spatial uncertainty in mapped meadow area (±R, ha), where R is the mapping precision estimated using a buffer-based approach around each meadow boundary. Dashed horizontal lines indicate decadal baseline conditions, calculated as the mean over the reference period (2001–2010). Data from Campbell et al. (2001), Reason et al. (2025).

absence at both fish sampling sites by 2014. Therefore, for the purposes of this study, we defined three disturbance phases: pre-disturbance, comprising 1991 and 2000, when seagrass was present and widespread; disturbance, comprising 2014, following almost the entire collapse of the meadow and when seagrass was absent at both sampling sites; and recovery, comprising 2023–2025, when seagrass biomass and area had approached pre-disturbance levels.

2.2. Sampling

Beam trawl sampling was conducted at Ellie Point and the Esplanade in Cairns Harbour during February, May, August, and November in 1991, 2000 and 2014. In the recovery period, sampling was conducted in May, August and November 2023, in all four sampling months in 2024, and in February and May 2025. These sampling months were

selected to capture seasonal variability in tropical coastal systems, broadly corresponding to the wet season (February), early dry or post-wet transition (May), dry season (August), and late dry or pre-wet transition (November), consistent with regional climate patterns in north Queensland (BOM, 2025). Sampling followed an established long-term monitoring protocol developed for assessing fish assemblages in shallow tropical seagrass meadows (Coles and Lee Long, 1985; Coles et al., 1993).

The beam trawl net opening measured 1.5 m in width and 0.5 m in height and was fitted with 2 mm mesh net and a tied cod end. At each site, four replicate trawls were undertaken along transects defined between predetermined points. Trawls were towed behind a vessel at approximately 0.75 m s^{-1} for 2.5 min, corresponding to a tow distance of ~100 m.

Sampling was undertaken at night during high tide and targeted periods of low lunar illumination (new moon), with sampling occurring within ±4 days of the new moon for all events. This timing was selected to maximise catchability, as reduced light levels limit net avoidance and increase fish activity within seagrass habitats, while high tide facilitates movement of nekton into shallow meadows, increasing their availability for capture (Guest et al., 2003). Site locations were originally established in 1991 and were subsequently adjusted where necessary to remain within seagrass habitat, based on estimated seagrass biomass (g DW m^{-2}), area (ha), distribution, and species compositions from the long-term seagrass monitoring program and aerial imagery (Reason et al., 2025).

Trawls that failed due to logistical constraints were excluded from analyses. Trawls in which no fish were captured were retained and assigned zero abundance and taxonomic richness. The beam trawl is inherently size-selective, with the small mesh size increasing retention of small-bodied and juvenile fishes, and may under-represent larger, more mobile taxa within the assemblage.

2.3. Specimen processing

Fish collected during beam trawl sampling were identified to the lowest taxonomic level based on morphological characteristics. Where possible, individuals were released after processing, while retained specimens were euthanised using an ice slurry and frozen for later laboratory identification. For each trawl, the total number of individuals, their lengths (nearest 0.1 mm), and taxonomic composition of the catch were recorded.

2.4. Molecular validation of taxonomic identity

Genomic DNA was extracted from a subset of specimens collected from beam trawl sampling during 2023 – 2025 for species taxonomic verification. Approximately 100 mg of tissue (fin clips or muscle) was preserved in ≥95% ethanol prior to extraction. DNA was extracted using a cetyltrimethylammonium bromide (CTAB) protocol adapted from Adamkewicz and Harasewych (1996) with minor modifications (see Supplementary Methods S1) and quantified using a Qubit Fluorometer (Thermo Fisher Scientific, Victoria, Australia).

A mitochondrial cytochrome *c* oxidase subunit I (COI) fragment (~650 bp) was amplified by endpoint PCR using the FishF1 and FishR1 primers as described by Ward et al. (2005). PCR amplification and Sanger sequencing were conducted by the Australian Genome Research Facility (AGRF; Brisbane, Australia).

Forward and reverse reads were quality-checked, trimmed, and assembled in Geneious Prime (v2026.0.2 Biomatters Ltd., Auckland, New Zealand). Identification of assembled COI sequences was performed using BLAST searches against the GenBank nucleotide database of the National Centre for Biotechnology Information (NCBI), Barcode of Life Data System (BOLD) and the National Biodiversity DNA Library guide (NBDL), using a ≥98% sequence similarity threshold for species-level assignment where possible.

2.5. Taxonomic standardisation

Taxonomic identifications were standardised prior to analysis to ensure consistent taxonomic resolution across the dataset. Individuals identified to species were retained at species level. Because no reference specimens remained from historical sampling, records with uncertain identifications (e.g. specimens labelled "sp.", "sp. 1", "sp. 2", "unknown", or "larval fish") were reassigned to the lowest reliable taxonomic level (genus, family, or order).

To avoid inflating richness estimates, multiple unresolved labels within the same taxonomic group (e.g. "Gobiidae sp. 1" and "Gobiidae sp. 2") were collapsed into a single taxonomic unit. Within each trawl, higher-level identifications were removed when a more resolved identification from the same lineage was present.

For richness analyses, consistently distinguished morphotypes were retained as separate observational units. For multivariate assemblage analyses, unresolved taxa were collapsed to a common higher taxonomic level to ensure comparability among samples and years.

2.6. Trophic group classification

Fish taxa were assigned to functional feeding groups based on published ecological classifications and family-level diet information (Froese and Pauly, 2026). Families were classified into five trophic groups: benthivores, carnivores, herbivores, omnivores, and planktivores. Benthivores were defined as taxa primarily feeding on infaunal and epifaunal prey associated with benthos. Carnivores were defined as taxa feeding primarily on fish and larger mobile invertebrates. Herbivores were defined as taxa primarily consuming plant material. Omnivores were defined as taxa with a mixed diet comprising both plant material and animal prey and planktivores were defined as taxa that primarily consume planktonic organisms, including zooplankton and phytoplankton (Froese and Pauly, 2026). Trophic group abundances were then summed for each trawl to produce a family-level functional composition matrix. Analyses were conducted at the family level to ensure consistency in functional assignment across taxa, particularly where species-level diet information is limited or variable among juvenile life stages. Because many fish species undergo ontogenetic dietary shifts, these trophic groups should be interpreted as broad family-level feeding groups rather than precise diet assignments for all juvenile individuals.

2.6.1. Statistical analyses

All statistical analyses were conducted in R v4.5.2 (R Core Team, 2025). Fish abundance (number of individuals per trawl) and taxonomic richness (number of taxa per trawl) were modelled using generalised linear mixed-effects models (GLMMs), fitted with the *glmmTMB* package (Brooks et al., 2017). Fish abundance was modelled with a negative binomial distribution with a log link to account for overdispersion, while taxonomic richness was modelled using a Poisson distribution with a log link.

Sampling period (pre-disturbance, disturbance, recovery), month (February, May, August, November) and site (Ellie Point and Esplanade) were included as fixed effects in both models. Site was included as a fixed effect because the study focused on direct comparisons between

two specific long-term monitoring meadows, rather than sites randomly sampled from a broader population of meadows. A random intercept of sampling event (defined as unique combinations of site x year x month) was included to account for non-independence among trawls conducted within the same sampling occasion (Zuur et al., 2009).

Candidate models with varying fixed-effect structures were compared using Akaike's Information Criterion (AIC), and final models were selected based on the lowest AIC (Appendix A, Table S2 and S8). For fish abundance, models including an interaction between sampling period and month were evaluated to account for potential seasonal variation in disturbance effects, and this interaction was retained in the final model. For taxonomic richness, seasonal variation was accounted for by including month as an additive fixed effect, but the sampling period × month interaction was not retained because it did not improve model fit based on AIC. Collinearity among predictors was assessed prior to model selection.

Model assumptions were evaluated using simulation-based residual diagnostics in the *DHARMa* package (Hartig, 2016), including tests for overdispersion, zero inflation, and residual uniformity. The significance of fixed effects was assessed using Type II Wald chi-square tests. Where disturbance period had a significant effect, pairwise comparisons were conducted using estimated marginal means with Tukey-adjusted p-values.

Trophic group abundances were analysed using GLMMs, following the same structure as for total fish abundance. Separate models were fitted for each trophic group (benthivores, carnivores, herbivores, omnivores, and planktivores), using the abundance of the focal trophic group per trawl as the response variable and a negative binomial distribution with a log link. Sampling period, month, and site were included as fixed effects, with sampling event retained as a random intercept. For each trophic group, both additive and interaction (period × month) model structures were evaluated, and the final model was selected based on AIC and residual diagnostics.

2.7. Multivariate assemblage and functional composition analyses

Taxonomic assemblage structure and functional composition were visualised separately using principal coordinates analysis (PCoA) based on Bray–Curtis dissimilarities in the *vegan* package (Oksanen et al., 2013). A trawl-by-taxa abundance matrix was constructed from beam trawl data. Low-occurrence taxa, defined as taxa occurring in two or fewer trawls were removed, and two trawls from Esplanade in August 2014 were excluded because they contained only five individuals each, represented solely by unresolved order-level taxa, making them uninformative for compositional analysis. Abundance data were log-transformed using log (x + 1) prior to analysis to reduce the influence of highly abundant taxa. Functional composition was analysed separately using a trawl-by-trophic group abundance matrix constructed from family-level trophic group assignments. Trophic group assignments were summed within each trawl and used to calculate Bray–Curtis dissimilarities. Patterns in functional composition were also visualised using PCoA.

For both taxonomic assemblage structure and functional composition, differences in composition were tested using permutational multivariate analysis of variance (PERMANOVA; 999 permutations) with disturbance period, month, and site as fixed factors. For both taxonomic assemblage structure and functional composition, additive and interaction models were evaluated, with the final model including a disturbance period × month interaction. Homogeneity of multivariate dispersions was assessed using PERMDISP. Where significant effects were detected, pairwise PERMANOVA comparisons were conducted between disturbance periods using the *pairwiseAdonis* package (Arbizu, 2020) with 999 permutations. Temporal patterns in trophic group abundance were additionally summarised as mean abundance (±SE) across months and disturbance periods for visualisation.

2.8. Functional traits and functional diversity

Functional diversity was quantified using functional dispersion (FDis) and functional richness (FRic) (Laliberté and Legendre, 2010). Functional dispersion measures the spread of taxa in multivariate trait space and functional richness estimates the amount of functional trait space occupied by taxa present in each assemblage. Both metrics were calculated at the trawl level using a trawl-by-taxon abundance matrix and a corresponding functional trait matrix.

Functional traits included trophic group, position in the water column and maximum body size. These traits were selected because they describe key differences in how taxa use seagrass habitats, feeding strategy, habitat use and body-size-related differences in ecological interactions. They were also available consistently across the full long-term dataset, allowing functional diversity to be compared among disturbance periods. Trophic group was classified as benthivore, carnivore, herbivore, omnivore and planktivore, while water-column position was classified as benthic, demersal, or pelagic. Trophic group and water-column position were assigned at the family level based on published ecological information (Froese and Pauly, 2026). Maximum body size was assigned at the taxon level and log-transformed prior to analysis because fish body size spans a wide range of values and can strongly influence trait dissimilarities. This transformation reduced the influence of very large-bodied taxa on the functional distance matrix (de Bello et al., 2013; Toussaint et al., 2016).

Pairwise functional distances among taxa were calculated using Gower distance from the mixed trait matrix. Functional dispersion and functional richness were then calculated using the dbFD function in the FD package in R (v1.0-12.3; Laliberté and Legendre (2010)). FRic was calculated as the convex hull volume occupied by taxa present in each trawl, while FDis was calculated as the abundance-weighted mean distance of taxa from the assemblage centroid. Trawls with too few taxa to calculate convex hull volume were excluded from FRic summaries but retained for FDis where possible.

Functional trait space was visualised using a Principal Coordinates Analysis (PCoA) based on pairwise functional distance matrix. The ordination was used to compare the distribution of taxa in functional trait space among disturbance periods and to support interpretation of changes in occupied trait space.

2.9. Indicator species

Indicator species analysis (IndVal) was conducted using the *indicspecies* package (Cáceres and Legendre, 2009) to identify taxa significantly associated with each disturbance period. Indicator values were calculated based on species specificity and fidelity, with statistical significance assessed using 999 permutations. The highest-ranking indicator taxa, based on IndVal scores and statistical significance, were first identified. For visualisation, a subset of these significant taxa was selected within each period, prioritising species with ecological or fisheries relevance (Coles et al., 1993; Froese and Pauly, 2026).

3. Results

Sampling spanned periods of seagrass disturbance and recovery between 1991 and 2025. A total of 167 beam trawl tows were conducted at

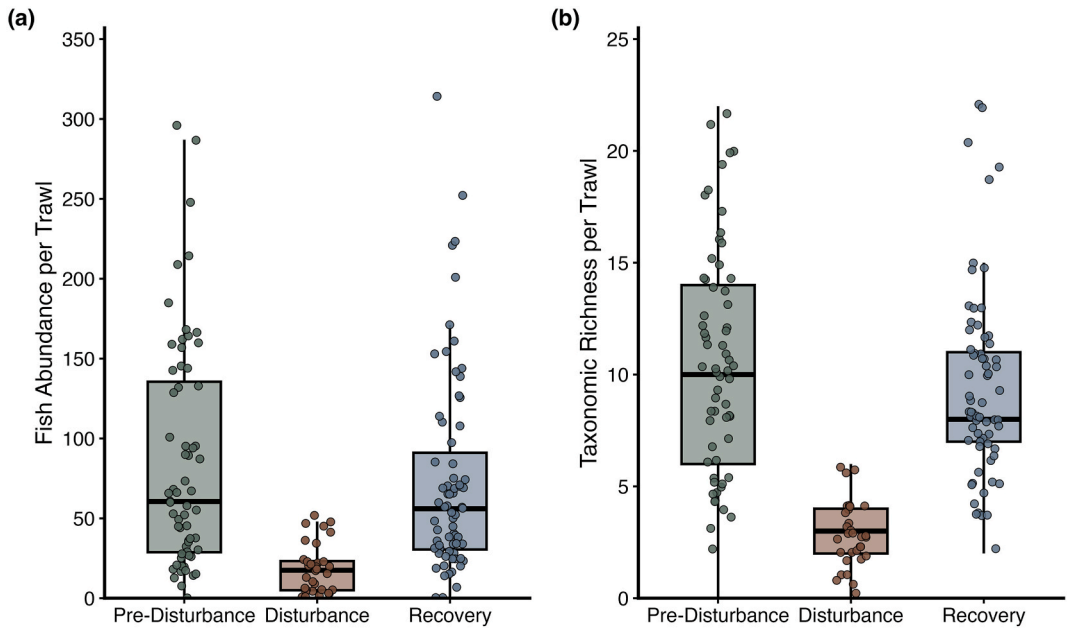

Fig. 3. Fish assemblage across disturbance periods in Trinity Inlet. Fish abundance per trawl (a) and taxonomic richness (b) per trawl across pre-disturbance, disturbance and recovery periods. Boxplots show the median, interquartile range and whiskers, with points representing individual trawl samples.

Ellie Point and Esplanade across six sampling years (1991, 2000, 2014, 2023, 2024 and 2025), resulting in the capture of 11,224 individuals representing 190 taxa from 47 families (Table S1). Taxonomic resolution varied, with 104 taxa identified to species level, 36 to genus level, 46 retained at family level, and four at order level.

Individual trawl tows captured a mean of 8.38 ± 5.18 taxa per tow, and 67.21 ± 65.16 individuals per tow (mean $\pm$ SD). Across all samples, Gobiidae, Sillaginidae and Tetraodontidae were among the most taxonomically diverse families. The most frequently recorded species were *Pelates quadrilineatus* (Fourline Striped Grunter; 19.5% of all individuals), *Terapon puta* (Spinycheek Grunter; 8.9%) and *Eubleekeria splendens* (Blacktip Ponyfish; 3.85%).

3.1. Abundance

Fish abundance varied significantly among disturbance periods (Wald, $\chi^2 = 71.57$, df $= 2$, $p < 0.001$; Fig. 3a) as well as among months ($\chi^2 = 32.61$, df $= 3$, $p < 0.001$) and was significantly higher at Esplanade

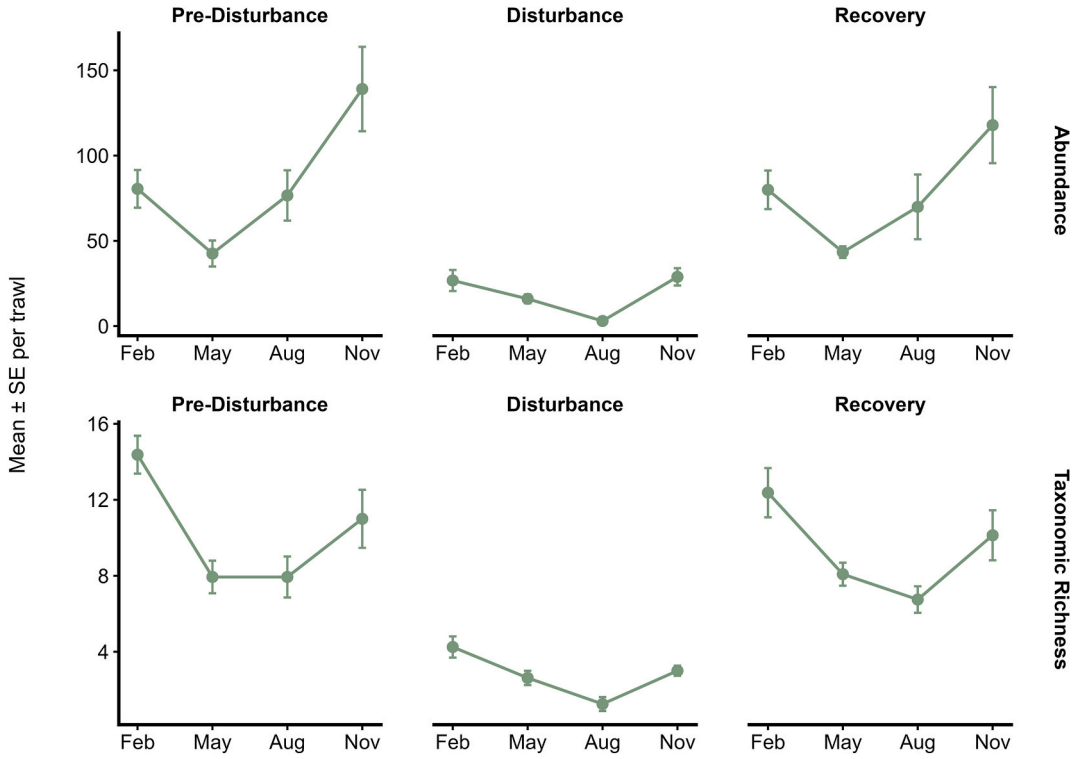

Fig. 4. Mean fish abundance and taxonomic richness per trawl across months (February, May, August, November) for pre-disturbance, disturbance and recovery periods. Points represent means and error bars show $\pm$ SE.

than Ellie Point ($\chi^2 = 15.02$, df = 1, $p = 0.001$), with a significant interaction between period and month ($\chi^2 = 18.07$, df = 6, p = 0.006; Table S3; Fig. 4).

Overall, abundance was significantly lower during the disturbance period compared to both pre-disturbance and recovery periods, while no significant difference was detected between pre-disturbance and recovery (Table S6). However, the significant interaction between period and month indicates that the magnitude of these differences varied seasonally.

Seasonal patterns differed among disturbance phases (Table S7; Fig. 4). During the disturbance period, abundance was significantly lower in August compared to February, May, and November (all $p < 0.01$), indicating a pronounced seasonal decline. In contrast, seasonal differences were weaker and largely non-significant during pre-disturbance and recovery phases, with only May and November differing significantly in both periods ($p < 0.05$).

Across all periods, abundance tended to be highest in November and February and lowest in May and August, although this pattern was most strongly expressed during disturbance. The most pronounced decline occurred in August, where abundance during disturbance was extremely low (2.95 ± 1.10 SE fish per trawl) compared to pre-disturbance (68.49 ± 15.30 SE) and recovery (49.59 ± 11.40 SE). Abundance was significantly higher at Esplanade than Ellie Point (Table S4), with a 1.72-fold greater abundance (estimate = 0.540 ± 0.14 SE, p < 0.001), and mean estimated abundances of 53.0 ± 6.5 SE and 30.9 ± 3.8 SE fish per trawl respectively.

3.2. Taxonomic richness

Taxonomic richness varied significantly among disturbance periods (Fig. 3b; Wald $\chi^2 = 93.50$, df = 2, $p < 0.001$) as well as month ($\chi^2 = 38.36$, df = 3, $p < 0.001$) and between sites ($\chi^2 = 15.19$, df = 1, $p < 0.001$; Table S9).

Pairwise comparisons of estimated marginal means (Table S11 and S12) showed that richness during disturbance was significantly lower than both pre-disturbance (ratio = 3.73, $p < 0.001$) and recovery periods (ratio = 0.30, $p < 0.001$). There was no significant difference between pre-disturbance and recovery (ratio = 0.90, $p = 0.43$). Mean richness per trawl declined from 9.75 ± 0.59 SE taxa pre-disturbance to 2.61 ± 0.33 during disturbance, before recovering to 8.78 ± 0.52.

Seasonally, richness per trawl differed significantly among months, with highest values observed in February (Table S13, Fig. 4). February richness was significantly higher than in May (ratio = 1.64, $p < 0.001$) and August (ratio = 1.77, $p < 0.001$), but did not differ significantly from November (ratio = 1.22, $p = 0.185$). Richness in November was significantly higher than in May (ratio = 0.74, $p = 0.014$) and August (ratio = 0.69, $p = 0.002$), whereas May and August did not differ significantly (ratio = 1.08, $p = 0.889$). Esplanade supported significantly higher species richness than Ellie Point (7.09 ± 0.45 SE vs 5.20 ± 0.35 SE taxa per trawl; ratio = 0.73, $p < 0.001$) (Table S11).

3.2.1. Assemblage structure

Following the exclusion of rare taxa, the final community matrix

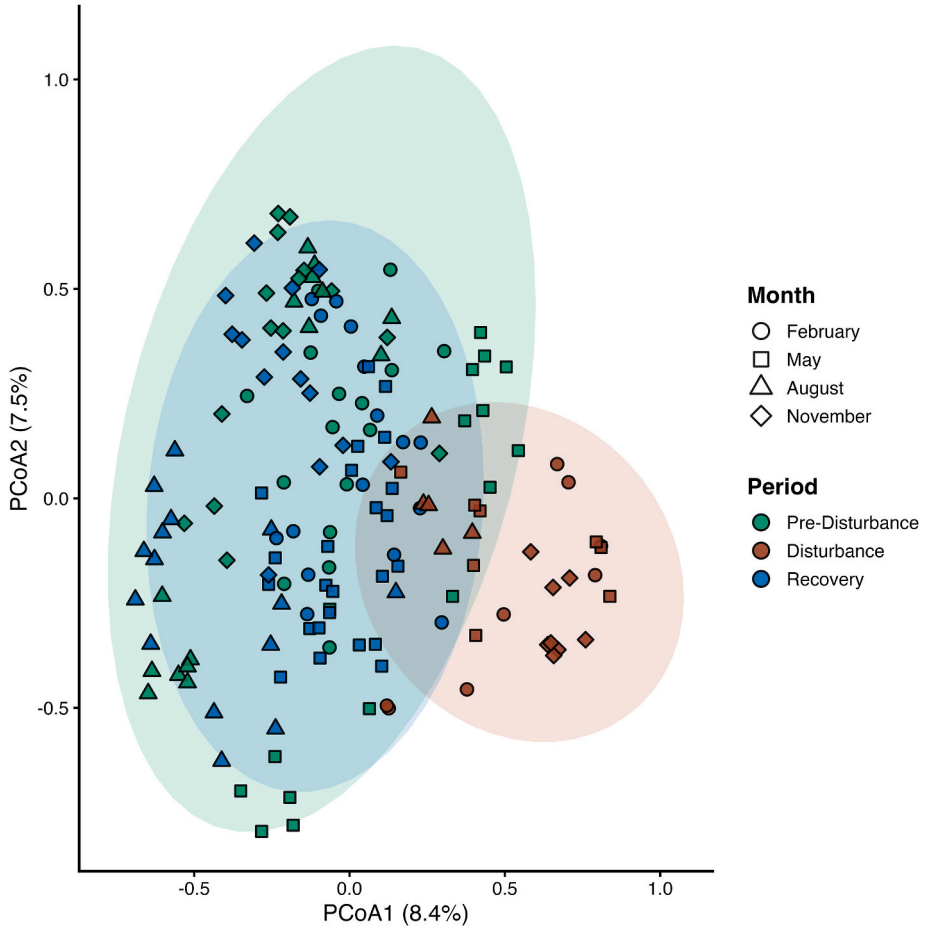

Fig. 5. Principal coordinates analysis (PCoA) of fish assemblage composition from beam trawl samples collected across three disturbance periods: pre-disturbance, disturbance and recovery, in Cairns Harbour. Ordination is based on Bray–Curtis dissimilarities calculated from log (x + 1)-transformed abundance data. Points represent individual trawl samples, coloured by disturbance period and shaped by month of sampling. Shaded ellipses represent 95% confidence regions for each disturbance period. Two trawls from Esplanade in August 2014 were excluded from the ordination because they each contained only five individuals, all identified only to order level, and were therefore considered uninformative for assemblage composition analysis.

comprised 104 taxa. Fish assemblage composition differed significantly among disturbance periods and months (PERMANOVA, Bray–Curtis dissimilarity; Period: $F_{2,153} = 14.71$, $R^2 = 0.14$, $p = 0.001$; Month: $F_{3,153} = 8.93$, $R^2 = 0.12$, $p = 0.001$; Table S14). Site also had a smaller but significant effect ($F_{1,153} = 4.76$, $R^2 = 0.02$, $p = 0.001$). A significant Period × Month interaction ($F_{6,147} = 3.70$, $R^2 = 0.09$, $p = 0.001$) indicated that seasonal patterns in assemblage composition varied among disturbance phases.

Multivariate dispersion did not differ significantly among disturbance periods (PERMDISP: $F_{2,157} = 2.20$, $p = 0.129$; Table S15), indicating that broad differences in assemblage composition among periods were not attributable to unequal dispersion. However, dispersion differed significantly among Period × Month groups (PERMDISP: $F_{11,148} = 5.25$, $p = 0.001$; Table S15), indicating that seasonal differences in assemblage variability may have contributed to the interaction effect.

Given the significant Period × Month interaction, pairwise PERMANOVA contrasts were conducted among disturbance periods within each sampling month (Table S16). Disturbance assemblages differed significantly from pre-disturbance assemblages in February ($R^2 = 0.33$, $p = 0.001$), May ($R^2 = 0.14$, $p = 0.005$), August ($R^2 = 0.25$, $p = 0.001$) and November ($R^2 = 0.40$, $p = 0.001$). Disturbance assemblages also differed significantly from recovery assemblages in February ($R^2 = 0.31$, $p = 0.001$), May ($R^2 = 0.16$, $p = 0.001$), August ($R^2 = 0.30$, $p = 0.001$) and November ($R^2 = 0.44$, $p = 0.001$). Pre-disturbance and recovery assemblages also differed significantly in each month, but with smaller effect sizes: February ($R^2 = 0.10$, $p = 0.001$), May ($R^2 = 0.08$, $p = 0.002$), August ($R^2 = 0.13$, $p = 0.002$) and November ($R^2 = 0.16$, $p = 0.001$). Overall, recovery assemblages remained significantly different from pre-disturbance assemblages, although these contrasts had smaller effect sizes than those involving the disturbance period.

Principal coordinates analysis based on Bray-Curtis dissimilarities supported these patterns, showing a shift in assemblage composition during the disturbance period, while pre-disturbance and recovery assemblages overlapped (Fig. 5). This overlap, together with the smaller pairwise effect size between pre-disturbance and recovery assemblages ($R^2 = 0.05$), suggests that assemblage composition partially recovered following disturbance, although assemblages had not fully returned to pre-disturbance conditions.

4. Functional composition

Functional composition differed significantly among disturbance periods ($F_{2,153} = 20.90$, $R^2 = 0.18$, $p = 0.001$), months ($F_{3,153} = 9.52$, $R^2 = 0.13$, $p = 0.001$) and sites ($F_{1,153} = 7.72$, $R^2 = 0.03$, $p = 0.001$; Table S17). A significant Period × Month interaction ($F_{6,147} = 5.72$, $R^2 = 0.13$, $p = 0.001$) indicated that seasonal patterns in functional composition varied among disturbance periods. Pairwise PERMANOVA comparisons showed that differences in functional composition were most consistent between disturbance and non-disturbance conditions (Table S18). Disturbance assemblages differed significantly from pre-disturbance and recovery assemblages across all months. In contrast, differences between pre-disturbance and recovery assemblages were weaker and varied seasonally, with no significant difference observed in August ($R^2 = 0.05$, $p = 0.218$) and only marginal differences in February ($R^2 = 0.09$, $p = 0.056$).

Multivariate dispersion differed significantly among disturbance periods (PERMDISP: $F_{2,156} = 3.49$, $p = 0.033$), with significantly higher dispersion during the disturbance period than the pre-disturbance period ($p = 0.022$). Dispersion also differed significantly among Period × Month groups ($F_{11,147} = 2.03$, $p = 0.030$; Table S19).

PCoA ordination (Fig. 6) supported these patterns, with disturbance samples showing partial separation from pre-disturbance and recovery samples, while recovery samples overlapped more strongly with pre-disturbance conditions.

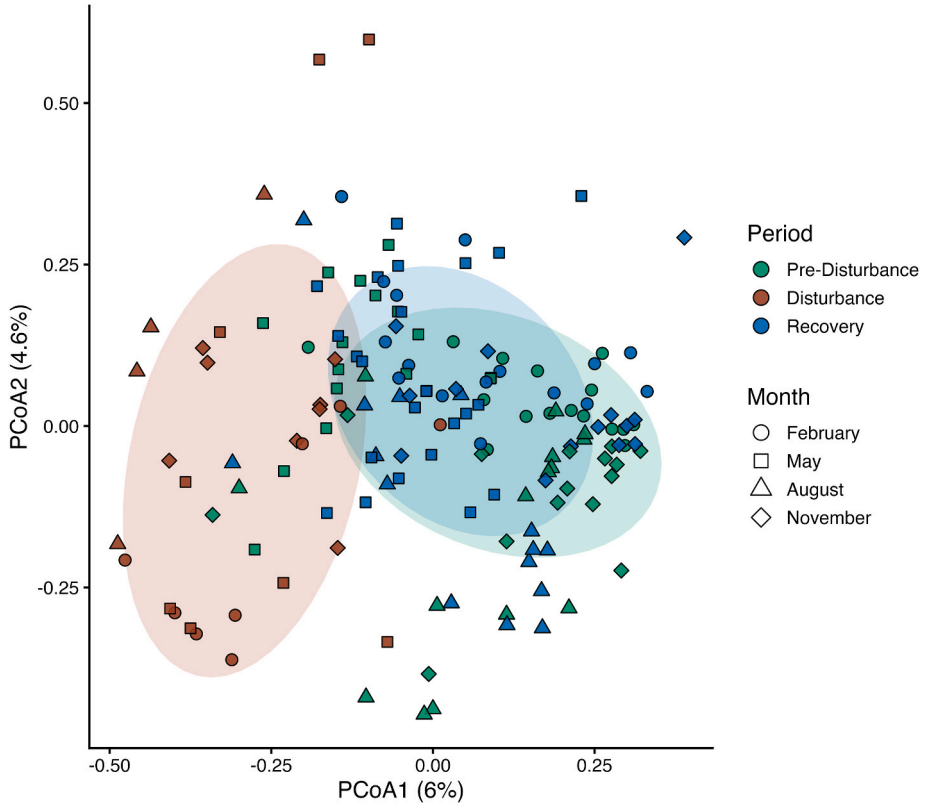

Fig. 6. Principal Coordinates Analysis (PCoA) ordination of functional composition based on Bray–Curtis dissimilarities of family-level trophic group abundance data. Points represent individual trawls, coloured by disturbance period and shaped by month. Ellipses show group dispersion.

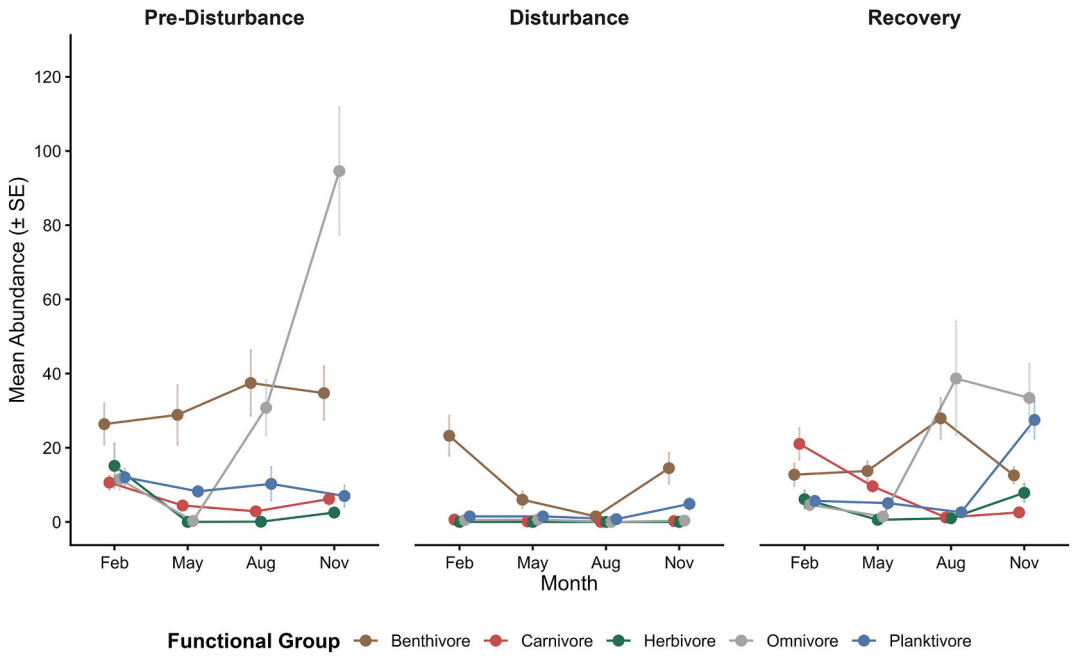

Fig. 7. Mean abundance (±SE) of fish trophic groups (individuals per trawl) across disturbance periods and months in Cairns Harbour.

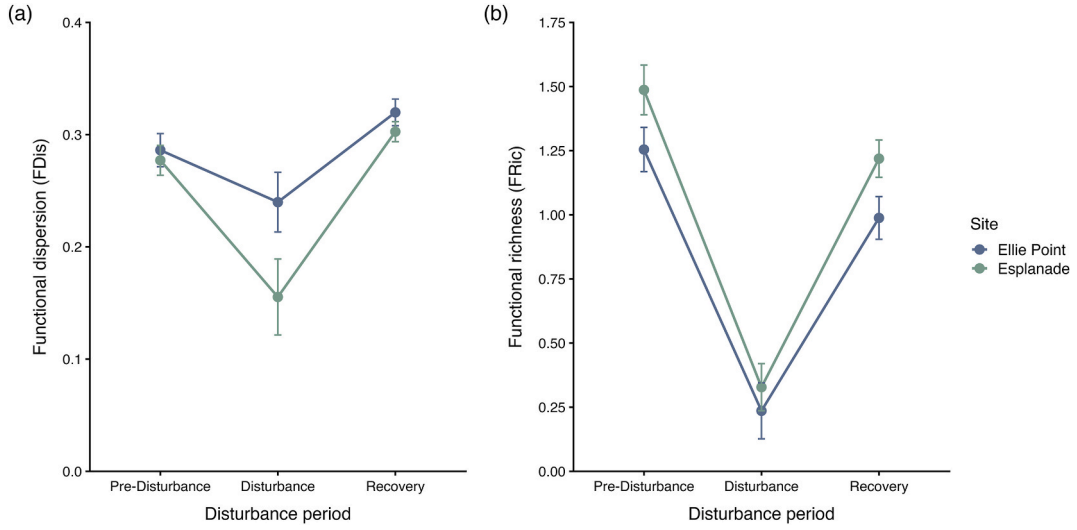

Fig. 8. Mean functional dispersion (a) and functional richness (b) were calculated at the trawl level for fish assemblages at Ellie Point and the Esplanade in Cairns Harbour. Points represent mean values for each site within each disturbance period, with error bars indicating ± standard error.

4.1. Trophic group responses

Trophic group responses varied across disturbance period and month (Table S20). Period and month had significant effects on most trophic groups. Significant interactions between period and month were detected for omnivores ($\chi^2 = 21.80$, $p = 0.001$), planktivores ($\chi^2 = 17.47$, $p = 0.008$), and benthivores ($\chi^2 = 29.71$, $p < 0.001$), indicating that seasonal patterns differed among disturbance periods. In contrast, carnivores showed significant additive effects of period ($\chi^2 = 33.80$, $p < 0.001$) and month ($\chi^2 = 25.53$, $p < 0.001$). Herbivores were absent during the disturbance event, and the model did not detect a significant overall effect of period ($p = 0.68$), although they varied significantly among months ($\chi 2 = 17.59$, p < 0.001).

Site effects were variable among trophic groups, with significant differences observed for benthivores ($\chi^2 = 18.54$, $p < 0.001$) and omnivores ($\chi^2 = 7.39$, $p = 0.007$), but not for carnivores or planktivores.

Pairwise comparisons indicated that abundance declined during the disturbance period for several trophic groups, although responses varied among months and were not consistent across all groups (Table S21). Omnivore abundance was significantly higher in the pre-disturbance period compared to the disturbance period in February ($p = 0.003$) and November ($p < 0.001$). In November, pre-disturbance abundance was also higher than recovery ($p = 0.047$), while recovery abundance was higher than during disturbance ($p < 0.001$). No significant

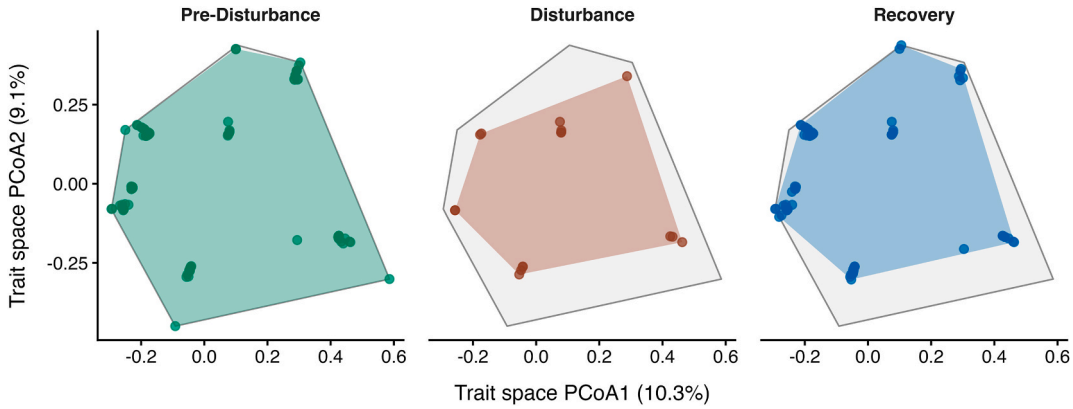

Fig. 9. Functional trait space occupied by fish taxa across disturbance periods. Distribution of taxa is shown in functional trait space, where axes represent the first two axes from a principal coordinates analysis (PCoA) on functional traits. The grey polygon shows the total observed trait space occupied by taxa across all disturbance periods. Coloured polygons show the trait space occupied within each disturbance period, and points represent taxa present in each period.

differences were detected among periods in May or August.

Planktivores were significantly more abundant in the pre-disturbance period compared to the disturbance period in February ($p = 0.003$), May ($p = 0.037$), and August ($p = 0.006$). In November, abundance was significantly higher in the recovery period compared to both pre-disturbance ($p = 0.009$) and disturbance periods ($p = 0.014$). Benthivore abundance showed similar declines, with significantly higher abundance pre-disturbance than during disturbance in May ($p = 0.015$) and August ($p < 0.001$). Herbivore abundance was higher in February than in May ($p = 0.002$) and August ($p = 0.008$), and higher in November than in May ($p = 0.026$). Although significant effects of period and month were detected, for carnivores pairwise comparisons were associated with high uncertainty.

Trophic group abundance declined during the disturbance period (Fig. 7). Benthivores and omnivores, which dominated during the pre-disturbance period showed marked reductions, with only partial recovery in some months. Recovery assemblages were characterised by a more even distribution of trophic groups, indicating a shift in trophic structure rather than a return to pre-disturbance conditions.

4.2. Functional traits and functional diversity

Mean functional dispersion (FDis) and functional richness (FRic) varied among disturbance periods and between sites (Fig. 8). Functional dispersion was lower during the disturbance period at both sites, with a more pronounced decline at the Esplanade, where mean FDis decreased from 0.28 pre-disturbance to 0.16 during disturbance (Fig. 8 a). Functional richness also declined strongly during the disturbance period, with mean FRic decreasing from 1.37 pre-disturbance to 0.29 during disturbance, indicating a reduction in occupied functional trait space (Fig. 8b).

During the recovery phase, FDis increased at both sites, exceeding pre-disturbance levels, with mean values of 0.32 at Ellie Point and 0.30 at the Esplanade. Functional richness also increased during recovery, reaching 1.11 overall, but remained below pre-disturbance values. This pattern was also visible in the trait-space PCoA (Fig. 9), where disturbance-period taxa occupied a smaller area of the overall observed trait space compared with pre-disturbance and recovery taxa. Overall, disturbance was associated with both a reduction in functional dispersion and functional richness, while recovery was characterised by increased functional dispersion, and a partial expansion of trait space.

5. Indicator species

Indicator species analysis identified 38 taxa significantly associated with disturbance periods (IndVal, 999 permutations, $p < 0.05$, Table S22). Pre-disturbance conditions had the greatest number of indicator taxa (16 species), *Glossogobius circumspectus* (IndVal = 0.58), *Sillago maculata* (IndVal = 0.38), and *Acanthopagrus berda* (IndVal = 0.36). Four species were strongly associated with the disturbance period, including *Gerres oyena* (IndVal = 0.77), *Amniataba percoides* (IndVal = 0.45) and *Polydactylus multiradiatus (*IndVal = 0.37). Six species were indicators of the recovery period, including *Pomadasys argenteus* (IndVal = 0.47) and *Alepes djedaba* (IndVal = 0.32). In addition, one species (*Devexim*entum *ruconius*) was associated with both pre-disturbance and disturbance periods.

Eleven species were associated with both pre-disturbance and recovery periods but were absent or rare during disturbance, including *Pelates quadrilineatus* (IndVal = 0.76), *Terapon puta* (IndVal = 0.69), and *Pomadasys kaakan* (IndVal = 0.61). These patterns were further supported by changes in abundance of selected indicator taxa across disturbance periods (Fig. 10).

Overall, indicator taxa showed contrasting responses among disturbance periods, with some taxa increasing during disturbance and others declining or showing limited recovery.

6. Discussion

The loss and subsequent recovery of a seagrass meadow in Cairns Harbour showed that recovery in fish abundance and taxonomic richness did not necessarily correspond with a return to the historical fish assemblage. Seagrass loss was associated with substantial declines in fish abundance (~84%) and taxonomic richness (~73%), yet both metrics returned to levels comparable with pre-disturbance conditions following meadow recovery over a decadal timescale. However, assemblage composition remained distinct from the historical baseline, indicating that increases in seagrass area and above-ground biomass were not accompanied by a full return of the previous fish community. Instead, the recovered meadow supported a reassembled assemblage with different taxonomic and functional characteristics.

This reassembly was also reflected in trophic structure, with disturbance and recovery associated with shifts in the relative abundance of key trophic groups. Seasonal dynamics further shaped fish assemblages, with higher abundance and richness observed during the wet and

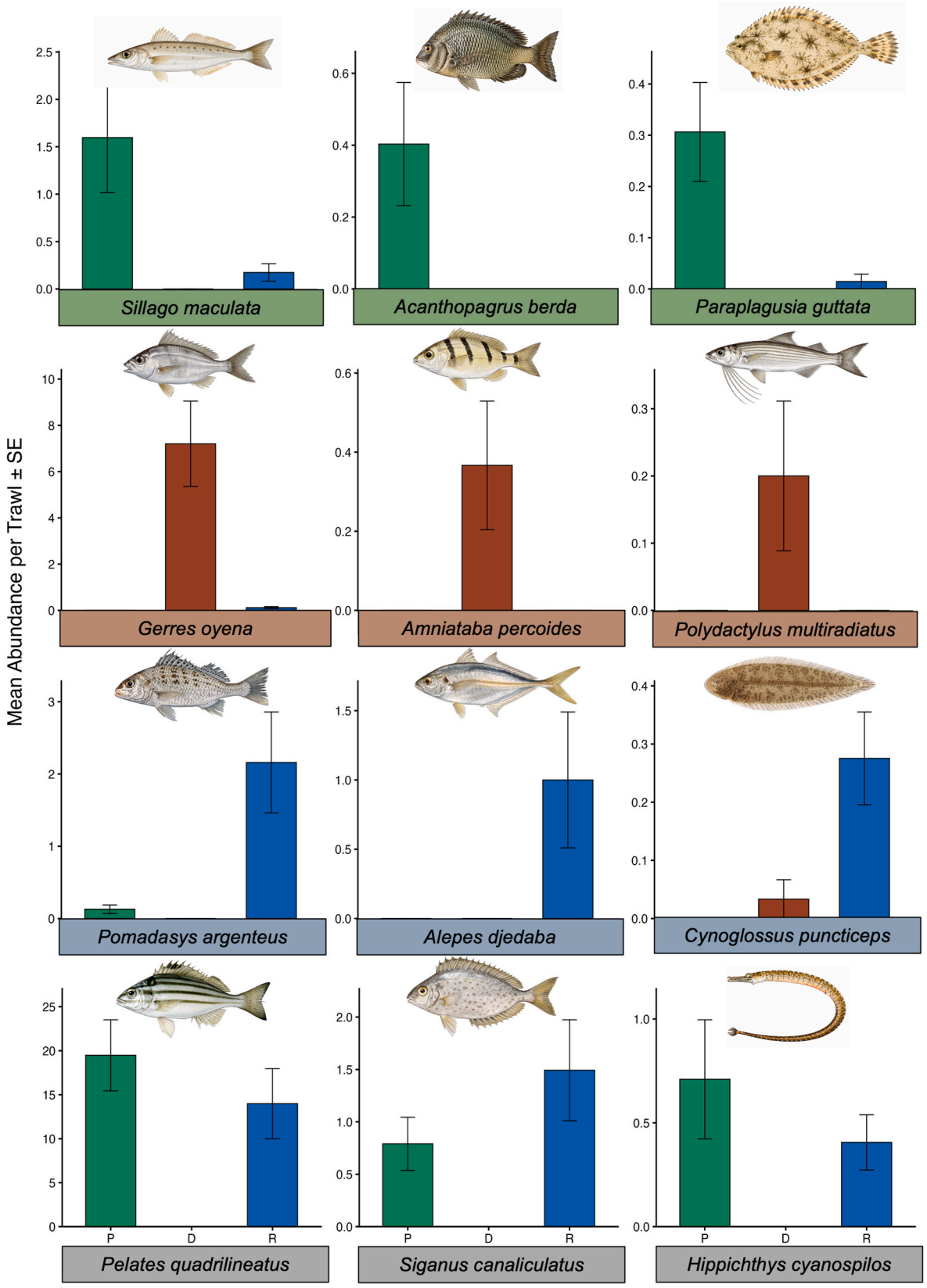

Fig. 10. Mean abundance per trawl (±SE) of selected indicator taxa across disturbance periods (P = Pre-disturbance, D = Disturbance, R = Recovery). Species were identified as significant indicators of disturbance period using indicator species analysis (IndVal, $p < 0.05$). Taxa are grouped as pre-disturbance-associated (green), disturbance-associated (brown), recovery-associated (blue), shared pre-disturbance and recovery taxa (grey). (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

transitional periods (February and November), likely reflecting increased productivity and recruitment in tropical seagrass ecosystems (Unsworth et al., 2008).

6.1. Disturbance and recovery of seagrass fish assemblages

Disturbance and recovery in marine ecosystems are often characterised by mismatches between the recovery of habitat structure and the response of associated faunal communities (Lotze et al., 2011). Seagrass meadows can recover in area and biomass over time, but associated fish assemblages do not always return to their original composition (Castro-Fernández et al., 2025a,b). Instead, recovery can be delayed, incomplete, or involve shifts in community structure driven by changes in recruitment, trophic interactions, and habitat connectivity (Lotze et al., 2011; McCauley et al., 2015). Globally, seagrass ecosystems have experienced widespread declines, and although recovery is increasingly documented, it is often variable and does not necessarily result in the full re-establishment of pre-disturbance communities (Orth et al., 2006; Dunic et al., 2021).

In this study, seagrass loss resulted in drastic declines in both fish abundance and taxonomic richness at sites previously within meadow footprints. Abundance decreased from 90.1 ± 16.8 fish per trawl to 14.2 ± 4.0 during disturbance, and richness declined from 9.75 ± 0.59 to 2.61 ± 0.33 taxa per trawl. These declines were likely strongly associated with the loss of structurally complex seagrass habitat, which reduces refuge availability, food resources, and recruitment success (Hughes et al., 2002; McCloskey and Unsworth, 2015). Similar patterns of seagrass loss and associated declines in fish communities have been documented globally (Hughes et al., 2002; Pihl et al., 2006; O'Leary et al., 2021), although the magnitude and duration of change observed in Cairns Harbour emphasise the sensitivity of tropical seagrass-associated fish communities to habitat degradation.

Following habitat recovery, both fish abundance and richness recovered to levels comparable to pre-disturbance conditions, indicating a recovery in overall assemblage size and diversity. This suggests that fauna are capable of responding to improved habitat conditions, likely facilitated by movement between adjacent habitats and recolonisation processes as seagrass structure and habitat improved (Henderson et al., 2017; Olson et al., 2019; Sievers et al., 2025).

Despite this recovery in abundance and richness, assemblage composition remained significantly different from pre-disturbance conditions, indicating a reorganisation of the fish community rather than a return to baseline composition. In Cairns Harbour, the disturbance resulted in an approximately 98% loss of intertidal seagrass area (McKenna et al., 2015), with limited recovery over several years (Reason et al., 2025). Such sustained habitat degradation may have disrupted key ecological processes, including recruitment, species interactions, and habitat connectivity, resulting in lasting changes to community structure (Orth et al., 2006; Pihl et al., 2006). However, this may partly reflect the way habitat recovery was assessed. Although above-ground biomass provides an integrated measure of seagrass abundance that incorporates aspects of canopy height and leaf density, seagrass area and biomass do not capture all components of structural habitat complexity. Finer-scale variables such as shoot density and leaf area can influence refuge availability, prey resources, and settlement habitat for juvenile fishes, but were not consistently available across the full time series (Heck and Orth, 1980; Gullström et al., 2008; Henderson et al., 2017; Castro-Fernández et al., 2025a,b). Consequently, the available measures of habitat recovery may not fully reflect the recovery of habitat quality for fish assemblages.

These findings are consistent with growing evidence that ecological recovery is often not linear, and that post-disturbance assemblages may reflect altered or transitional states rather than a direct return to pre-disturbance conditions (Pihl et al., 2006; Sobocinski et al., 2013; Castro-Fernández et al., 2025a,b; Garcia et al., 2025). In some cases, prolonged or severe disturbance can lead to shifts towards alternative community states, particularly where habitat loss is extensive and recovery trajectories are constrained (Scheffer et al., 2001; Stuart-Smith et al., 2021).

Changes in assemblage structure may also reflect altered connectivity between seagrass meadows and adjacent habitats. Many seagrass-associated fish species rely on movement between mangroves, estuaries, and coastal reefs during different life stages (Nagelkerken et al., 2015; Gilby et al., 2018). Disturbance to seagrass habitats may disrupt these linkages, limiting recruitment and slowing community recovery, contributing to the persistence of altered assemblage composition (Henderson et al., 2017).

6.2. Trophic reorganisation and species-specific responses

Changes in trophic composition are a key ecological response to disturbance, reflecting shifts in trophic structure, with wider implications for ecosystem functioning and resilience (Orth et al., 2006; Hempson et al., 2018; Stuart-Smith et al., 2021). In seagrass habitats, trophic groups are closely associated with prey availability and habitat structure, with seagrass meadows supporting high densities of benthic invertebrates (Heck and Orth, 1980; Nakamura and Sano, 2005; Jones et al., 2021).

In this study, disturbance was associated with widespread declines across trophic groups, particularly benthivores, herbivores, and omnivores, which were more abundant under pre-disturbance conditions. These groups are typically associated with structured seagrass habitats and benthic foraging, suggesting that habitat degradation and reduced seagrass area likely constrained their feeding opportunities and resource availability during disturbance (Campbell et al., 2011; McCloskey and Unsworth, 2015). The size-selective nature of the beam trawl, which favours the capture of small-bodied and juvenile fishes, may have contributed to an under-representation of larger, more mobile taxa occupying higher trophic levels (McNeill and Bell, 1992; French et al., 2021b; Philpott et al., 2025).

In contrast, recovery was characterised by increases in omnivores and planktivores, alongside a more even distribution of trophic groups. This suggests that recovery involved a shift in trophic structure rather than a simple return to pre-disturbance trophic organisation. Although overall abundance and richness returned to levels comparable with the pre-disturbance period, the relative contribution of trophic groups differed, indicating that recovered assemblages supported a different balance of feeding strategies. These patterns are consistent with evidence that species turnover can drive trophic restructuring and alter functional redundancy following disturbance (Clavel et al., 2011; Garcia et al., 2025).

Seasonal variation further influenced these patterns, with trophic composition varying significantly among months, particularly under pre-disturbance conditions, and showing greater variability during recovery. This is consistent with studies demonstrating that seasonal dynamics and variation in seagrass structure can drive shifts in functional diversity and resource use (Gomes et al., 2025).

Indicator species analysis revealed distinct species-specific responses across disturbance phases, consistent with the broader shifts in species composition and trophic structure. Species such as *Gerres oyena* were significantly associated with the disturbance period, reflecting a broader pattern in which opportunistic species with flexible habitat use and feeding strategies become increasingly prevalent in degraded systems (McKinney and Lockwood, 1999). This shift suggests that disturbance can promote generalist-dominated assemblages, with consequences for the distribution of trophic roles within seagrass-associated communities (Clavel et al., 2011; Iacarella et al., 2018; Stuart-Smith et al., 2021).

In contrast, several taxa were associated with pre-disturbance and recovery conditions, reflecting stronger links to seagrass habitat structure. Notably, the pipefish *Hippichthys cyanospilos* was associated with both periods, suggesting a strong dependence on structurally complex seagrass habitat. Pipefish are highly specialised, relying on vegetation

for camouflage, feeding, and protection, and their absence during disturbance likely reflects the loss of suitable habitat (York et al., 2006; O'Leary et al., 2021). More broadly, many estuarine fish depend on structurally complex habitats for settlement and refuge, and the temporary loss of seagrass likely reduced recruitment success during disturbance (Burfeind et al., 2009; Williams et al., 2016). The reappearance of these taxa during recovery suggests that the return of habitat structure was an important driver of assemblage change (McCloskey and Unsworth, 2015).

Importantly, recovery trajectories were not consistent across taxa. While some species returned following disturbance at lower abundances than pre-disturbance levels (e.g. *Pelates quadrilineatus*), other species increased during recovery, including herbivorous taxa such as *Siganus canaliculatus*, which are closely associated with seagrass habitats (Hoey et al., 2013). This indicates shifts in species dominance rather than a uniform return to baseline conditions. This is further supported by the emergence of recovery-associated indicator taxa, such as *Pomadasys argenteus* and *Alepes djedaba,* suggesting a partial return of taxa occupying demersal and pelagic positions (Froese and Pauly, 2026). Together, the shifts in taxonomic composition and trophic structure indicate that disturbance drives strong species-level filtering, resulting in reorganisation of assemblage structure and ecological function.

Such shifts are consistent with patterns observed in systems undergoing regime shifts, where disturbance drives transitions to alternative community configurations with different functional characteristics (Graham et al., 2015; Hempson et al., 2018; Stuart-Smith et al., 2021; Cook et al., 2022). These changes suggest a broader reorganisation of trophic structure within the system, rather than recovery of the original functional configuration (Pihl et al., 2006; Sobocinski et al., 2013; Stuart-Smith et al., 2021). Changes in resource availability and habitat structure can favour taxa with broader feeding or habitat-use flexibility, while more specialised or higher trophic-level taxa may decline, resulting in altered trophic organisation (Clavel et al., 2011; Graham et al., 2015).

Trait-based functional diversity patterns provided further evidence of ecological restructuring beyond shifts in species composition (Laliberté and Legendre, 2010; Mouillot et al., 2013; Mao et al., 2021). Functional dispersion was reduced during the disturbance period, suggesting that the taxa present were more tightly grouped in trait space. The lower functional richness observed during disturbance indicates reduced occupation of functional trait space during habitat loss. During functional recovery, functional dispersion exceeded pre-disturbance levels, suggesting an expansion into trait space occupied by a different combination of species and functional roles. Together, the functional richness and functional dispersion results indicate reorganisation rather than a return to baseline conditions, with potential implications for ecosystem functioning and trophic interactions within seagrass ecosystems (Stuart-Smith et al., 2021; Garcia et al., 2025; Sha et al., 2026).

6.3. Environmental drivers: habitat variability and seasonality

Fish assemblages exhibited strong seasonal variation, with the highest abundance and richness patterns observed during November and February, and the lowest during May and August. However, these seasonal patterns did not correspond directly with periods of maximum seagrass biomass, suggesting that temporal variation in fish assemblages was not driven solely by habitat availability or structural complexity.

In tropical north Queensland, November occurs near the end of dry season and represents a transitional period into the wet season. This period may coincide with relatively high seagrass biomass and habitat structure, as well as the onset of seasonal recruitment into coastal habitats (Robertson and Duke, 1987; McKenzie, 1994; Kwak and Klumpp, 2004; Ralph et al., 2007). Elevated abundance and richness during November may therefore reflect the combined influence of suitable habitat conditions and early recruitment pulses. In contrast, February occurs during peak wet season conditions, characterised by increased water temperature, freshwater input, nutrient availability and reduced water clarity (McKenzie, 1994; Davis et al., 2012; da Silva et al., 2021). Although these conditions can reduce seagrass biomass through light limitation, they may also enhance larval supply and recruitment of juvenile fishes into coastal habitats, explaining the high abundance and richness in February despite lower seagrass biomass.

Conversely, periods of higher seagrass biomass observed in the dry season did not correspond to peak fish abundance or richness, particularly in August. This mismatch suggests that habitat availability alone does not explain seasonal assemblage patterns. Instead, seasonal pulses of larval recruitment, coupled with variability in environmental conditions such as turbidity and freshwater input, likely influenced temporal patterns in fish assemblages (da Silva et al., 2021; Compain et al., 2025).

Over the multi-decadal period examined in this study, changes in fish assemblage composition may also have been influenced by broader environmental variability. Long-term changes in sea temperature, freshwater flow, turbidity, nutrient availability, salinity and chlorophyll-a can all affect estuarine and coastal fish assemblages through effects on recruitment, physiological tolerance, prey availability and habitat use (Abrahams and Kattenfeld, 1997; O'Leary et al., 2021; Guo et al., 2022; Lourenço et al., 2023; Itsukushima and Kano, 2025). Although the timing and severity of seagrass loss in Cairns Harbour provide a strong basis for linking declines in fish abundance and richness to habitat disturbance, the absence of an undisturbed control meadow and long-term environmental covariates limit our ability to attribute compositional reorganisation solely to changes in seagrass habitat. The differences between pre-disturbance and recovery assemblages likely reflect the combined influence of prolonged seagrass loss, seasonal recruitment dynamics, and broader environmental change (Comte et al., 2021).

Seagrass habitat condition nevertheless remains important in structuring fish assemblages. Changes in seagrass biomass and area during the recovery period likely contributed to the differences observed in assemblage composition, particularly because recovery was spatially variable across sites (Castro-Fernández et al., 2025a,b). Given the importance of structural complexity in supporting faunal assemblages (Gullström et al., 2008; Jones et al., 2021), prolonged habitat loss in Cairns Harbour likely constrained the return of species reliant on dense seagrass habitat. Periods of high seagrass biomass can also support greater densities of epifauna associated with seagrass blades, increasing both food availability and refuge for juvenile fishes (Edgar and Robertson, 1992; Bologna and Heck, 1999).

Together, these results suggest that fish assemblage dynamics in tropical seagrass systems are shaped by the interaction between seasonal recruitment processes and habitat condition (Gullström et al., 2008; Gilby et al., 2018; Gross et al., 2019; Ruesink et al., 2019). Seasonal recruitment likely drives short-term peaks in abundance and richness, while seagrass structure and recovery dynamics influence which taxa persist, return, or remain absent following disturbance (Barletta et al., 2008; Pichler et al., 2017).

6.4. Conservation and management implications

These findings have important implications for the nursery function of tropical seagrass meadows. Reduced abundance and diversity of juvenile fishes during disturbance periods indicate a reduced capacity of these habitats to support early life stages (McCloskey and Unsworth, 2015). Given that the nursery role of seagrass systems is closely linked to habitat structure and condition, prolonged habitat loss or incomplete recovery may compromise their ability to function as effective nurseries (Heck et al., 2003; Orth et al., 2006).

Although fish abundance and richness recovered to pre-disturbance levels, the persistence of altered assemblage composition suggests that nursery function may not be fully restored following disturbance within the timeframes of this study (Lefcheck et al., 2019). These observed shifts in assemblage composition raise the possibility of longer-term

changes in community structure, including the increased dominance of disturbance-tolerant and generalist species, which may alter trophic interactions, prey use, and the contribution of seagrass meadows to fisheries recruitment (McKinney and Lockwood, 1999; Clavel et al., 2011; Iacarella et al., 2018). This suggests that recovery assessments that are based only on seagrass area, above-ground biomass, or total fish abundance may not indicate full ecological recovery. Changes in species composition and trophic roles may result in the meadow supporting different fish assemblages and provide a different nursery function than before disturbance (Pihl et al., 2006; Iacarella et al., 2018).

From a management perspective, these findings emphasise that recovery of seagrass extent alone may not guarantee full ecological recovery of associated faunal communities (Castro-Fernández et al., 2025a,b). However, growing evidence from seagrass restoration studies suggests that active habitat restoration can accelerate the return of biodiversity and ecosystem function (McSkimming et al., 2016; Tanner et al., 2021). For example, restored meadows have been shown to rapidly recover key ecosystem services (Orth et al., 2020), support increasing fish abundance and diversity over time (Gagnon et al., 2023; Hardison et al., 2023) and facilitate early faunal recolonisation even before full habitat maturity is reached (McSkimming et al., 2016). While this study suggests that full ecological recovery may take longer than full habitat recovery, together, these studies suggest that restoration combined with natural recovery may play a role in promoting both structural and functional recovery of seagrass-associated fish assemblages.

7. Conclusion

This study demonstrates that seagrass loss can result in substantial declines in fish abundance and taxonomic richness, followed by recovery to pre-disturbance levels after an extended period of habitat decline. However, within the timeframe examined here, this recovery was not accompanied by a full return to pre-disturbance assemblage composition, indicating a restructuring of the fish community rather than complete ecological recovery. Species-specific responses and shifts in trophic structure and trait-based functional diversity reinforced this pattern, with some taxa absent during disturbance exhibiting variable re-establishment during recovery, suggesting ongoing changes in recruitment, habitat use, and community structure.

Seasonal variation also played a key role in structuring assemblages, with higher abundance and richness during November and February, likely driven by increased productivity and recruitment pulses characteristic of tropical seagrass systems. These temporal patterns further highlight the importance of considering seasonality when assessing disturbance and recovery trajectories.

Together, these findings demonstrate that the recovery of seagrass habitats does not necessarily result in the immediate recovery of associated faunal communities. Instead, during the recovery period captured in this study, fish assemblages were characterised by shifts in species composition, trophic structure, and functional diversity, indicating ecological reorganisation rather than a full restoration of the original assemblage. However, it remains possible that continued habitat recovery and additional time may allow further convergence towards pre-disturbance assemblage structure.

This multi-decadal dataset provides valuable insight into disturbance and recovery dynamics in tropical seagrass habitats, highlighting that assessments of ecosystem recovery must consider not only abundance and richness estimates, but also changes in community composition, functional diversity, and temporal dynamics.

Ethics and permit approvals

All sampling procedures were conducted in accordance with relevant regulatory approvals, operating under the Queensland Department of Agriculture and Fisheries (DAF) General Fisheries Permits (#114026 and #259152), the Great Barrier Reef Marine Park Authority (GBRMPA; permit G23/48334.1), and James Cook University Animal Ethics approval (A1787 and A2896).

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CRediT authorship contribution statement

Darcy E. Philpott: Conceptualization, Data curation, Formal analysis, Funding acquisition, Investigation, Project administration, Validation, Visualization, Writing – original draft, Writing – review & editing. **Robert G. Coles:** Conceptualization, Data curation, Funding acquisition, Investigation, Methodology, Supervision, Validation, Writing – review & editing. **Sarah Omundsen:** Data curation, Investigation, Validation, Writing – review & editing. **Michael A. Rasheed:** Conceptualization, Funding acquisition, Project administration, Supervision, Writing – review & editing. **Timothy M. Smith:** Data curation, Supervision, Validation, Visualization, Writing – review & editing. **Warren J. Lee Long:** Conceptualization, Investigation, Methodology, Validation, Writing – review & editing. **Marcus Sheaves:** Data curation, Investigation, Validation, Writing – review & editing. **Len J. McKenzie:** Data curation, Investigation, Methodology, Validation, Writing – review & editing. **Tonia Sankey:** Investigation, Validation, Writing – review & editing. **Paul H. York:** Conceptualization, Data curation, Funding acquisition, Investigation, Methodology, Project administration, Supervision, Validation, Visualization, Writing – review & editing.

Declaration of competing interest

The authors declare the following financial interests/personal relationships which may be considered as potential competing interests: Darcy Philpott reports financial support was provided by Holsworth Wildlife Research Endowment Equity Trustees Charitable Foundation. Darcy Philpott, Paul York, Michael Rasheed reports financial support was provided by North Queensland Bulk Ports Corporation. Paul York, Michael Rasheed, Tim Smith reports financial support was provided by Australian Research Council Grant. If there are other authors, they declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.ecss.2026.110155.

Data availability

All survey data needed to replicate the study, and statistical analyses are available as supplementary material. Consensus mtDNA COI haplotypes generated for taxonomic validation are available in NCBI Bank under accession numbers: PZ100018–100029 and PZ240397-240408.

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