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The functional diversity of fish assemblages in the vicinity of oil and gas pipelines compared to nearby natural reef and soft sediment habitats

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ABSTRACT

As the offshore hydrocarbon industry matures and decommissioning activities are expected to increase, there is a requirement to assess the environmental consequences of different pipeline decommissioning options. Previous research on fish and other ecological components associated with pipelines has focused on examining species richness, abundance and biomass surrounding structures. The extent to which subsea pipelines mimic or alter ecosystem function compared with nearby natural habitats is unknown. We analyse differences in fish assemblage biological trait composition and the functional diversity at exposed shallow-water subsea pipelines, nearby natural reef and soft sediment habitats, using mini stereo-video remotely operated vehicles (ROV). Habitats significantly differed in assemblage trait composition. The pipeline and reef habitats shared a more similar functional composition and had the presence of key functional groups required for the development and maintenance of healthy coral reef systems. The reef habitat had the greatest functional diversity, followed by the pipeline habitat and soft sediment habitat respectively.

1. Introduction

The marine environment is facing increasing pressures and today, 60% of the world's major marine ecosystems that underpin livelihoods have been degraded or are being used unsustainably (UNESCO, 2020). Increasingly, over the next few decades, the offshore oil and gas industry will continue its decline. Currently there are more than 7,500 oil and gas structures (OGSs) in the waters of 53 countries that are approaching the end of field life and will require some form of decommissioning (Fowler et al., 2018). The planning and execution of decommissioning offshore OGSs is a relatively new challenge for the industry, its regulators, and governments worldwide. The process requires judgement on whether it is socially, economically, and ecologically beneficial to apply derogation (leave in place) or, partially or completely remove these infrastructures. There is growing evidence that OGSs can support a high abundance and diversity of sessile invertebrates and fish, including species that are considered commercially and recreationally important and/or are of high conservation value (Schramm et al., 2021; Harvey et al., 2021; McLean et al., 2022a).

Different regions of the world have taken different approaches to decommissioning. However, in alignment with international obligations (i.e., the United Nations Convention on the Law of the Sea (UNCLOS) and the Convention on the Prevention of Marine Pollution by Dumping of Wastes and Other Matter (London Convention), complete removal of infrastructure is required in most countries, including Australia (Hamzah, 2003). Although full removal of infrastructure is the default decommissioning option in Australia, other options include: (1) partial (range from almost complete removal where infrastructure is removed near to the seafloor through to minimal removal, e.g., where only platform topsides are removed); (2) remain in situ (infrastructure is left in place); or (3) reefing (using decommissioned infrastructure to form an artificial reef) (Shaw et al., 2018). Current Australian Government policy states that any proposed deviation from complete removal of offshore oil and gas infrastructure must deliver an equal or better environmental, safety and well integrity outcomes, compared to complete removal (Australian Government Department of Industry, Science, Energy and Resources (DISER), 2018). Environmental assessments fall broadly into two groups: benefits – such as ecological or fishery

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(Macreadie et al., 2011), and risks – such as release and dispersal of contaminants (Fowler et al., 2018). With increasing evidence that OGSs have the potential to function as artificial reefs, regulators in Australia are currently reviewing permissible alternatives to the "base case" regulatory default of complete removal (Melbourne-Thomas et al., 2021).

Investing in research to address knowledge uncertainty is one way to demonstrate awareness of the range of issues that can also underpin the selection of decommissioning options for assets. Previous ecological studies have predominantly focused on examining species richness, abundance and biomass surrounding platforms. For example, Friedlander et al. (2014) reported a higher diversity and biomass of fishes and rocky invertebrates on platforms in West Africa compared to the surrounding natural region, dominated by soft sediment communities. Ajemian et al. (2015) in the north-western Gulf of Mexico (GOM) shelf reported structure type (toppled and partially removed jackets) and relief to influence species richness and community structure, where inhabiting species varied from large transient piscivores to small herbivorous reef fishes. A recent study by Harvey et al. (2021) estimated that the biomass of fish associated with seven standing platforms in the Gulf of Thailand was at least four times higher per unit area than some of the world's most productive coral reefs. However, community composition and food web structure has been reported to differ between natural and artificial reef systems, with artificial reefs being described as having "novel attributes"; where an ecosystem has been altered by human activity and has distinct ecological characteristics not found at natural sites in the region (Hobbs et al., 2014; Elden et al., 2019). For example, oil and gas platforms can act as "stepping-stones" in soft sediment dominated environments by facilitating the presence of fish and invertebrate species that might not otherwise occur in these areas (Consoli et al., 2013; Friedlander et al., 2014; Nishimoto et al., 2019). A study by Elden et al. (2019) stated that in the case where a novel ecosystem has emerged from the presence of offshore platforms with potentially significant ecological value, they should be classified and managed using the novel ecosystems concept using existing decommissioning decision analysis models as a base, which recognises the value of the new ecosystem functions and services and allows for the ecosystem to be managed in its novel state.

Subsea pipelines have been installed in all major hydrocarbon basins across the globe to support the offshore oil and gas industry and are used for transporting products such as crude oil or natural gas. Despite the prevalence of subsea pipelines, research is only beginning to understand the interactions between pipelines and local ecosystems (Bond et al., 2018a; Redford et al., 2021; Schramm et al., 2021). Like jackets, oil and gas pipelines lying exposed on the seabed can function as "artificial reefs," providing habitat for fish and benthic species (Rouse et al., 2019). A study by Schramm et al. (2021) reported that the biomass of fish on pipelines located on the Northwest shelf of Western Australia was, on average, 20 times greater than soft sediments, and was similar to natural reefs. However, the community composition of fish associated with pipelines was distinct from those associated with natural habitats, suggesting that similar to previous studies on platforms, there is the emergence of a novel ecosystem.

An aspect that has received little attention is how assemblages associated with pipelines function compared to natural communities. A self-sustaining and self-regulating ecosystem is deemed "functional" if it represents a significant component of ecosystem health and provides ecosystem services that benefit society (Barabás et al., 2017). Understanding the structure of communities may reveal critical insights into their functioning, such as the role of keystone species, ecological engineers, species interactions and resilience to stressors such as climate change (Sebastián-González et al., 2021). Although community composition may differ between natural and artificial habitats resulting in novel ecosystems, those ecosystems may function in a similar way, which must be investigated to determine habitat value. This will improve our understanding of the resilience to stressors, allow for the potential conservation of species that might have been reduced in natural habitats due to multiple stressors, and to ensure that a harmful novel ecosystem does not evolve and begin to negatively impact natural habitats (e.g., the presence of species that would otherwise not occur in the region or increased mortality rates or reduced fitness) (McLean et al., 2019; Komyakova et al., 2021). Elliott and Birchenough (2022) derived a cause and consequence conceptual model for man-made structures and identified ecosystem functioning as part of a main category of cause and effect (base support for biota). Another study by McLean et al. (2022b) identified the influence of man-made structures on ecological function as a priority research question on the influence of oil and gas infrastructure on seascape connectivity.

Species traits, regarded as any property of organisms that influence performance (McGill et al., 2006), offer an ideal framework to better understand the mechanisms driving assemblage structure. Establishing causal links between species traits and ecosystem functions is challenging, especially when multifunctionality is considered (Bellwood et al., 2018), and it is impossible to empirically examine links to specific functions for all traits held by all species. However, every link established is an invaluable step forward to improving our understanding of ecosystem dynamics in high-diversity ecosystems. The analysis of traits therefore offers a first step in the evaluation of broad-scale trends that may be functionally relevant (Mouillot et al., 2013; Cresson et al., 2019). The use of functional traits is especially important in the current scenario of global environmental change and regions/habitats where descriptions of functional ecology are hampered by gaps in the autecological knowledge of fish fauna (Ribeiro et al., 2019; Pombo-Ayora et al., 2020), such as the newly established habitats associated with decommissioned structures.

Understanding of the ecological role of subsea pipelines is crucial for an assessment of decommissioning options. In this study, we examined the assemblage trait diversity, functional composition and diversity of fish assemblages associated with exposed shallow-water subsea pipelines and nearby natural reef and soft sediment habitats using mini stereo-video ROVs. This will improve our understanding of the ecosystem dynamics associated with the pipeline habitat in relation to natural habitats and can provide information on the habitat value of these structures.

2. Methods

2.1. Study area and sampling technique

Study area and sampling technique are described in detail in Schramm et al. (2021). In summary, two mini ROVs fitted with a stereo-video system (stereo-video ROVs) were used to survey fish associated with a network of subsea pipelines, natural reefs, and soft sediment habitats located near Thevenard Island, Western Australia (Figs. 1 and 2). The network of pipelines was approximately 20–32 years of age with a diameter range of 89–720 mm, having a combined length of 132 km. Depth of pipelines ranged from 0 to 20 m, connecting nine platforms (three tripods and six monopods) to onshore facilities. The sampled depths of the pipeline ranged from 10.6 to 20 m. Other structures associated with the pipeline, such as concrete mattresses and tie downs were also examined as part of the pipelines in this study. Marine growth had not been cleaned from the pipelines since installation.

For the pipelines, on average per transect: 5% (2.33 ± 0.72 m, average ± SE) was free span above the seafloor, 55% (27.62 ± 2.10 m, average ± SE) was more than half-exposed, 33% (16.40 ± 2.02 m, average ± SE) was more than half-buried, and 7% (3.66 ± 0.93 m, average ± SE) was completely buried. Pipeline surveys were completed between 08:30 and 17:00 h to minimise the effects of diel changes in fish behaviour on data collected (Myers et al., 2016; Bond et al., 2018b). GIS maps combined with recent hydrographic survey data were used to identify the position of exposed segments of pipeline around Thevenard Island. Live feed from the ROV camera and attached multibeam sonar were then used to locate pipelines in situ. The ROV operated approximately 1.4 ± 0.05 m from the pipeline on one side only, with the system

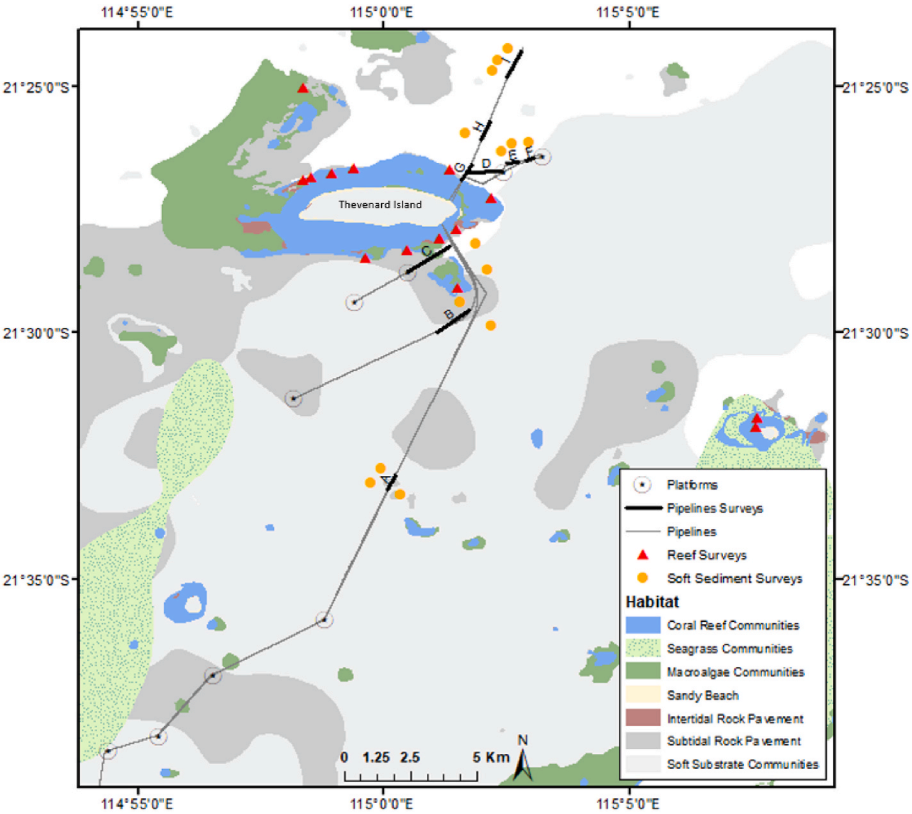


Fig. 1. Location of exposed subsea pipelines surveyed and surrounding reef and soft sediment sites, including habitat characterisation, in the vicinity of Thevenard Island, Western Australia. Pipeline surveys are labelled A to I according roughly from distance to the mainland.

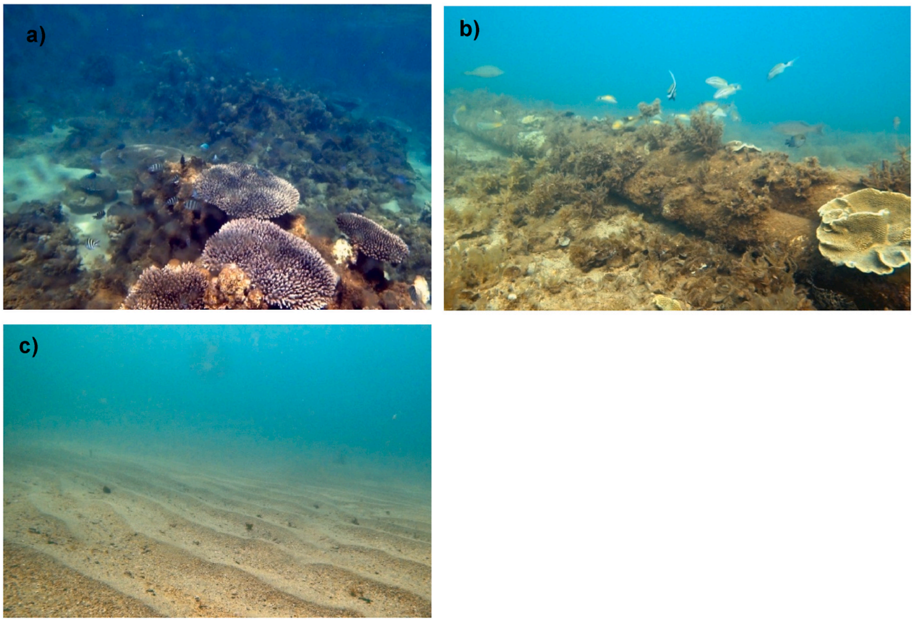


Fig. 2. Representative captured images of the three habitats: **a)** reef, **b)** pipeline, and **c)** soft sediment.

angled approximately 25° (23.05 ± 0.77°) towards the pipeline to enable a field of view of any undercut sections between the pipe and the seafloor. The system was operated at an average fight speed of approximately 0.54 ± 0.04 m/s. Each pipeline transect surveyed encompassed an area 5 m wide × 50 m long (250 m^2).

Natural reefs (hard substrate with coral cover and/or macro algae) and soft sediment (bare sand) habitats in the surrounding area, in water depths of 3.7–18.5 m, were surveyed simultaneously with the pipeline network to provide ecological context to the data obtained from the pipelines. Surveys in natural habitats were undertaken >500 m away from the pipeline or any artificial structure, such as platforms. The ROV was operated from an anchored vessel and was continuously flown for approximately 25 min in an expanding square design around the vessel (Goswami et al., 2017; Shaw et al., 2018). Fishing pressure in the area was minimal. The imagery was split into 5 × 50 m transects (250 m^2) with a 20 m separation between transects as per the pipelines. Surveys in natural habitats were similarly undertaken between 08:30 and 17:00 h.

The total area of each habitat type (pipeline, natural reef, and soft sediment) analysed was standardised to 10,000 m^2 to ensure that functional group analysis was not a result of different sampling areas, which would be affected by patchy fish distribution. Surveys of pipeline were done over different sections (see Fig. 1), and pipeline surveys E and F were combined for random transect selection due to an insufficient area per survey, hereby referred to as E/F. Imagery was analysed from eight pipeline surveys: A, B, C, D, E/F, G, H and I, thirteen sites in reef habitat, and fourteen sites in soft sediment habitat. The species identified at each habitat is shown in Table S1.

Stereo-video systems were calibrated before and after fieldwork using the software package ‘CAL’ (SeaGIS CAL) following well established protocols and guidelines (Shortis et al., 2009; Boutros et al., 2015). All fish counts and identifications were made in EventMeasure Stereo Version 5.25 (https://www.seagis.com.au/event.html). To maintain a defined unit area of sampling across image analyses a horizontal and vertical constrained field of view was set to 2.5 m in either direction of the centre point ($x = 5$ m, $y = 5$ m), with a depth (z) range to 7 m. All individuals were counted within this defined sampling area, and those that were observed outside this area were not included in the data set.

2.2. Trait selection and classification

A subset of nine traits across four functions of interest were selected to act as proxies for functions, encompassing multiple processes potentially shaping the communities at each habitat. Traits were selected based on their ecological relevance and data availability, as the most valuable traits are those that are available for most species (Costello et al., 2015). Functions of interest were selected to represent how fish species utilise their environment (Table 1) (Ladds et al., 2018), and included traits of:

1) Diet

Diet determines a species position in the food web and species-species interactions at the selected habitats. Resource partitioning within communities can be assessed by the classification of species into feeding guilds (Table 1) according to the type of prey consumed, providing information on the trophic niche occupied by species in assemblages’ organisation (Albouy et al., 2011; da Silva et al., 2019; Cresson et al., 2019).

2) Morphology

Morphology traits describe how species move around their environment, which may indicate aspects of behaviour, habitat use and the range of food sources. Morphology has been used largely as a proxy of functional traits in many taxa and recent studies have reported a strong association between morphological and ecological traits, and significant relationships between diversity indices computed on morphological and ecological traits (Côte et al., 2022). When feeding guilds are used to assess resource partitioning, it has been reported that diet data should be complemented with morphological traits (Albouy et al., 2011; Reecht et al., 2013; Ladds et al., 2018). This is because species in the same guild will inevitably differ in some subtle aspects of resource use (da Silva et al., 2019). Feeding habits, diet composition, and food consumption in fishes have been related to various morphological characteristics, notably the mouth shape (Karpouzi and Stergiou, 2003; da Silva et al., 2019; Carrington et al., 2021), body length (Gravel et al., 2016; Hadj-Hammou et al., 2021), body form (da Silva et al., 2019; Delariva and Neves, 2020) and caudal fin shape (Carrington et al., 2021) (Table 1). Morphology traits are expected to indicate the types of consumed prey and/or feeding strategies adopted by species (Albouy et al., 2011; Dolbeth et al., 2016), providing information on ecological specialisation of species to the use of core resources (Adite and Winemiller, 1997; Ramírez-Ortiz et al., 2017).

Table 1

Diet, habitat, morphology and life history traits included in the analysis.

Trait	Function of interest	Categories	References
Feeding guild	Diet	Herbivore; Planktivore; Omnivore; Corallivore; Invertivore; Generalist Carnivore; Piscivore	Schramm et al. (2021); Froese and Pauly (2022)
Maximum depth	Habitat	Shallow (0–20.1 m); Medium (20.2–54.6 m); Deep (54.7–148.4 m); Very deep (148.5–403.4 m);	Ladds et al. (2018); Froese and Pauly (2022)
Maximum body length	Morphology	Small (0–20.1 cm), Medium (20.2–54.6 cm); Large (54.7–148.4 cm); Very large (148.5+ cm)	Ladds et al. (2018); Froese and Pauly (2022)
Mouth shape	Morphology	Upper/Lower/ Terminal/Retractable/ Tubular/Funnel	Marenkov (2018)
Body form	Morphology	Anguilliform; Compressed-deep; Compressed-elongate; Compressed-laterally; Elongate-deep; Fusiform; Globiform; Ovate; Stout	Bergbauer and Kirschner (2014); Allen et al. (2015); Froese and Pauly (2022)
Caudal fin shape	Morphology	Emarginate/Forked/ Lunate/Pointed/ Rounded/Truncate	Bergbauer and Kirschner (2014); Allen et al. (2015); Froese and Pauly (2022)
Egg dispersal	Life history	Demersal/Pelagic	Jan (2000); Gravel et al. (2016); Froese and Pauly (2022)
Resilience	Life history	High (<15 months), Medium (1.4–4.4 years), Low (4.5–14 years), Very low (>14 years)	Froese and Pauly (2022)
Forage period	Life history	Diurnal/Nocturnal	Nagelkerken et al., (2000); Durville et al., (2003); Bergbauer and Kirschner (2014); Allen et al. (2015); Froese and Pauly (2022); Collins et al. (2022)

3) Habitat

Habitat traits define how a species use their environment. For example, the presence of reef-associated species (shallow depth; Table 1) at the structure may be indicative of an environment with the physical and environmental resources to accommodate reef fish. Understanding the vertical space that a species occupy can also inform us of potential intraspecific competition at the structure (Munday et al., 2001).

4) Life history

Life history traits primarily reflect species reproductive strategies and longevity which may be indicative of abundance and resilience in the environment. Oil and gas structures have been reported to attract fish for breeding purposes (Madgett et al., 2022). For example, demersal egg laying species can spawn within filamentous algal habitat which is abundant on many structures (Saunders et al., 2013; Schutter et al., 2019) or onto hard substrate such as pebbles, shells, and artificial materials (Navarrete-Fernández et al., 2014). Egg dispersal therefore provides information on how species may be interacting with the ecosystem associated with the structure for key life stages (Table 1). Resilience is calculated using a number of parameters (e.g., growth coefficients, exploitation rate, length class, natural mortality (Froese and Pauly, 2022; Table 1) and reflects how a species/population can tolerate impacts without irreversible change in its outputs or structure (Mohamed et al., 2021). This may be important for predicting future assemblage structure and functional stability. Forage period was selected as a life history trait as diel patterns in movement behaviour have been shown to differ between fish species present on oil and gas structures and natural reefs (McLean et al., 2022b).

Nine traits (feeding guild, maximum depth, maximum body length, mouth shape, body form, caudal fin shape, egg dispersal, resilience and forage period) across four functions of interest (diet, habitat, morphology and life history) (Table 1) were assigned to each species. The majority of trait information was obtained from Fishbase (Froese and Pauly, 2022), including feeding guild, maximum length, maximum depth, forage period and resilience. Maximum depth and maximum body length categories are described in Ladds et al. (2018). Mouth shape, body form and caudal fin shape were obtained visually using the stereo video footage (Figure S1(a-d)), images on Fishbase and guides (Bergbauer and Kirschner, 2014; Allen et al., 2015). Mouth shape categories were derived from Marenkov (2018). Additional literature was selected to add the egg dispersal and forage period information for species when this trait information was missing from Fishbase (Table 1). A higher taxonomic level was used in this case, but unlike the other traits, egg dispersal and forage period are mainly consistent across a family, e.g., Pomacentridae species are diurnal foragers and demersal spawners. A table containing the trait profiles for each species is available in the supplementary information (Table S2). Figure S1(a-d) demonstrates stereo-video snapshot examples of the fish morphology assessment.

2.3. Statistical analysis

2.3.1. Assemblage trait distributions

Statistical analyses for the trait composition percentage (%) of each habitat (Habitat: three levels; pipeline, reef, soft sediment) were undertaken in PRIMER 7 with PERMANOVA + add on (Anderson et al., 2008) and visualised using pie charts. The pie chart segment size indicates the percentage of individuals at each habitat possessing a particular trait.

The initial matrix had species as variables and transects as samples. Species traits were included as indicators and habitat as factors. The matrix for calculating assemblage trait distributions was formed by summing the factor and indicator levels, with traits as the variables and habitat as the samples. A one-way PERMANOVA was used to determine if trait distributions across habitats significantly differed from one another (Habitat: three levels; pipeline, reef, soft sediment). When a statistical difference was found ($P < 0.05$, using 9999 permutations), a post-hoc pairwise comparison was done. P values from pairwise tests are indicated using $P_{(pairwise)}$. Dominant traits contributing to the dissimilarity (>50%) of each habitat pairwise comparison were identified using SIMPER analyses.

2.3.2. Functional composition and diversity

Statistical analyses for the multivariate assemblage were undertaken in PRIMER 7 with PERMANOVA + add on (Anderson et al., 2008). The multivariate assemblage matrix was formed by summing the indicator levels, resulting in traits as the variables and transects as the samples. Data treatment of assemblage trait data included applying a fourth root transformation to down weight the influence of more common traits over those rarely recorded across the data set. A Bray Curtis similarity matrix was used for analysis of compositional dissimilarity. Principal coordinates analysis (PCO) was used to visually represent differences in the abundance of trait assemblages among habitats.

Functional groups (clusters by habitat) were derived using methods described and recommended in Ladds et al. (2018) using the R package "nomclust", where multiple linkage methods and distance matrices were tested on the clustering of nominal fish traits. Having nominal data prevents the usage of some measures, such as Euclidean distances, as they assume an inherent ordering within variables. A Goodall distance matrix with the average linkage method was selected to measure the pairwise similarities between species based on their trait values. A similarity value was assigned based on the normalised similarity between the two observations, where the similarity value was higher if a category occurs infrequently. This method takes into account that individuals attributes occur stochastically and independently in a population (Ladds et al., 2018).

The optimal number of clusters ("functional groups") was evaluated by the Pseudo F coefficient based on the entropy (PSFE), a measure of entropy of the between- and within-cluster variability (Equation (1)).

$$PSFE(k) = \frac{(n-k)[nWCE(1) - nWCE(k)]}{(k-1)nWCE(k)} \tag{1}$$

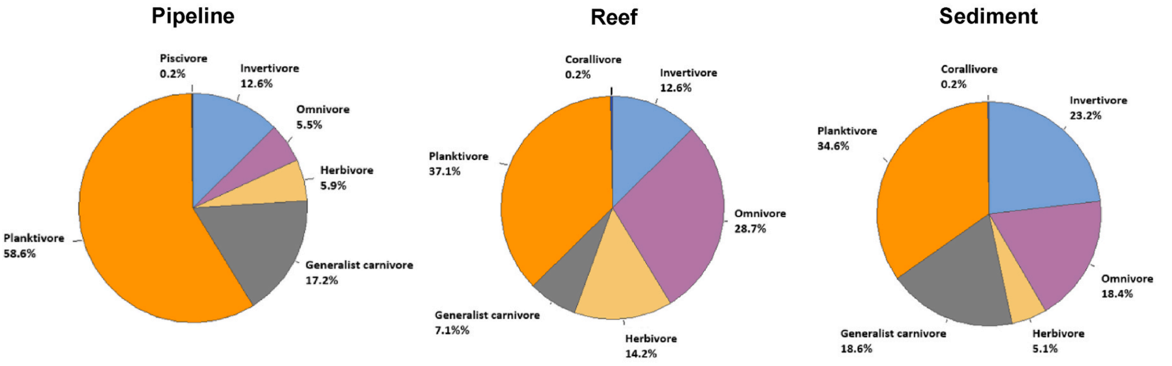
Equation (1): Pseudo F coefficient based on the entropy (PSFE): n = number of observations, k = number of clusters, nWCE(1) = variability in the whole dataset, nWCE(k) = within-cluster variability in the k-cluster solution (Šulc, 2016; Ladds et al., 2018).

To visually represent the functional diversity at each habitat, the non-linear dimensionality technique t-Distributed Stochastic Neighbour Embedding (t-SNE) with a partition around medoids (PAM) clustering algorithm was used to construct a two-dimensional scatter plot in which each point represents a species (Van Der Maaten, 2014; Ladds et al., 2018). Nonlinear dimensionality reduction was selected to discard any correlated information and recover only the varying information (rotation and scale). Non-linear dimensionality reduction methods were able to describe more variance in data compared to linear methods with the same number of dimensions, and t-SNE is a widely used nonlinear dimensionality reduction technique primarily used for data exploration and visualising high-dimensional data (Spiwok and Kříž, 2020; Simões and Pierce, 2021).

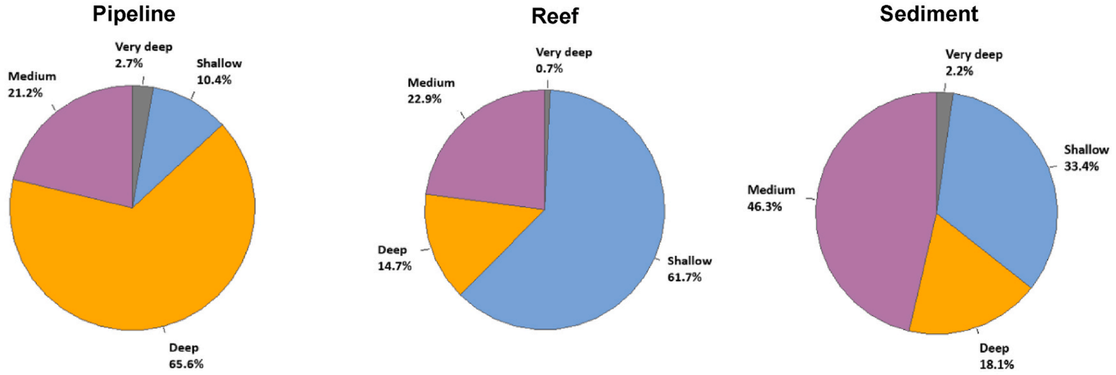
Species with similar trait profiles were clustered together in the same defined "functional group". A 95% confidence ellipse was applied to visually represent the functional groups. The 95% confidence ellipse was defined by the variance of the underlying population relating to the confidence interval. The medoid of each cluster was determined using the partition around medoids (PAM) algorithm. The medoid was the centrally located point in the cluster, defined as the species in the cluster whose average dissimilarity to all the species in the cluster was minimal (Lawrence and Fernandes, 2022). The medoid species was used as a group representative trait profile.

Three functional diversity indices were considered in this study: Gini-Simpson, Rao's Quadratic entropy, and Functional Redundancy. The Gini-Simpson index was used to quantify the community diversity of a habitat, accounting for the number of species and their relative abundance (Happel, 2022). Rao's quadratic entropy was based on the proportion of the abundance of species present in a community and some measure of dissimilarity among them (Karadimou et al., 2016). Functional redundancy was calculated as the difference between Rao's quadratic entropy and species diversity based on the functional dissimilarity (Floyd et al., 2022). The index values were between 0 and 1 as they incorporate proportional abundances and are only meaningful when conducting a within-index comparison. The three diversity indices were calculated using the "SYNCSA" package on R version 1.3.4 (Debastiani and Pillar, 2012). This package has been used in previous studies to calculate the functional diversity and redundancy of fish communities (McLean et al., 2019; Payan-Alcacio et al., 2021; Brumm et al., 2021). Data normality was tested using an Anderson-Darling test and a one-way non-parametric ANOVA (Kruskal-Wallis test) was carried out to establish significant differences of functional indices between

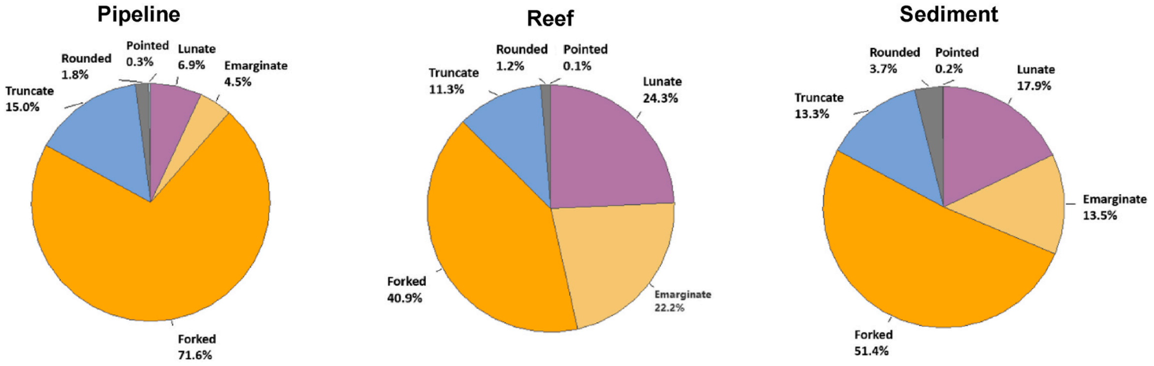
a) Feeding guild



b) Maximum depth



c) Caudal fin shape



d) Egg dispersal

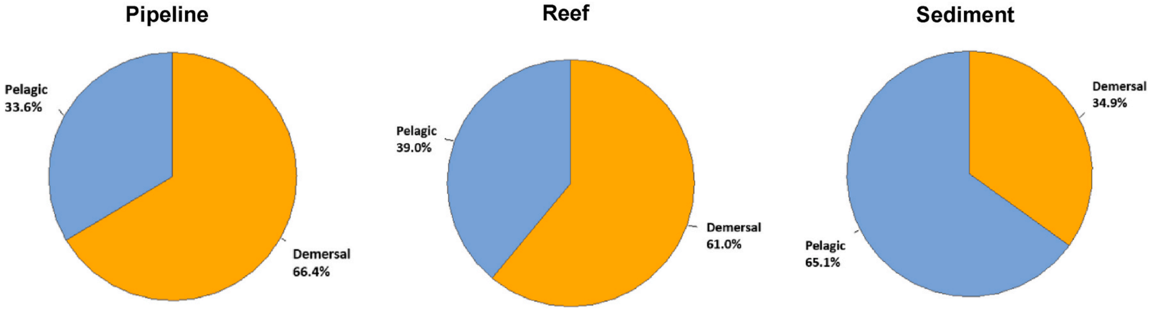


Fig. 3. Pie chart of the trait (%) within each habitat displaying a) feeding guild (Schramm et al. (2021); b) maximum depth; c) caudal fin shape; and d) egg dispersal.

habitats. Results were presented for each diversity index using an individual value plot, demonstrating the median for descriptive purposes.

3. Results

3.1. Assemblage trait distributions

Trait distributions among habitats are presented using a pie chart (Fig. 3a–d). The charts of four traits (one per function of interest) are included in the text (feeding guild, maximum depth, caudal fin shape, and egg dispersal). The other five traits are presented in the supplementary information (Figures S1a-e). There were observable differences in assemblage trait distribution across the three habitats (Fig. 3a–d, Figures S1a-e), with all traits being significantly different among habitats (PERMANOVA: $P < 0.001$). These have been discussed further below.

Feeding guild comprised of invertivores, omnivores, herbivores, generalist carnivores, planktivores, corallivores, and piscivores (Fig. 3a). Each habitat supported significantly different feeding guilds (PERMANOVA: $P < 0.001$). Feeding guild was also significantly different for each habitat pairwise comparison ($P_{(pairwise)} = <0.001$). The reef habitat had a higher percentage of omnivores, herbivores and corallivores than the other two habitats, accounting for 28.7%, 14.2% and 0.2% of the total trait percentage distribution, respectively (Fig. 3a). The pipeline habitat had a higher percentage of planktivores, generalist carnivores and piscivores than the other two habitats, accounting for 58.6%, 17.2% and 0.2% of the total trait percentage distribution (Fig. 3a). Soft sediment had a higher percentage of invertivores than the reef and pipeline habitats, accounting for 23.2% of the total trait percentage distribution (Fig. 3a). Trait distribution was reflected in the habitat group dissimilarities, where planktivores contributed to the between-group dissimilarity for all three habitats pairwise comparisons (Table 2). Omnivores contributed to the between-group dissimilarity for pipeline and reef and reef and soft sediment pairwise comparisons and herbivores contributed to the between-group dissimilarity for the pipeline and reef pairwise comparison (Table 2).

Maximum depth (m) comprised of “Shallow” (0–20.1 m), “Medium” (20.2–54.6 m), “Deep” (54.7–148.4 m) and “Very deep” (148.5+ m) (Fig. 3b, Table 1). Each habitat supported significantly different maximum depths (PERMANOVA: $P < 0.001$). Maximum depth was also significantly different for each habitat pairwise comparison ($P_{(pairwise)} = <0.001$). The pipeline habitat had a higher percentage of individuals with a “Deep” depth, accounting for 65.6% of the total trait percentage distribution (Fig. 3b). Soft sediment had a higher percentage of “Medium” depth species, accounting for 46.3% of the total trait percentage distribution (Fig. 3b). The reef habitat had a higher percentage of “Shallow” depth species, accounting for 61.7% of the total trait percentage distribution (Fig. 3b). “Shallow” depth contributed to the between-group dissimilarity for all three habitats pairwise comparisons (Table 2). “Deep” depth contributed to the between-group dissimilarity for the pipeline and reef and pipeline and soft sediment habitats (Table 2).

Maximum length comprised of “Small” (0–20.1 cm), “Medium” (20.2–54.6 cm), “Large” (54.7–148.4 cm), and “Very large” (148.5+ cm) (Figure S2a, Table 1). Each habitat supported significantly different maximum lengths (PERMANOVA: $P < 0.001$). Maximum length was also significantly different for each habitat pairwise comparison ($P_{(pairwise)} = <0.04$). Pipeline and reef habitats had a higher percentage of “Small” individuals than the soft sediment habitat, contributing to 66.6% and 63.9% of the total trait percentage distribution, respectively (Figure S2a). Soft sediment had a higher percentage of “Medium” individuals than the other habitats, accounting for 51.1% of the total trait percentage distribution (Figure S2a). “Small” maximum length contributed to the between-group dissimilarity for all three habitats pairwise comparisons (Table 2).

Mouth shape comprised of upper, lower, terminal, retractable, tubular and funnel (Figure S2b, Table 1). Each habitat supported significantly different mouth shapes (PERMANOVA: $P < 0.001$). Mouth shape was also significantly different for each habitat pairwise comparison ($P(\text{pairwise}) = <0.02$). Upper was the dominant mouth shape at the three habitats, accounting for 73.2% of the total trait percentage distribution at the pipeline, 66.9% at the reef and 62.7% at the soft sediment (Figure S2b). Upper mouth shape contributed to the between-group dissimilarity for all three habitats pairwise comparisons (Table 2).

Body form comprised of anguilliform, compressed-deep, compressed-elongate, compressed-laterally, elongate-deep, fusiform, globiform, ovate and stout (Figure S2c, Table 1). Each habitat supported significantly different body forms (PERMANOVA: $P < 0.001$). Body form was similar between pipeline and reef habitats ($P_{(pairwise)} = 0.306$), with both habitats having individuals with significantly different body forms than soft sediment habitat ($P_{(pairwise)} < 0.001$). Ovate was the dominant

Table 2
SIMPER pairwise comparison (average dissimilarity (%), contributing traits and percentage contribution) within the pipeline, natural reef, and soft sediment habitat assemblages.

SIMPER			
Pairwise comparison	Average dissimilarity (%)	Traits >50%	% Contribution
Pipeline, Reef	37.21	Omnivore	4.52
		Planktivore	4.52
		Emarginate caudal fin shape	4.40
		Shallow (0–20.1 m max. depth)	4.40
		Demersal egg dispersal	4.22
		Ovate body form	4.19
		Small maximum length	4.03
		Upper mouth shape	3.83
		Deep (54.7–148.4 m max. depth)	3.63
		High resilience	3.41
		Lunate caudal fin shape	3.39
		Forked caudal fin shape	3.38
		Herbivore	3.35
Pipeline, Soft sediment	49.63	Upper mouth shape	5.45
		Ovate body form	5.23
		Small maximum length	4.86
		Demersal egg dispersal	4.75
		Planktivore	4.62
		Deep (54.7–148.4 m max. depth)	4.56
		High resilience	3.97
		Medium resilience	3.97
		Forked caudal fin	3.88
		Shallow (0–20.1 m max. depth)	3.47
		Diurnal	3.41
		Truncate caudal fin shape	3.40
Reef, Soft sediment	51.89	Ovate body form	5.62
		Shallow (0–20.1 m max. depth)	5.61
		Upper mouth shape	5.22
		Omnivore	4.90
		Small maximum length	4.83
		Demersal egg dispersal	4.74
		Emarginate caudal fin shape	4.64
		Medium resilience	3.87
		Lunate caudal fin shape	3.68
		High resilience	3.51
		Diurnal	3.35
		Planktivore	3.24

body form at the three habitats, accounting for 66.8% of the total trait percentage distribution at the pipeline, 67.6% at the reef and 33.7% at the soft sediment (Figure S2c). Soft sediment had a higher percentage of individuals with a fusiform body form (22.3%) than the reef (5.1%) and pipeline (3.3%) habitats (Figure S2c). An ovate body form contributed to the between-group dissimilarity for all three pairwise comparisons (Table 2).

Caudal fin shape comprised of six groups: emarginate, forked, lunate, pointed, rounded and truncate (Fig. 3c, Table 1). Each habitat supported significantly different caudal fin shapes (PERMANOVA: $P < 0.001$). Caudal fin shape was also significantly different for each habitat pairwise comparison ($P_{(pairwise)} = <0.001$). Caudal fin shape was dominated by a forked shape, accounting for 71.6% of the total trait percentage distribution at the pipeline habitat, 51.4% at the soft sediment and 40.9% at the reef (Fig. 3c). Reef habitat had a higher percentage of individuals with a lunate (24.3%) and emarginate (22.2%) caudal fin shape than the pipeline and soft sediment habitats (Fig. 3c). Pipeline habitat had a higher percentage of fishes with a truncate caudal fin shape (15.0%) than the soft sediment (13.3%) and reef (11.3%) (Fig. 3c). An emarginate and lunate caudal fin shape contributed to the between-group dissimilarity for the reef and pipeline and reef and soft sediment habitats (Table 2).

Egg dispersal comprised of pelagic and demersal (Fig. 3d, Table 1). Each habitat supported species with a significantly different egg dispersal (PERMANOVA: $P < 0.001$). Egg dispersal was similar between pipeline and reef habitats ($P_{(pairwise)} = 0.271$); with both habitats having individuals with a significantly different egg dispersal than the soft sediment habitat ($P_{(pairwise)} < 0.001$). Pipeline and reef habitats had a higher percentage of demersal laying species than the soft sediment habitat, contributing to 66.4% and 61.0% of the total trait percentage distribution, respectively (Fig. 3d). Demersal egg dispersal contributed to the between-group dissimilarity for all three habitats pairwise comparisons (Table 2).

Resilience comprised of "Very low" (>14 years), "Low" (4.5–14 years), "Medium" (1.4–4.4 years), and "High" (<15 months) (Figure S2d, Table 1). Each habitat supported significantly different resilience values (PERMANOVA: $P < 0.001$). Resilience was similar between pipeline and reef habitats (P(pairwise) = 0.103; with both habitats having a significantly different resilience value than soft sediment habitat ($P_{(pairwise)} < 0.001$). "High" resilience dominated the total trait percentage distribution at the three habitats, accounting for 74.9% at the pipeline, 74.3% at the soft sediment, and 66.8% at the reef (Figure S2d). Soft sediment habitat had a higher percentage of individuals with a "Low" resilience compared to the reef and pipeline habitats (Figure S2d). "High" resilience contributed to the between-group dissimilarity for all three habitats pairwise comparisons (Table 2).

Forage period comprised of two groups: diurnal and nocturnal (Figure S2e, Table 1). Each habitat supported species with significantly different forage period (PERMANOVA: $P < 0.001$). Forage period was similar between pipeline and reef habitats ($P_{(pairwise)} = 0.121$); with both habitats having individuals with a significantly different forage period than soft sediment habitat ($P(_{pairwise}) < 0.001$). A diurnal forage period dominated the total trait percentage distribution at the three habitats, accounting for 95.5% at the reef, 93.4% at the soft sediment and 91.6% at the pipeline (Figure S2e). Forage period did not contribute to the between-group dissimilarity (Table 2).

3.2. Functional diversity

3.2.1. Multivariate assemblage

Trait composition differed among habitats (PERMANOVA: $P < 0.001$) with each habitat being distinct from one another ($P_{(pairwise)<}0.001$). The pipeline and reef habitats were however more overlapped in trait space and had a tighter clustering compared to the soft sediment (Fig. 4). This suggests that on a functional level, the pipeline and reef habitats were more similar, and may indicate that they share more specific physical (e.g., structural complexity) and environmental conditions (e.g., hydrodynamics, resulting food resources).

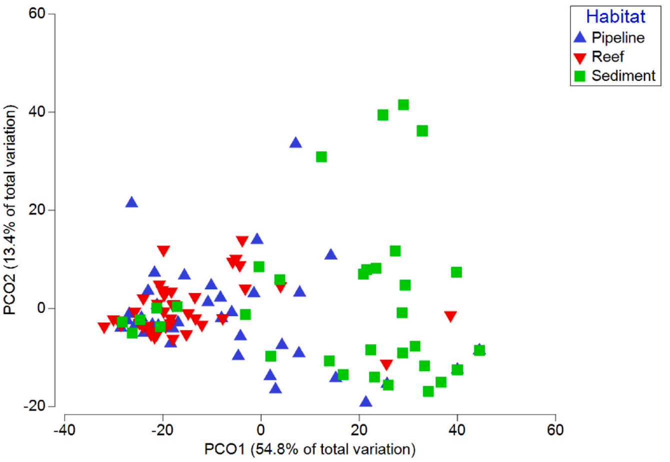


Fig. 4. PCO ordination of the assemblage trait matrix between three habitats. Traits contributing to the average dissimilarity (%) between habitats are shown in Table 2.

3.2.2. Clusters by habitat

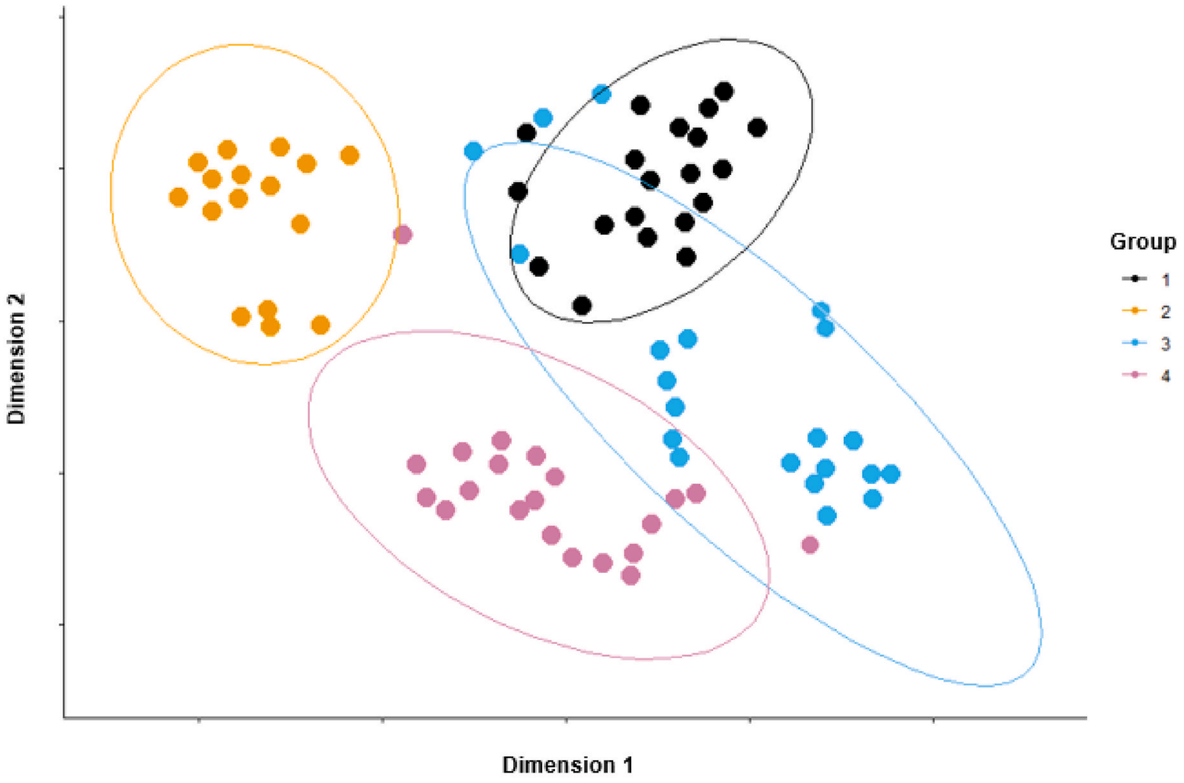
To represent fish functional groups within each of the three habitats (pipeline, reef, soft sediment), cluster analyses were performed on functional groups. The optimal number of clusters (functional groups) was evaluated by Pseudo F coefficient based on the entropy (PSFE) and visually represented using t-SNE with 95% confidence ellipse. The species composition of each group is listed below the t-SNE plot in their corresponding group colours, with the medoid species of each group highlighted in the list.

Within the pipeline habitat, four functional groups were represented (Fig. 5), most with a separation of species within the groups. Group 1 (black) was composed of twenty species (Fig. 5) across four families (Labridae, Scaridae, Balistidae and Pomacanthidae). Fifteen species belonged to the family Labridae. The medoid species was *Choerodon vitta* (redstripe tuskfish) (Fig. 5), with the trait profile of: "Medium" depth, diurnal foraging invertivore, with a "Small" body length, terminal mouth shape, elongate-deep body form with a truncate caudal fin shape, pelagic egg dispersal and a "Medium" resilience.

Group 2 (orange) was composed of sixteen species (Fig. 5) across five families (Pomacentridae, Tetradontidae, Glaucosomatidae, Ostraciidae and Labridae). Ten species belonged to the family Pomacentridae. The medoid species was *Pomacentrus milleri* (Miller's damselfish) (Fig. 5), with the trait profile: "Shallow" depth, diurnal foraging omnivore, with a "Small" body length, upper mouth shape, ovate body form with an emarginate caudal fin shape, demersal egg dispersal and a "High" resilience.

Group 3 (light blue) was composed of twenty-one species (Fig. 5) across nine families (Serranidae, Lutjanidae, Carangidae, Pomacanthidae, Acanthuridae, Chaetodontidae, Haemulidae, Plotosidae and Holocentridae). The medoid species was *Epinephelus multinotatus* (white-blotched grouper) (Fig. 5), with the trait profile of: "Deep" depth, nocturnal foraging generalist carnivore, with a "Medium" body length, upper mouth shape, stout body form with a truncate caudal fin shape, pelagic egg dispersal and a "Medium" resilience.

Group 4 (purple) was composed of twenty-one species (Fig. 5) across nine families (Lethrinidae, Mullidae, Carangidae, Nemipteridae, Cirrhitidae, Pempheridae, Pomacanthidae, Caesionidae and Siganidae). The medoid species was *Pentapodus porosus* (Northwest Australian whiptail) (Fig. 5), with the trait profile: "Medium" depth, diurnal foraging generalist carnivore, with a "Medium" body length, terminal mouth shape, elongate-deep body form with a forked caudal fin shape, pelagic egg dispersal and a "High" resilience.



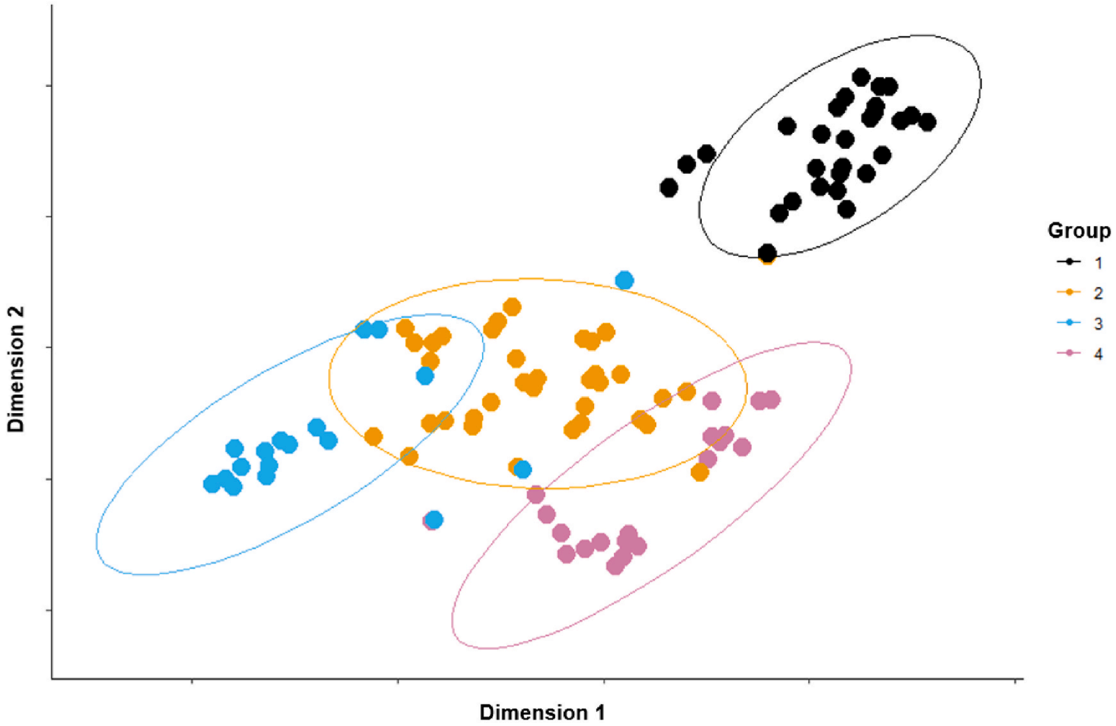
Group 1	Group 2	Group 3	Group 4
Abalistes stellatus	*Abudefduf bengalensis*	*Acanthurus grammoptilus*	*Atule mate*
Anampses lennardi	*Amphiprion clarkii*	*Carangoides fulvoguttatus*	*Cirrhitichthys aprinus*
Chaetodontoplus duboulayi	*Arothron hispidus*	*Cephalopholis boenak*	*Gnathanodon speciosus*
Cheilio inermis	*Arothron mappa*	*Chaetodon auriga*	*Lethrinus atkinsoni*
Chelmon marginalis	*Canthigaster valentini*	*Diagramma pictum*	*Lethrinus laticaudis*
Choerodon cauteroma	*Chromis fumea*	*Diploprion bifasciatum*	*Lethrinus lentjan*
Choerodon cephalotes	*Dascyllus trimaculatus*	*Epinephelus bilobatus*	*Lethrinus nebulosus*
Choerodon cyanodus	*Glaucosoma magnificum*	*Epinephelus fasciatus*	*Lethrinus punctulatus*
Choerodon schoenleinii	*Neopomacentrus aktites*	*Epinephelus merra*	*Mulloidichthys vanicolensis*
Choerodon vitta	*Ostracion cubicus*	*Epinephelus multinotatus*	*Parupeneus barberinoides*
Coris caudimacula	*Pomacentrus coelestis*	*Epinephelus quoyanus*	*Parupeneus indicus*
Halichoeres margaritaceus	*Pomacentrus limosus*	*Lutjanus carponotatus*	*Parupeneus spilurus*
Halichoeres melanochir	*Pomacentrus milleri*	*Lutjanus quinquelineatus*	*Pempheris oualensis*
Labroides dimidiatus	*Pomacentrus nagasakiensis*	*Lutjanus sebae*	*Pentapodus porosus*
Leptojulis cyanopleura	*Pomacentrus vaiuli*	*Lutjanus vitta*	*Pentapodus vitta*
Scarus ghobban	*Thalassoma amblycephalum*	*Paraplotosus butleri*	*Pomacanthus semicirculatus*
Scarus schlegeli		*Pomacanthus imperator*	*Pterocaesio chrysozona*
Stethojulis bandanensis		*Pomacanthus sexstriatus*	*Scolopsis monogramma*
Stethojulis interrupta		*Sargocentron rubrum*	*Selaroides leptolepis*
Thalassoma lunare		*Scomberoides lysan*	*Siganus fuscescens*
		Symphorus nematophorus	*Upeneus tragula*

Fig. 5. Pipeline habitat: Visual representation of the relationships among four functional diversity trait groups displayed in two dimensions as the result of t-SNE. Group species composition are listed below the t-SNE plot in their corresponding group colour. Medoid species are highlighted within the list.

Within the reef habitat, four groups were identified (Fig. 6). Group 1 (black) was composed of twenty-nine species (Fig. 6). The majority of species (nineteen) were part of the Pomacentridae family. The medoid species was *Pomacentrus limosus* (muddy damsel) (Fig. 6), with the trait profile: "Shallow" depth, diurnal foraging omnivore, with a "Small" maximum body length, upper mouth shape, ovate body form with a forked caudal fin shape, demersal egg dispersal and a "High" resilience. Other group species belonged to the families Siganidae, Caesionidae, Tetradontidae, Latridae, Mullidae, Pempheridae and Gobiidae.

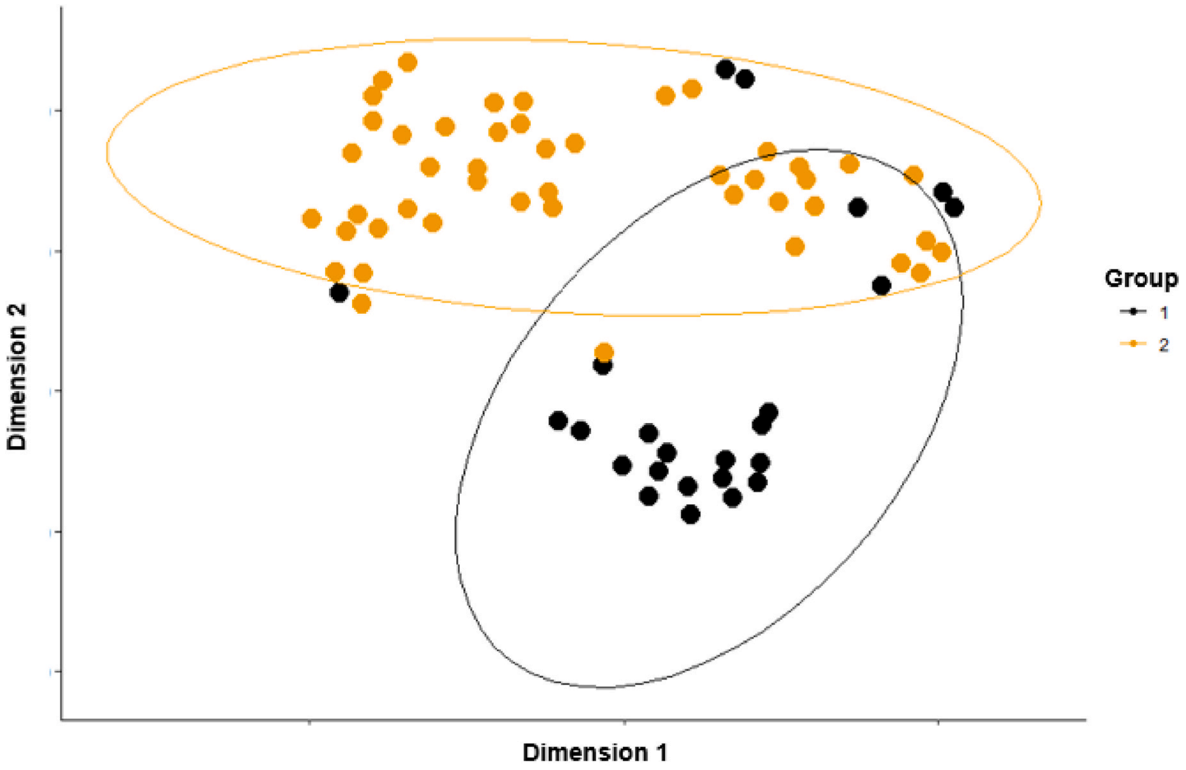
Group 2 (orange) was composed of thirty-six species (Fig. 6) across eight families (Labridae, Scaridae, Acanthuridae, Lethrinidae, Mullidae, Nemipteridae, Balistidae, and Tetradontidae). Seventeen species belonged to the Labridae family. The medoid species was *Thalassoma lutescens* (yellow-brown wrasse) (Fig. 6), with the trait profile: "Medium" depth, diurnal foraging invertivore, with a "Medium" maximum body length, terminal mouth shape, elongate-deep body form with a lunate caudal fin shape, pelagic egg dispersal and a "Medium" resilience.

Group 3 (blue) was composed of eighteen species (Fig. 6) across eight



Group 1	Group 2	Group 3	Group 4
Abudefduf bengalensis	*Acanthurus grammoptilus*	*Acanthurus triostegus*	*Anampses melanurus*
Abudefduf septemfasciatus	*Anampses caeruleopunctatus*	*Cephalopholis boenak*	*Aspidontus taeniatus*
Caesio cuning	*Anampses geographicus*	*Diagramma pictum*	*Centropyge tibicen*
Canthigaster valentini	*Anampses lennardi*	*Epinephelus bilobatus*	*Chaetodon adiergastos*
Cheilodactylus gibbosus	*Anampses meleagrides*	*Epinephelus fasciatus*	*Chaetodon aureofasciatus*
Chromis fumea	*Arothron stellatus*	*Epinephelus malabaricus*	*Chaetodon auriga*
Chromis viridis	*Cheilio inermis*	*Epinephelus rivulatus*	*Chaetodon citrinellus*
Chromis weberi	*Chlorurus microrhinos*	*Lethrinus nebulosus*	*Chaetodon lunula*
Dascyllus aruanus	*Chlorurus sordidus*	*Lutjanus carponotatus*	*Chaetodon trifascialis*
Dascyllus reticulatus	*Choerodon cauteroma*	*Lutjanus fulviflamma*	*Chelmon marginalis*
Dascyllus trimaculatus	*Choerodon cyanodus*	*Lutjanus lemniscatus*	*Halichoeres melanochir*
Neoglyphidodon melas	*Choerodon schoenleinii*	*Lutjanus monostigma*	*Halichoeres nebulosus*
Neoglyphidodon nigroris	*Coris caudimacula*	*Lutjanus quinquelineatus*	*Heniochus acuminatus*
Neopomacentrus aktites	*Ctenochaetus striatus*	*Paraplotosus butleri*	*Labroides dimidiatus*
Neopomacentrus azysron	*Epibulus insidiator*	*Pomacanthus sexstriatus*	*Leptojulis cyanopleura*
Parupeneus spilurus	*Gomphosus varius*	*Scolopsis affinis*	*Parachaetodon ocellatus*
Pempheris schwenkii	*Hemigymnus fasciatus*	*Scolopsis bilineata*	*Pomacanthus semicirculatus*
Pomacentrus amboinensis	*Hemigymnus melapterus*	*Symphorus nematophorus*	*Stethojulis bandanensis*
Pomacentrus coelestis	*Hologymnosus doliatus*		*Stethojulis strigiventer*
Pomacentrus limosus	*Lethrinus atkinsoni*		*Zebrasoma scopas*
Pomacentrus milleri	*Lethrinus laticaudis*		
Pomacentrus moluccensis	*Naso unicornis*		
Ptereleotris evides	*Parupeneus barberinoides*		
Pterocaesio chrysozona	*Parupeneus indicus*		
Siganus canaliculatus	*Pentapodus porosus*		
Siganus doliatus	*Pseudodax moluccanus*		
Siganus trispilos	*Scarus ghobban*		
Stegastes nigricans	*Scarus prasiognathos*		
Stegastes obreptus	*Scarus psittacus*		
	Scarus rivulatus		
	Scarus schlegeli		
	Scolopsis monogramma		
	Sufflamen chrysopterum		
	Thalassoma hardwicke		
	Thalassoma lunare		
	Thalassoma lutescens		

Fig. 6. Reef habitat: Visual representation of the relationships among four functional diversity trait groups displayed in two dimensions as the result of t-SNE. Group species composition are listed below the t-SNE plot in their corresponding group colour. Medoid species are highlighted within the list.



Group 1	Group 2	Group 2
Abudefduf bengalensis	Acanthurus grammoptilus	Lethrinus laticaudis
Aurigequula longispina	Anampses geographicus	Lethrinus punctulatus
Canthigaster valentini	Anampses meleagrides	Lutjanus carponotatus
Chaetodon lunula	Chaetodontoplus duboulayi	Lutjanus lemniscatus
Chromis fumea	Cheilinus chlorourus	Parachaetodon ocellatus
Hoplolatilus cuniculus	Chelmon marginalis	Parapercis nebulosa
Neoglyphidodon melas	Chlorurus sordidus	Parupeneus heptacanthus
Neopomacentrus aktites	Choerodon cauteroma	Parupeneus indicus
Neopomacentrus azysron	Choerodon cephalotes	Pentapodus porosus
Parupeneus spilurus	Choerodon cyanodus	Pentapodus vitta
Plagiotremus tapeinosoma	Choerodon schoenleinii	Plectorhinchus polytaenia
Pomacanthus semicirculatus	Choerodon vitta	Pomacanthus imperator
Pomacanthus sexstriatus	Coris aygula	Scarus ghobban
Pomacentrus coelestis	Ctenochaetus striatus	Scarus rivulatus
Pomacentrus limosus	Epinephelus bilobatus	Scarus schlegeli
Pomacentrus milleri	Epinephelus fasciatus	Scolopsis bilineata
Psammoperca datnioides	Gymnothorax thrysoideus	Scolopsis monogramma
Ptereleotris microlepis	Halichoeres melanochir	Stethojulis strigiventer
Pterocaesio chrysozona	Halichoeres nebulosus	Sufflamen chrysopterum
Siganus doliatus	Halichoeres prosopeion	Thalassoma lunare
Siganus lineatus	Hemigymnus melapterus	Thalassoma lutescens
Stegastes nigricans	Heniochus acuminatus	Upeneus tragula
Stegastes obreptus	Labroides dimidiatus	
Thalassoma amblycephalum	Lethrinus atkinsoni	

Fig. 7. Soft Sediment habitat: Visual representation of the relationships among two functional diversity trait groups displayed in two dimensions as the result of t-SNE. Group species composition are listed below the t-SNE plot in their corresponding group colour. Medoid species are highlighted within the list.

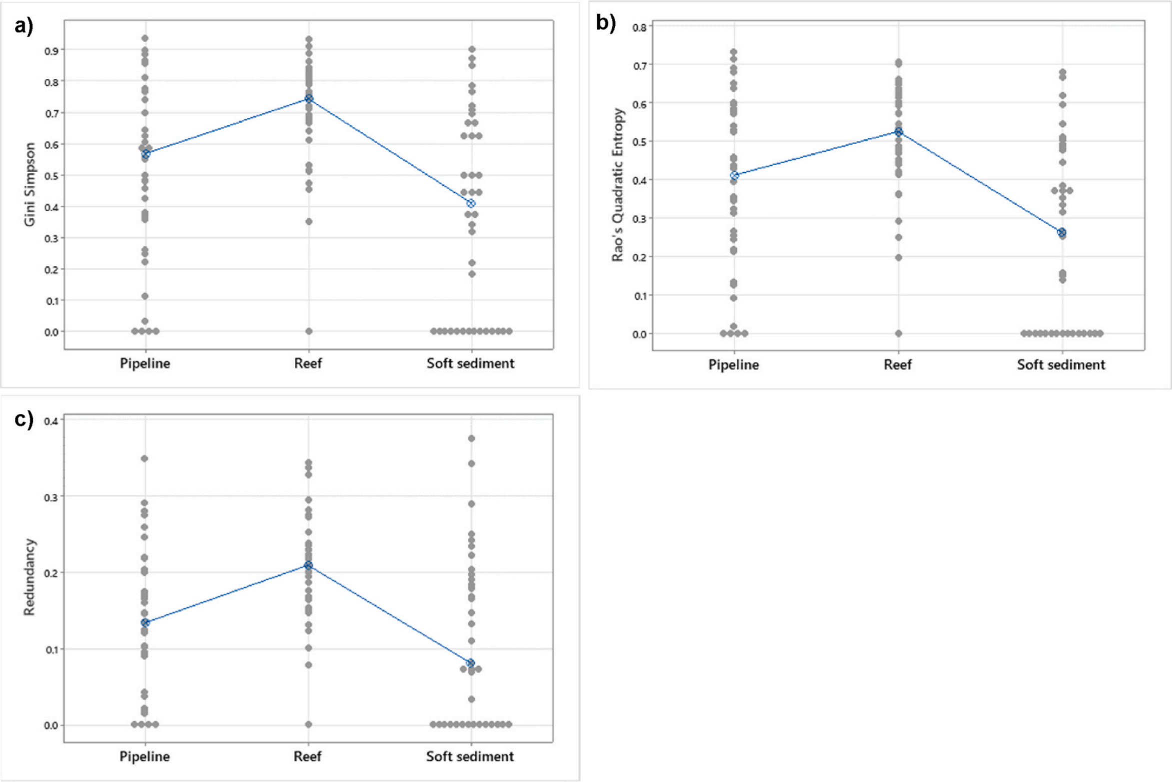


Fig. 8. a) Gini-Simpson index; b) Rao's Quadratic Entropy; and c) Functional Redundancy calculated for each habitat.

families (Lutjanidae, Serranidae, Nemipteridae, Acanthuridae, Haemulidae, Lethrinidae, Plotosidae and Pomacanthidae). The medoid species was *Lutjanus carponotatus* (Spanish flag snapper) (Fig. 6), with the trait profile: "Deep" depth, nocturnal foraging generalist carnivore, with a "Medium" body length, upper mouth shape, stout body form with a truncate caudal fin shape, pelagic egg dispersal and a "Medium" resilience.

Group 4 (purple) was composed of twenty species (Fig. 6) across four families (Chaetodontidae, Labridae, Mullidae and Blenniidae). Eight of the group species belonged to the Labridae family and eight species belonged to Chaetodontidae. The medoid species was *Chaetodon adiergastos* (Philippine butterflyfish) (Fig. 6), with the trait profile: "Medium" depth, diurnal foraging invertivore, with a "Small" body length, tubular mouth shape, laterally compressed body form with a truncate caudal fin shape, pelagic egg dispersal and a "High" resilience.

There were only two defined groups within the soft sediment habitat (Fig. 7), with a large number of species occupying each group (Fig. 7). The groups were considerably spread across both dimensions with considerable group overlap (Fig. 7). Group 1 (black) was composed of twenty-four species and Group 2 (orange) was composed of forty-six species (Fig. 7), both covering a large variety of families.

The medoid species of Group 1 was muddy damsel (Fig. 7), with the trait profile: "Shallow" depth, diurnal foraging omnivore, with a "Small" body length, upper mouth shape, ovate body shape with a forked caudal fin, demersal egg dispersal and a "High" resilience. The medoid species of Group 2 was *Anampses geographicus* (geographic wrasse) (Fig. 7), with the trait profile: "Medium" depth, diurnal foraging invertivore, with a "Medium" body length, terminal mouth shape, elongate-deep body shape with a truncate caudal fin, pelagic egg dispersal and a "Medium" resilience.

This variation and group overlap is likely due to the lack of specific physical and environmental conditions, where species identified were more likely "passing by" than fulfilling a particular ecological niche.

3.2.3. *Univariate*

Dimensionality-reduction techniques provide a qualitative picture of functional diversity, but do not give absolute insight into the distribution of traits within a specific site. A quantitative measurement was required to complement trait dissimilarity in two-dimensional space, to describe an assemblage and indicate ecosystem functionality. The analysis of functional indices (Gini-Simpson, Rao's Quadratic Entropy and Functional Redundancy) between habitats was used to measure community diversity, functional diversity and redundancy (Fig. 8).

Reef habitat had the highest proportion for all three indices (median: Gini-Simpson = 0.74; Rao = 0.52; Redundancy = 0.21) (Fig. 8). This was followed by the pipeline habitat (median: Gini-Simpson = 0.57; Rao = 0.41; Redundancy = 0.13) and soft sediment habitat (median: Gini-Simpson = 0.41; Rao = 0.26; Redundancy = 0.08) (Fig. 8). The Gini Simpson, Rao's Quadratic entropy and Functional Redundancy proportions for all three habitats were significantly distinct ($p < 0.05$).

4. Discussion

The results of this study show that the functional composition differed among habitats, with each habitat being distinct from one another. The pipeline and reef habitats were however more overlapped in multivariate space than the assemblage composition described in Schramm et al. (2021), had the least variation, and the most similar habitat pairwise trait assemblage (lowest % dissimilarity). Schramm et al. (2021) also reported a higher overlap between pipeline and soft sediment habitats than between reef and pipeline habitats for assemblage composition. Although the pipeline habitat had an assemblage composition more similar to soft sediment habitats, on a functional level, the pipeline and reef habitats were more similar and may indicate that they share more specific physical (e.g., structural complexity) and environmental conditions (e.g., hydrodynamics, resulting food resources).

Each habitat supported significantly different traits, with the pipeline habitat having a higher percentage of nocturnal foraging, generalist carnivores and piscivores with a truncate caudal fin than the reef and soft sediment habitats. Generalist feeding strategies are favoured in stressful or variable environments where flexibility in ecological traits is beneficial (Beaudoin et al., 2001). Generalist carnivores may impart stability on food webs using readily available, alternative energy pools (Laske et al., 2018). The pipeline habitat also had a higher percentage contribution of planktivores than the reef and soft sediment habitats. In contrast to generalist feeding, planktivorous species are specialist feeders having a limited diet and occupy a narrow niche and are classed as "trophic drivers" of global coral reef fish diversity patterns, connecting primary producers to the rest of the food chain (Siqueira et al., 2021). This agrees with the findings reported in Paxton et al. (2019), where planktivores, piscivores and generalist feeders were more abundant on artificial reefs along the eastern USA composed of shipwrecks and concrete blocks, whereas herbivores were more abundant on natural reefs. Another study by Zhang et al. (2021) on the differences in trophic structure and trophic pathways between artificial reef and natural reef ecosystems along the coast of the North Yellow Sea, China, demonstrated a strong predator–prey relationship between planktivores and piscivores using isotopic signatures. This relationship may explain why piscivores were only detected at the pipeline habitat in this study, where there was the highest percentage of planktivores. The benefit of optimising the production of planktivorous fish will depend on an artificial reef's management objectives (e.g., fishing opportunities and/or habitat offsets). For reefs deployed to provide fisheries benefits, increasing the presence and production of targeted species is a key objective. Optimising the production of planktivores at the pipeline habitat may promote this by increasing the presence of piscivorous fish, which are targeted by fisheries in many marine ecosystems (Soudijn et al., 2021).

Champion et al. (2015) reported that the deployment of man-made structures can be beneficial to planktivorous species mainly due to the refuge provided, allowing for safer foraging conditions. This refuge effect was identified for the nocturnal species in this study, where the presence of nocturnal foraging fishes (mainly generalist carnivores such as Lutjanids (snappers) and Ephinephelids (groupers)) suggests that as well as offering a significant food source, the pipelines appear to support numerous species refuge for diurnal resting and protection. McLean et al. (2019) similarly reported that fish appeared to be utilising pipeline spans as refuges.

The pipeline and reef habitats had species with a significantly different body form, egg dispersal, forage period and resilience to the soft sediment habitat. This was primarily due to the higher number of damselfish species (Family: Pomacentridae) at the reef and pipeline habitats, who share a small ovate body form, demersal egg dispersal, diurnal forage period and high resilience. Damselfish are a major component of a coral reef community (Cooper and Westneat, 2009) and are considered key components of reef food chains, transferring energy from the pelagic zone to the reef environment (Pinnegar and Polunin, 2006). These fishes also provide indirect ecological benefits, moderating bleaching susceptibility of their coral hosts (increasing resilience to multiple stressors), facilitating recruitment sites for some reef fishes and coral and constraining starfish population upsurges and associated coral declines (Cowan et al., 2016; Chase et al., 2018). The specific niche requirements of damselfish were reflected in the multivariate analysis, where the pipeline and reef habitats had damselfish grouped in a single functional group (Group 2 at the pipeline and Group 1 at the reef). The higher percentage of demersal egg laying fishes at the pipeline habitat may suggest the potential for secondary production, as many species spawn within filamentous algal habitat, which is abundant on many oil and gas structures (Saunders et al., 2013; Schutter et al., 2019), or directly on hard substrate such as pebbles, shells, and artificial materials (e.g., pipeline surface or concrete mattresses) (Navarrete-Fernández et al., 2014).

Not all species were functionally grouped with taxonomical related species. For example, species within the Familiy Labridae were dispersed across two functional groups at the pipeline and reef habitats due to their different trait profiles (mainly differences in feeding guilds and maximum depths). This supports the findings from other studies on natural reef habitats, where the classification of species within functional groups often transcends taxonomic boundaries (Hoeinghaus et al., 2007; Córdova-Tapia and Zambrano, 2016; Wang et al., 2019).

The reef habitat had a higher value of community diversity, functional diversity and functional redundancy than the pipeline habitat. The pipeline habitat did however have defined functional groupings, where species were separated within the groups, suggesting the presence and development of a range of conditions necessary for the persistence of species and specific ecological roles (Polechová and Storch, 2019). This is a valuable indicator of ecosystem change (Labadessa et al., 2013). The higher value of the diversity indices at the reef habitat was no surprise, as temporal change is an inherent characteristic of all ecosystems and the reef was much older and more established than the pipeline habitat (Hadj-Hammou et al., 2021). It is generally accepted that following the construction of artificial reefs, the fish community will be disturbed and reach a new equilibrium within one to five years (Guo et al., 2015; Zhang et al., 2021). A common thread throughout the literature is that more time is needed for the community to develop on artificial reefs than natural reefs. Future management plans may wish to consider extending monitoring programs longer than five years (Paxton et al., 2019; Harrison and Rousseau, 2020; Brochier et al., 2021; Blanar et al. 2021; Higgins et al., 2022). The pipeline habitat was also less topographically complex than the natural reef habitat, with fewer crevices and interstitial spaces, which is a strong predictor of reef fish abundance, biomass, species richness, and trophic structure (Darling et al., 2017). Nevertheless, the fish communities on pipelines we studied have developed over time (20–32 years) to function more similarly to the natural reef, though we still detect differences between the artificial and natural systems, with the pipelines having "novel attributes".

The vulnerability, resistance, and resilience of marine ecosystems to global stressors are of major concern as they support an array of essential services, including habitat for species, pollution control, recreation and tourism, shoreline stabilisation and erosion control, and carbon sequestration (Barbier, 2017). Governments, organisations, scientists, and communities are trying to find alternatives that can mitigate the environmental, economic, and social challenges caused by industrialisation (Oliveira and Pereira, 2021) by seeking to restore and balance nature (Lafortezza et al., 2018; Albert et al., 2019; Wilson et al., 2020; Palialexis et al., 2021). Traditional conservation measures, such as no take-zones, reserves, and marine protected areas have been used for decades (Sala and Giakoumi, 2018; Humphreys and Clark, 2020; Medrano et al., 2020), but attention has progressively shifted toward active restoration methods in response to accelerating coral decline (Higgins, Metaxes and Scheibling, 2022). In response to this, we need ways to better characterise ecological community change, beyond just basic measures of abundance and diversity of species. To fully understand pressure response, habitat value, and ultimately improve conservation planning for artificial reefs such as those associated with oil and gas structures, studies need to focus on functions of fish that are linked to their ecological roles in aquatic ecosystems.

As society enters a time where much oil and gas infrastructure has reached the end of its working life, deciding whether to completely remove these structures from the seafloor or to leave in situ as an artificial reef is imminent for many nations and corporations (Bull and Love, 2019). In both tropical and temperate environments, jackets and pipelines are reported to yield greater species richness than nearby natural habitats (Claisse et al., 2014; Bond et al., 2018c; Wright et al., 2020; Harvey et al., 2021; Schramm et al., 2021; Alexander et al., 2022), and increasing evidence suggests that offshore oil and gas structures provide significant ecosystem services (Elden et al., 2019). Fish communities are key to ecosystem functioning, and fisheries management requires a better knowledge of fish community responses, particularly in terms of how species traits respond to anthropogenic pressures and environmental changes (Hobbs et al., 2014; Murgier et al., 2021; Hadj-Hammou et al., 2021). Thus, a trait-based approach to estimate the functional diversity of a system is needed, and to our knowledge this approach has never been applied to study the functional ecology of artificial habitats associated with decommissioned oil and gas structures, which has been identified as a priority knowledge gap in the environmental assessment of decommissioning options (Elliott and Birchenough, 2022; McLean et al., 2022b). Understanding how species interact with the pipeline habitat compared to nearby natural habitats can provide information on the habitat value of these structures, which can be used in the decision-making process for decommissioning. This will improve our understanding of the resilience to stressors and ensure that novel attributes do not result in an "ecological trap" (increased mortality rates or reduced fitness), negatively impacting natural habitats (McLean et al., 2019; Komyakova et al., 2021).

The findings of this study show that there is habitat value for the pipelines being left in situ. There was the presence of multiple functional groups required for the development and maintenance of healthy coral reef systems and fish utilised the pipelines for key life-history stages, indicating that pipelines may help ecological communities resist/be resilient to stressors. Refuge use and the presence of a diverse range of feeding strategies are indicators of a healthy reef system associated with the pipeline habitat and to our knowledge, the presence of planktivorous communities at pipelines has not been previously documented. There is growing evidence to suggest that a balance of predation risk and foraging success influences the association and production of fish with reefs (both natural and artificial) (Folpp et al., 2020; Neely et al., 2021) and further research is required to understand the impact of artificial reef areas created by oil and gas structures specifically on marine food web structure.

CRediT authorship contribution statement

Alethea S. Madgett: Investigation, Conceptualization, Methodology, Formal analysis, Visualization, Writing - original draft, Writing - review & editing. Euan S. Harvey: Funding acquisition, Supervision, Data collection, Data curation, Formal analysis, Project administration, Software, Writing - review & editing. Karl D. Schramm: Data curation, Data collection, Formal analysis, Software, Writing - review & editing. Travis S. Elsdon: Funding acquisition, Formal analysis, Project administration, Writing - review & editing. Michael J. Marnane: Funding acquisition, Project administration, Data collection, Writing - review & editing.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data will be made available on request.

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Appendix A. Supplementary data

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