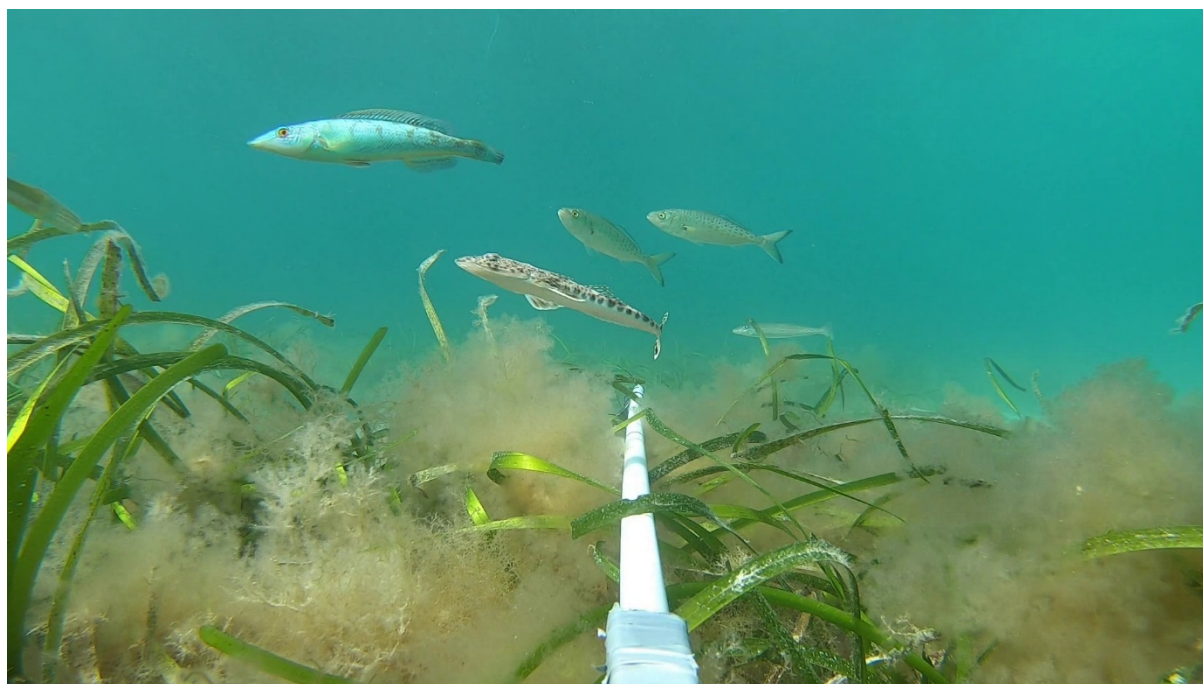


# Investigation of Marine Parks performance using fish counts and refined functional traits

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Final Report to the Department for Environment and Water

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## Executive summary

- Trait-based analysis is a relatively new approach in marine community ecology that value-adds onto traditional taxonomic-based metrics of abundance. For marine fish communities, there has been a very focused set of traits that are repeatedly used by researchers to understand contribution of fish to ecosystem functioning. Our investigation here, was to rigorously assess a more complete set of traits that are applicable to marine fish communities, to establish a refined, more informative set of traits that could be used as a complementary tool in fish community assessments, particularly in this case for Marine Park zoning performance.
- We used the Coffin Bay estuary as a case study to assess the influence of trait selection and taxa choice on the outcomes of spatio-temporal variations in fish assemblages.
- Findings from the detailed assessment of trait selection and taxa choice are provided in Appendix 1. Generally, it was found that using broader taxa datasets (i.e. all nekton) showed a greater ability to distinguish spatio-temporal differences compared to datasets containing only fish, but that was due to dominant scavenging taxa such as crabs. Also, a refined number of ecologically-relevant traits (e.g. nine traits in this case) can be more informative and resource-efficient than the standard three traits used in most studies or than a comprehensive sets of 25 traits. Herein, we used these findings to quantify and compare fish assemblages only without the inclusion of dominant scavenging macroinvertebrates such as crabs (i.e. that may be an effect of the BRUVS method used) across the Coffin Bay Marine Park Zones using a refined dataset of nine traits.
- We assessed if there were any differences in fish assemblages and traits between General Managed Use Zones, Habitat Protection Zones, and Sanctuary Zones across three bays within Coffin Bay using data obtained in 2015 and 2019.
- Overall, we found no difference between Marine Park zones or years for either the trait-based or the traditional assemblage-based analyses. However, species richness was higher in General-Managed Use Zones compared to Sanctuary Zones.
- Our results provide baseline data for fish assemblages and trait information within the first five years since Marine Parks were implemented in South Australia and thus will be beneficial for future assessments of the performance of zoning in Coffin Bay. Overall outcomes from Appendix 1 can be used to guide future trait-based analyses in their approach to trait selection and taxa choice.

## Introduction

Trait-based analysis is a relatively new approach in marine community ecology that value-adds onto traditional taxonomic-based metrics of abundance. Historically, trait-based approaches are steeped in tradition from the terrestrial and freshwater ecological sciences (e.g. Wellborn et al. 1996, Grime et al. 1997). Yet, the application of traits to marine ecosystems is gaining momentum, but often requires a complete understanding of the available traits that can be used in assessments of ecological communities (Bremner 2008; Lam Gordillo 2020). For marine fish communities, there has been a very focused set of traits (e.g. Reef Life Surveys, Stuart-Smith et al. 2013, Coleman et al. 2015, Stuart-Smith et al. 2018) that are repeatedly used by researchers to understand contribution of fish to ecosystem functioning.

The application of biological or functional trait analyses to assemblage data of ecological communities helps understanding of the functioning of aquatic organisms (Culhane et al. 2014; Henriques et al. 2016) and can improve our assessment of marine park performance (Coleman et al. 2015, Villnas et al. 2018). Following the implementation of marine reserves, noticeable changes in taxa abundance and richness may take >5 years for targeted species and >15 years for non-targeted species (Babcock et al. 2010). In comparison, Coleman et al. (2015) compared 18 marine reserves of various ages against unprotected zones detecting consistent trait differences across the fish assemblage in four-year-old reserves, that were not detectable using taxa abundance alone. However, the diverse range of traits used across studies hinders comparisons while the dearth of information for some fish species limits the ability to use some traits.

The Coffin Bay ecosystem is a complex set of shallow bays (< 15 m) with large areas of bare sand and seagrass (e.g. *Zostera* spp.). Throughout the Coffin Bay ecosystem, there are a complex set of General Managed Use (three), Habitat Protection (two) and Sanctuary (five) zones ([www.marineparks.sa.gov.au](http://www.marineparks.sa.gov.au)). The zoning and focus on the assessment in this study focuses on those different zones across three separate locations; Port Douglas, Mount Dutton and Kellidie Bay based on previous ecological (Whitmarsh 2019) and oceanographic flow modelling (Kaempf and Ellis 2015) studies.

In the first assessment based on Brad Martin's honours thesis, we investigated the effects of trait selection and taxa choice on the ability to detect variations in fish assemblages (Appendix 1; Brad Martin's Honours thesis). Four trait datasets were analysed and compared to the assemblage-only data across the five bays and two sampling years (2015 vs. 2019): a combination of either all nekton (37 species) or fish only (30 species), and a comprehensive set of traits (25 traits) or the standard three traits used by Reef Life Surveys. This was the first study of its kind to assess the influence of trait and taxa selection for assessing changes in temperate marine fish assemblages. Our results showed that the nekton and fish assemblage could identify general spatio-temporal patterns, but the nekton assemblage was dominated by scavenging crab. Based on the fish assemblages alone, a subset of nine ecologically-relevant traits were determined as adequate (i.e. based on reduction of traits through autocorrelation and SIMPER analyses procedures) to assess spatio-temporally changes and was likely to yield the best result while not being overly time intensive.

Our overall aim was to rigorously assess a more complete set of traits that are applicable to marine fish communities to establish a refined, more informative set of traits that could be used as a complementary tool in fish community assessments, particularly in this case for Marine Park zoning

performance. Based on the nine ecologically-relevant traits for fish assemblages established from Brad Martin's honours project, we used these aspects to quantify and compare Marine Park Zones spatially in 2019 and spatio-temporally between 2015 (Whitmarsh 2019) and 2019 in Coffin Bay.

## Methods

### *Data collection and video processing*

BRUVS were deployed during the austral spring on the 20<sup>th</sup> – 23<sup>rd</sup> of September 2019 and were compared to those conducted on the 17<sup>th</sup> – 18<sup>th</sup> of September 2015 (Whitmarsh 2019). Thirty and 46 deployments were undertaken in 2015 and 2019 respectively. In 2015, six replicate deployments were conducted across five sites with 16 additional deployments added in 2019 across three of the sites (Kellidie Bay, Mount Dutton, and Port Douglas South) to allow for comparisons of four replicate deployments across all three Marine Park zone types (Figure 1). All simultaneous deployments were separated by a minimum distance of 250 m to minimise the overlap of bait plumes and reduce the likelihood of organisms moving between replicates (Langlois et al. 2012). Surveys were conducted during daylight hours (08:00 – 17:00) with BRUVS deployed for a minimum soak time of 60 minutes and baited with 500 g of minced sardines. Videos were subsequently analysed with EventMeasure using standard practices. Still images of the habitat for each deployment were analysed with Benthobox (see Whitmarsh (2019) for additional details).

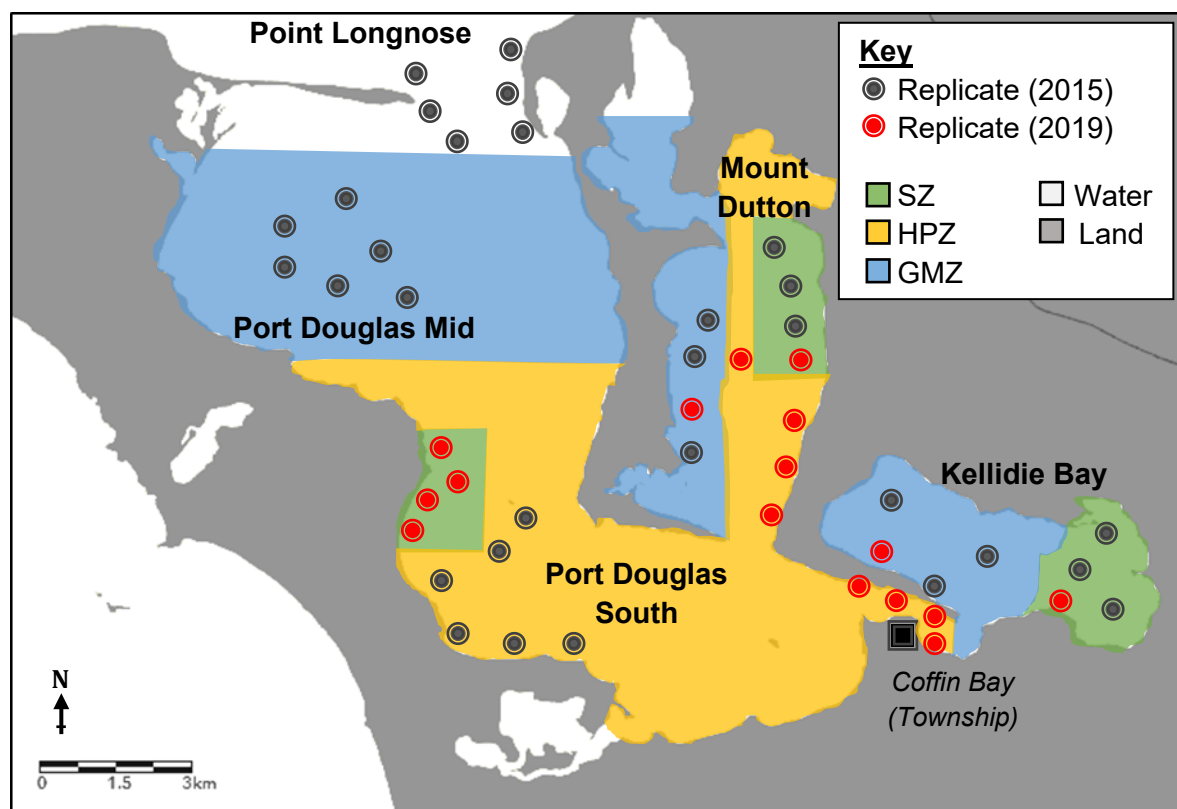


Figure 1: BRUVS locations within Coffin Bay, South Australia. Yellow = 2015 and 2019 surveys; Red = 2019 survey only. SZ, Sanctuary Zone; GMZ, General Managed Use Zone; HPZ, Habitat Protection Zone.

### *Data analyses*

Trait datasets were created and refined as per the methods explained by Martin (2020). From these initial investigations of traits datasets, it was determined that the reduced, three trait set (e.g. used by Reef Life Survey Australia) in combination with an additional subset of six traits, would be the most appropriate fish trait categories for Marine Park assessments in Coffin Bay. Thus, the following nine traits were included in the analysis: maximum body length; water column position; trophic group (temperate); gregariousness; defence structure; mouth position; body shape; conspicuousness; and fisheries value.

Habitat cover (excluding % open water) from most deployments (i.e. excluding the 16 additional replicates taken only in 2019) were analysed using Euclidean distance matrices with the following design: Year (Random; 2 levels) and Site (Random; 5 levels). Pairwise tests were used to determine which pairs of sites were significantly different at the  $p < 0.05$  level.

Two datasets were used and analysed (Figure 2): (1) four BRUVS replicates from each zone type (General Managed Use, Habitat Protection, and Sanctuary Zone) within each of three bays (Kellidie Bay, Mount Dutton Bay, and Port Douglas Bay;  $N = 36$ ) were used to compare fish assemblages across zones; and (2) a spatially smaller dataset ( $N = 24$ ) excluding Port Douglas because its Sanctuary Zone (Thorny Passage SZ-1) was not assessed in 2015.

For both datasets, fish assemblages and the traits dataset were analysed separately with Bray-Curtis similarity matrices created based on dispersion-weighted data. PERMANOVA analyses were conducted using the following two designs: the 2019 data with Site (Random; 3 levels) and MPA Zone (Fixed; 3 levels); and the 2015 v 2019 year comparisons with Year (Random; 2 levels); Site (Random; 2 levels); and Protected Status (Fixed; 2 levels). For each dataset, a dummy variable of one was added to address the problem of paired absences. Data were displayed visually using a non-metric Multi-Dimensional Scaling (nMDS) plot. Where analyses had low numbers of unique permutations ( $<100$ ), Monte-Carlo  $P$  values were used instead of the traditional  $P$  values to account for the lower unique permutations. Total abundance and number of species were also analysed using the same two PERMANOVA designs for each of the fish assemblages and traits datasets based on Euclidean distance matrices. However, analyses could not be run on the 2015 v 2019 data for number of species due to the low numbers recorded in some replicates across years.

Species which may potentially be responding to Marine Parks zoning protection were identified from EconSearch (2018) including King George Whiting, *Sillaginodes punctatus*, and Australian salmon, *Arripis* spp.. Other species of commercial or recreational value were not consistently abundant enough throughout Coffin Bay in space and time to run analyses. These species abundance counts were analysed using the same two PERMANOVA designs (i.e. 2019 only and across years) as per the other univariate analyses.

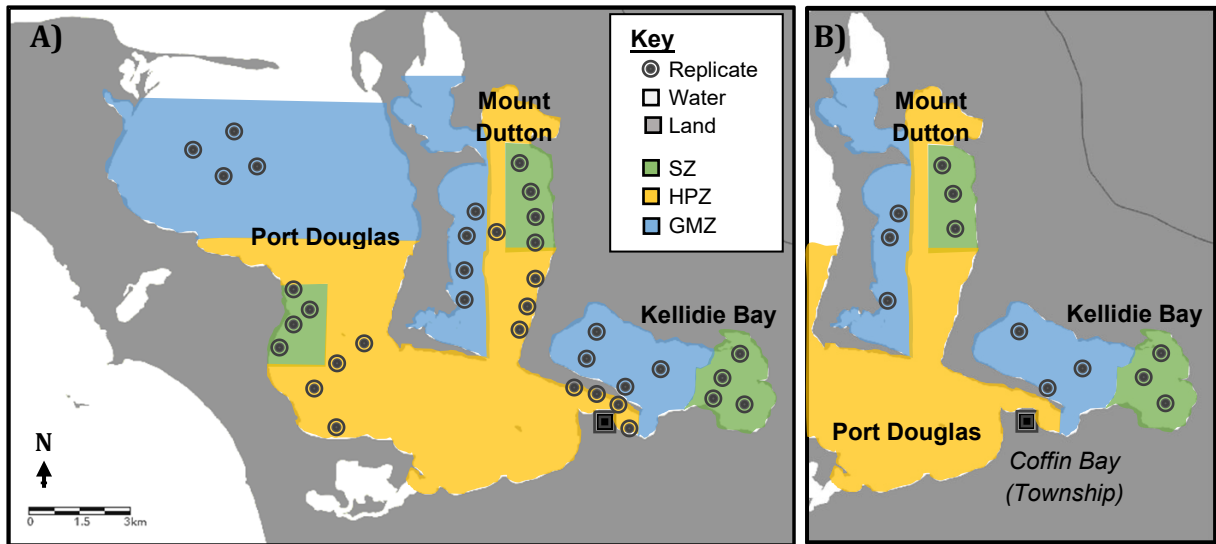


Figure 2: Location of replicates deployed for A) the spatial comparison of Marine Park zones in 2019 across three bays and B) the spatio-temporal comparison of zones between 2015 and 2019 within Kellidie Bay and Mount Dutton.



## Results

### Habitat

Habitat types in Coffin Bay included unconsolidated sandy areas or vegetated areas including seagrass and macroalgae cover (Figure 3). Habitat cover (%) varied significantly across sites (Pseudo- $F = 7.10$ ,  $P = 0.001$ ) but was consistent across years (Pseudo- $F = 0.85$ ,  $P = 0.45$ ). Kellidie Bay habitats were only significantly different to Mount Dutton Bay and no other sites, while all other site pairs were significantly different from each other (Table 1).

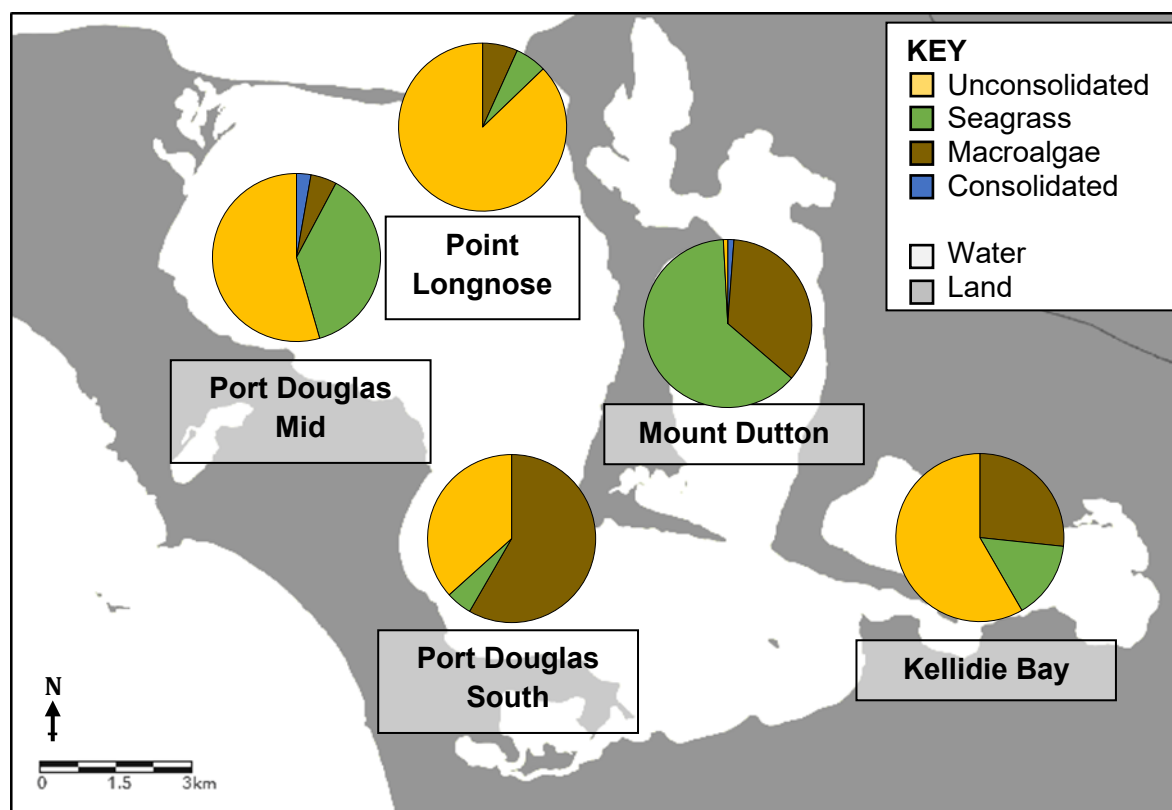


Figure 3: Mean % cover for each habitat type (excluding % open water).

Table 1: Pairwise PERMANOVA tests for differences between sites using habitat percentage cover for 2015 and 2019 BRUVS surveys combined. Unique permutations ranged from 9933 – 9957. Significant values are shown in bold.

Pairs	t	P
KB & MD	3.23	<b>0.0005</b>
KB & PDM	1.18	0.2475
KB & PDS	1.40	0.1454
KB & PL	1.61	0.0791
MD & PDM	2.83	<b>0.0021</b>
MD & PDS	2.89	<b>0.0009</b>
MD & PL	5.97	<b>0.0001</b>
PDM & PDS	2.29	<b>0.0118</b>
PDM & PL	2.03	<b>0.0473</b>
PDS & PL	3.00	<b>0.0052</b>

### Description of fish assemblage

In total, 1,234 individuals from 39 nekton species were observed across all deployments in 2019. Of those 39 species, contributions were from; 27 teleost fishes, two chondrichthyans, four decapod crustaceans, two cephalopods, two other invertebrate species, one sealion, and one aquatic bird. Abundant species included: hardyheads, *Atherinosoma microstoma*; Australian salmon, *Arripis* spp.; rock crab, *Nectocarcinus integrifrons*; and whittings, *Neodax balteatus*, *Sillaginodes punctatus*, and *Haletta semifasciata*. All subsequent analyses in this report were conducted on the teleost and chondrichthyan assemblage alone (but see further assessment including larger macroinvertebrates in Martin 2020).

### Univariate analyses of Marine Park Zones

No significant differences were observed for the total abundance of individuals between Marine Park Zones for either the 2019 or across years datasets (Table 2, Figure 4). In 2019 alone, fish species richness was greater in General Managed Use Zones and there were significant differences identified between zones, with pairwise tests indicating those differences were between General-Managed Use Zones and Sanctuary Zonest (Table 2).

Both individual fish species analysed, *Arripis* spp. and *Sillaginodes punctatus*, showed no significant differences between Marine Park Zones in 2019 or across years (Table 2).

Table 2: A) Summary of results from PERMANOVA tests for univariate analyses. An X indicates that the test was not significant, while numbers in bold show P value where significance was detected. A - indicates the test was not performed. Interactions were not significant and thus are not shown. B) Pairwise test from the significant factor of MPA Status for Number of species. GMUZ = General-Managed Use Zone, HPZ = Habitat Protection Zone, SZ = Sanctuary Zone.

A) Data	2019 only			2015 vs 2019		
	Test	Site	MPA Status	Year	Site	MPA Status
Total abundance		X	X	X	<b>0.048</b>	X
Number of species		<b>0.003</b>	<b>0.04</b>	-	-	-
<i>Arripis</i> spp.		<b>0.006</b>	X	X	X	X
<i>Sillaginodes punctatus</i>		X	X	X	X	X

B) Number of species	t	P(MC)
GMUZ vs. HPZ	3.19	0.086
GMUZ vs. SZ	7.76	<b>0.006</b>
HPZ vs. SZ	0.25	0.839

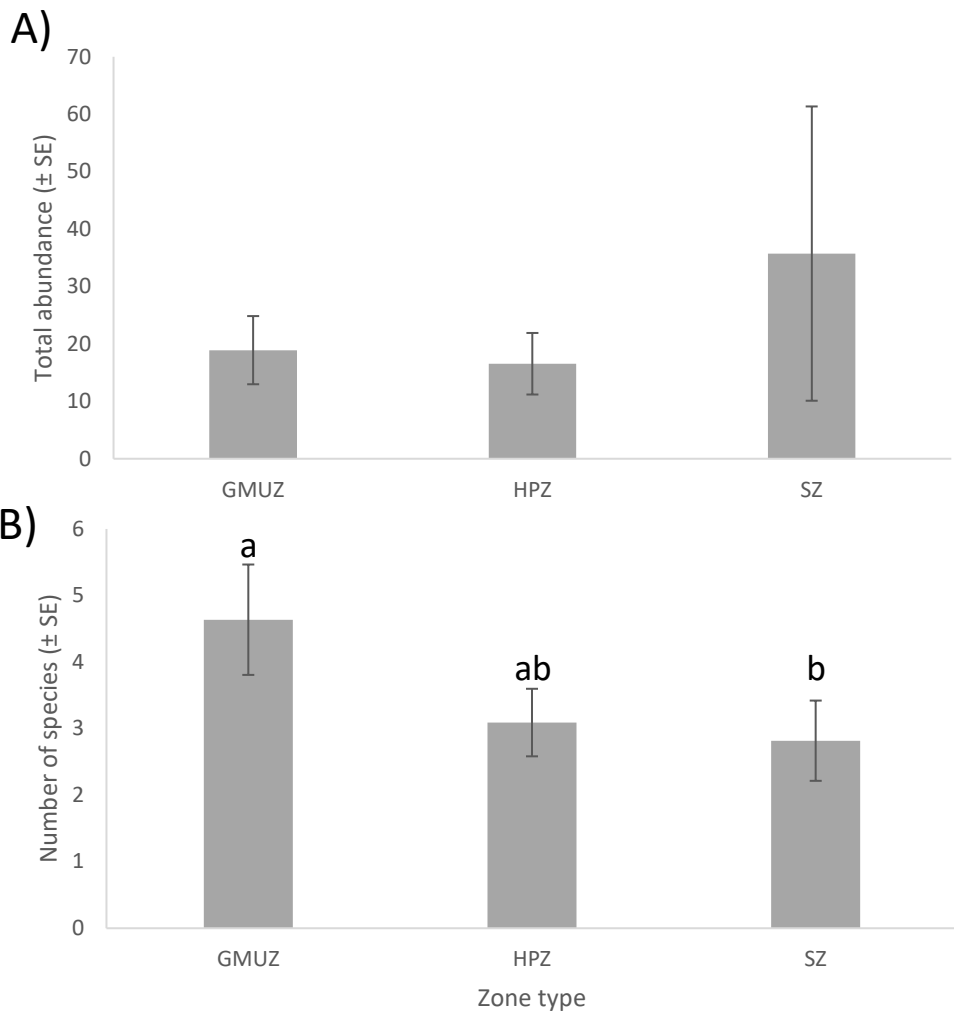


Figure 4: For the 2019 spatially expanded dataset A) shows the mean total abundance per zone with B) the mean number of species. Letters indicate significant differences. GMUZ = General-Managed Use Zone, HPZ = Habitat Protection Zone, SZ = Sanctuary Zone.

*Investigation of Marine Park Zones by fish assemblage and trait data*

No significant differences between Marine Park zones were identified for either fish assemblages or trait compositions in the expanded 2019 spatial dataset (Table 3, Figure 5). Also, there was no significant difference between protection status (i.e. zones) across years (Table 4, Figure 6).

Assessment of differences in fish assemblages and traits between separate bays are discussed in Martin (2020; Appendix 1) and thus are not discussed herein.

Table 3: PERMANOVA analyses for assemblages and trait datasets for 2019 across three zone types (GMU, HPZ, SZ) and three bays (Kellidie Bay, Mount Dutton, Port Douglas). Unique permutations ranged from 991 – 998. Significant values are shown in bold.

Factor	Assemblage				Traits			
	df	MS	Pseudo-F	P(perm)	Df	MS	Pseudo-F	P(perm)
Site	2	5777.5	3.47	<b>0.001</b>	2	7323.7	3.76	<b>0.001</b>
Zone	2	2098.4	1.15	0.4	2	2352	1.21	0.36
Site x Zone	4	1827.1	1.10	0.35	4	1941.5	1.00	0.52
Residual	24	1666.2			24	1948.5		

Table 4: PERMANOVA analyses for comparisons between 2019 and 2015 for assemblages and trait datasets for Kellidie Bay and Mount Dutton only. Unique permutations ranged from 3 – 999, thus Monte-Carlo P values were used. Significant values are shown in bold.

Factor	Assemblage				Traits			
	df	MS	Pseudo-F	P(MC)	df	MS	Pseudo-F	P(MC)
Year	1	1504.7	0.81	0.59	1	1813.4	1.27	0.38
Site	1	7586.2	4.09	0.07	1	9036.3	6.31	<b>0.0361</b>
Status	1	3465.7	1.80	0.19	1	4205	1.33	0.32
Year x Site	1	1854.2	1.30	0.25	1	1431.6	0.75	0.55
Year x Status	1	1585.7	0.80	0.62	1	2073	0.56	0.74
Site x Status	1	1439.1	0.73	0.65	1	3825.7	1.04	0.48
Year x Site x Status	1	1971.2	1.38	0.23	1	3672.8	1.92	0.08
Residual	16	1430.6			16	1913.3		

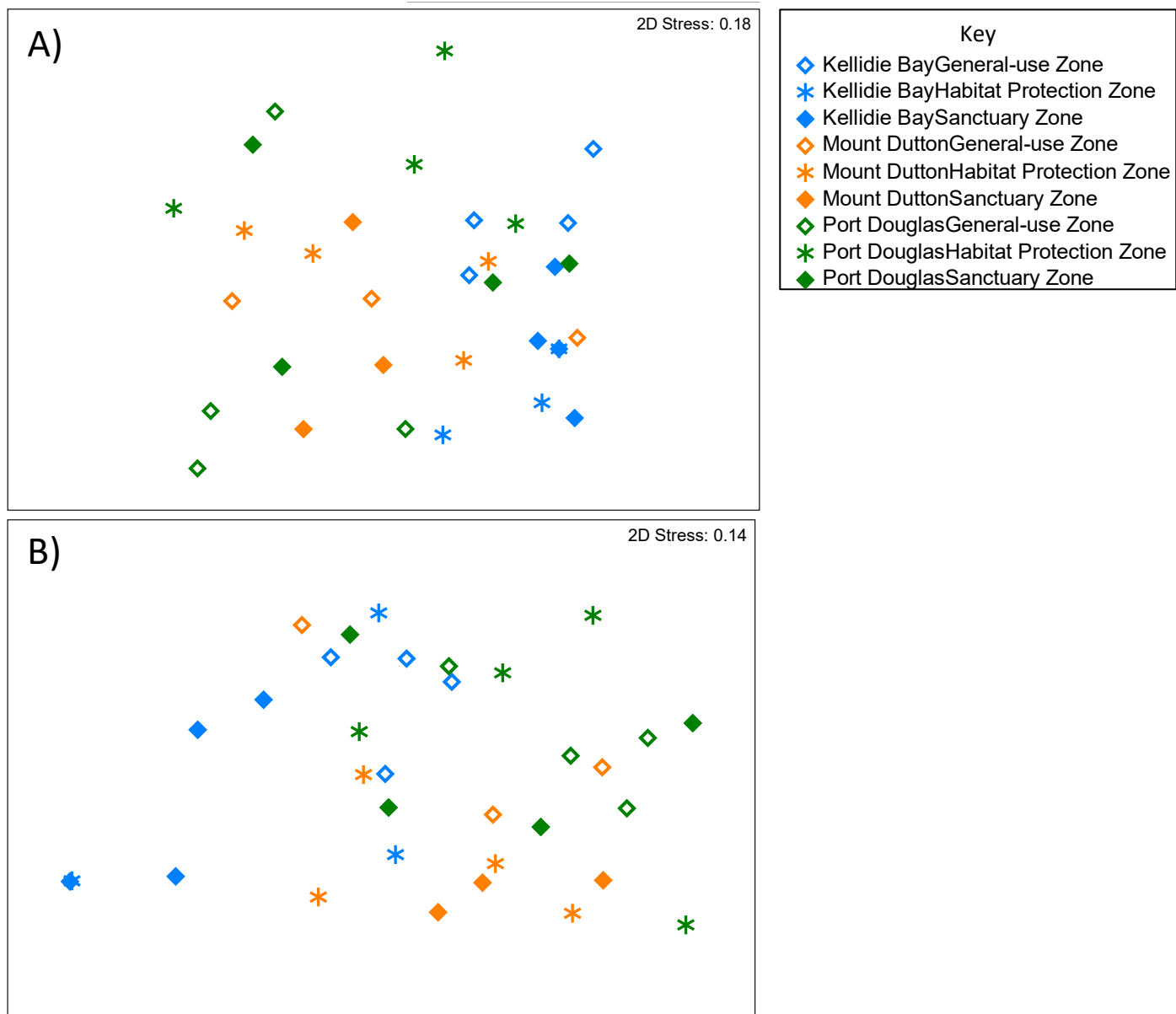


Figure 5: nMDS plot showing the 2019 expanded zonation study for A) the assemblage dataset and B) the trait dataset.

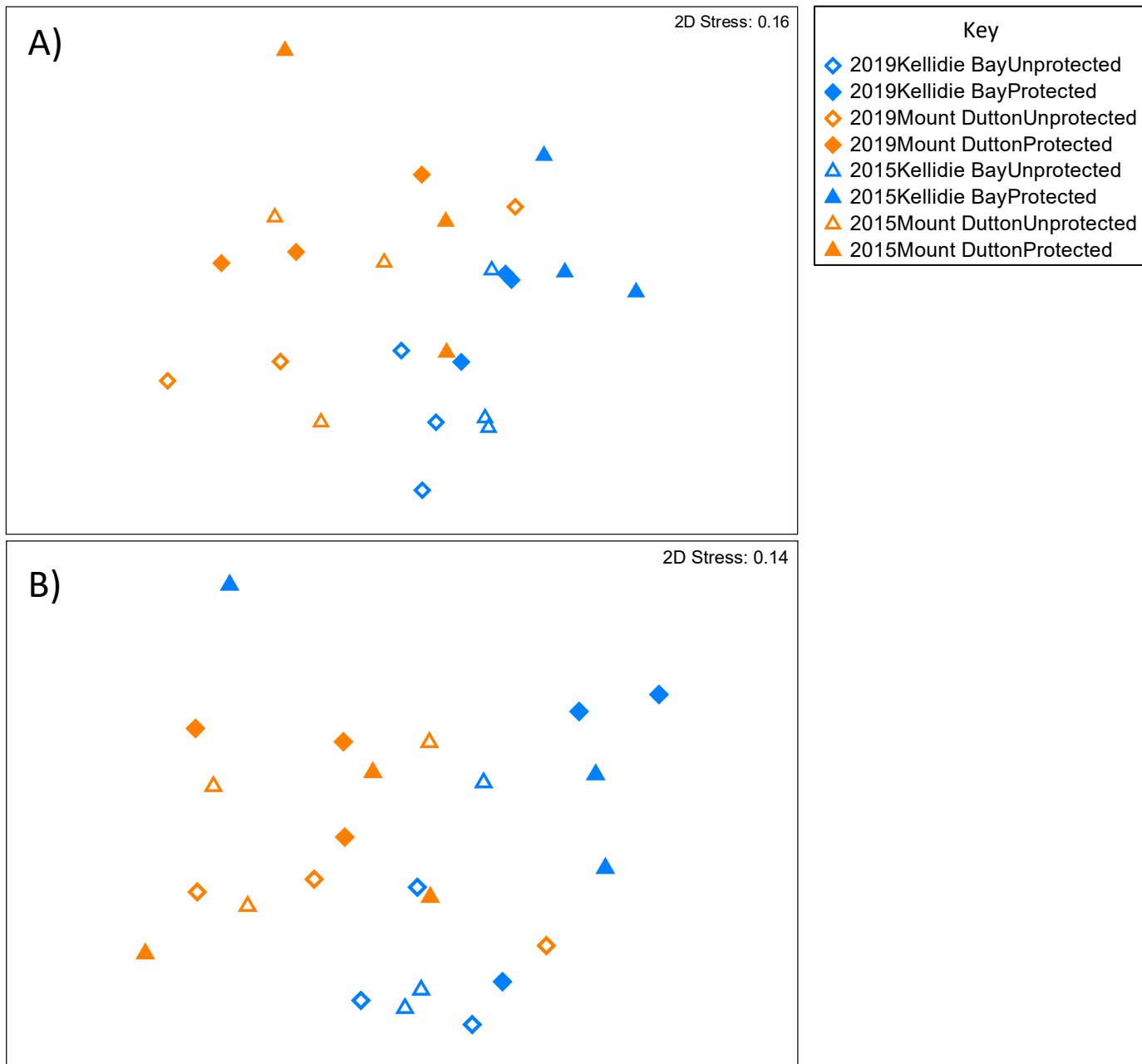


Figure 6: nMDS plot showing restricted zonation set across years for A) the assemblage dataset (+d) and B) the trait dataset.

## Discussion

Overall, no fish assemblage or trait differences were identified between Marine Park zones for either the spatially expanded 2019 dataset or for the temporal comparison between 2015 and 2019. Both traits and assemblage data of the sampled fish showed similar results for Marine Park zones indicating there was no observable difference for Coffin Bay Sanctuary Zones in the short time since zoning implementation 5 years prior. There was, however, significant differences in the number of fish species in 2019 between the General-Managed Use Zone and Sanctuary Zones, with greater numbers in the unprotected area.

There are a number of potential factors which may be attributable to the overall lack of difference between Marine Park zones in Coffin Bay including the size and age of zones, the type of fish species present, and the types of anthropogenic pressures present in Coffin Bay. The Thorny Passage Marine Park is still relatively young with enforcement of zones only coming into effect in October 2014; 11 months before the original BRUVS sampling date in 2015. Thus, the latest sampling in 2019 was only completed 4 years and 11 months after enforcement commenced. Studies have shown the effects of protection may not be observable for up to 15 years with the reliability to detect effects increasing with each year of age (Claudet et al. 2008, Molloy et al. 2009, Vandeperre et al. 2011). Similarly, the size of reserves may also be attributable to detecting effects of zoning with larger reserves often yielding better results (Claudet et al. 2008). The Sanctuary Zones in Coffin Bay are relatively small covering less than 5 km<sup>2</sup> for each zone and thus may not protect larger, more mobile species which are likely to have home ranges that extend outside this zone (e.g. King George whiting, *S. punctatus*, gummy sharks, *Mustelus antarcticus*, and flathead, *Platycephalus* spp.).

The fish species present in Coffin Bay may also influence the performance of the Marine Park Zones, or our ability to detect change. Of all fish sampled in our study, only 1% of individuals were considered sedentary in their home range, with 58% considered mobile and 40% considered wide-ranging, indicating larger reserves may be required for adequate protection of such individuals. There were also a large number of individuals (30%) observed that are considered non-target species for fisheries, however, the majority of individuals were classified as either by-product (20%) or targeted (50%) indicating that protection from fishing should benefit such species. Temperate species are also considered to have long larval durations and can be slow to mature (Laurel & Bradbury 2006, O'Connor et al. 2007) although these traits were unable to be included in our analysis due to a lack of reliable data for many species. Fish species with slow maturation and long larval stages may not adequately be protected by relatively young and small Marine Park zones and as such we found no differences in the individual species we assessed.

The fishing pressure and enforcement in Coffin Bay could also be contributing to the lack of differences between Marine Park zones. While Coffin Bay experiences higher fishing pressure with peak tourism in summer months due to recreational fishing, the relatively low fishing pressure at other times of the year may reduce the overall effectiveness of protection, due to the overall limited presence of this impact (EconSearch 2018). Further, the remoteness of Coffin Bay and fluctuations in recreational fishing pressure throughout the year make it difficult to consistently assign resources to educate and enforce the complex zoning throughout the bays.

The trait-based analyses we conducted provided further confirmation of results from the assemblage-based datasets, with no detectable difference between traits in Coffin Bay Marine Park

zones. However, trait-based analyses were able to identify idiosyncratic differences between some site pairs which were sometimes undetectable using assemblage-based data alone. Continued analyses using the refined trait dataset will allow for value-adding analyses at relatively low cost for future studies in Coffin Bay. Martin (2020; Appendix 1) highlights the importance of trait-based analyses in Coffin Bay and the differences observed from assemblage datasets in more detail.

### Conclusions and future research

Overall, there were no detectable effects of Marine Parks zoning protection on fish assemblages in Coffin Bay for either assemblage- or trait-based data. Future studies should incorporate additional sampling in other sites and zones within Coffin Bay and increase replicate numbers within those zones to provide a better overview of fish species and their variability in space and time. The use of stereo-BRUVS may also add some benefit as accurate size information can be gathered. However, there are limitations with this approach in Coffin Bay due to the shallow nature of the bays, particularly for many sanctuary zones. We also recommend that future assessments of fish assemblages in Coffin Bay and elsewhere in South Australia should include the addition of trait based information to improve the biological and functional understanding of marine ecosystem change across the complex Marine Park zoning network throughout the state.



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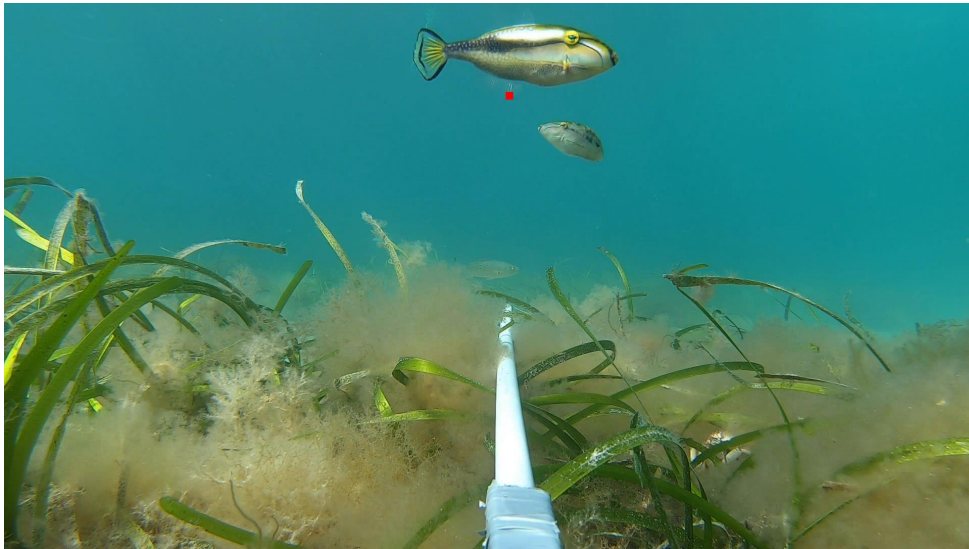
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## Appendix 1

# **Taxonomic scope and trait selection influence outcomes of nekton assessments**



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Presented in partial fulfilment of the requirements for the Bachelor of Science (Honours) (Enhanced Program for High Achievers), Flinders University, Australia.

**May 2020**

## I. Declaration

I certify that this thesis does not incorporate without acknowledgement any material previously submitted for a degree or diploma in any university; and that to the best of my knowledge and belief does not contain any material previously published or written by another person except where due reference is made in the text.

**Bradley Martin 25/05/2020**

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# Taxonomic scope and trait selection influence the outcomes of nekton assessments

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**ABSTRACT:** Marine monitoring programs are increasingly implementing trait-based approaches to understand spatio-temporal changes in community assemblages and their responses to environmental and anthropogenic pressures. Ultimately, an objective of trait-based ecology is to achieve ‘generality’, whereby trait-analyses are applied across different taxa, environments, and sites. Here, I evaluated the influence of taxonomic scope and trait selection on trait-based monitoring by examining estuarine nekton assemblages surveyed using baited remote underwater video stations (BRUVS). In 2015 and 2019, 39 taxa were documented from five sites across the inverse estuary of Coffin Bay, South Australia. This study compared a broad (all nekton) versus narrow (fish only) taxonomic scope, and also assessed few traits (restricted traits set) against all traits available (full trait set), with four trait datasets in total. I found that a broad taxonomic scope detected the only temporal differences and could identify general spatial variations of trait diversity. However, a narrow taxonomic scope determined finer trait differences between sites. I also found similar results using the restricted and full trait sets for both the fish and nekton assemblages, with full trait set identifying additional traits that were relevant to characterising spatio-temporal variation. Overall, the findings indicate that the number of traits selected is less important than the types of traits themselves.

**KEY WORDS:** trait analysis • monitoring • indicators • redundancy • biodiversity

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# 1. INTRODUCTION

Marine and estuarine environments worldwide are subject to an increasing number and intensity of environmental and anthropogenic pressures (Crain et al. 2008), often occurring concurrently (Halpern et al. 2007). To address ecological impacts and effectively manage marine biodiversity, it is vital to apply holistic approaches that explain faunal community responses to selective pressures rather than only quantifying changes in species abundance (Bremner et al. 2006, Claudet et al. 2010, Mouillot et al. 2013). Increasingly, this has evoked the assessment of trait diversity as a compliment to taxonomic diversity. Measuring the diversity and composition of traits has been vital to addressing critical ecological questions and determining spatio-temporal trends and changes in marine assemblages (Bremner et al. 2003, Micheli & Halpern 2005, Litchman et al. 2007).

Trait diversity can be generally described as the extent of trait differences between taxa (Dencker et al. 2017). Conceptually, each species is defined by a specific set of traits which are measurable attributes at the individual or species level (Bremner et al. 2003, Violle et al. 2007). Traits can be morphological (e.g. size and shape), physiological (e.g. growth-related or thermal constraints), phenological (e.g. maximum body size, fecundity), or behavioural (e.g. gregariousness, trophic group) (Bremner et al. 2006, Mouillot et al. 2013). Together, combinations of ecologically important traits can describe the ecological niche of each species, or 'what they do' to influence the functioning of ecosystem processes (Bremner et al. 2003, Petchey & Gaston 2006). Trait diversity can indicate the status and relationships associated with ecological processes, and can be interpreted as trait richness and evenness, or can be weighted using measures of abundance or biomass (Bremner 2008). Trait-analysis was pioneered in freshwater and terrestrial systems (e.g. Wellborn et al. 1996, Grime et al. 1997). However, over the past decade, the use of trait diversity on marine assemblages has rapidly

1 increased with application across a broad range of taxa, including benthic invertebrates  
2 (Bremner et al. 2003), plankton (Litchman et al. 2007), fish (King & McFarlane 2003),  
3 macroalgae (Jänes et al. 2016), and coral (Garrabou & Harmelin 2002).

4 Assessments of marine assemblages have traditionally focused on measures of species richness,  
5 abundance and biomass, which rely only on the taxonomic identity of each taxon. The use of  
6 taxonomic diversity in assessing spatio-temporal patterns has limitations that can be addressed  
7 using trait diversity (Bremner et al. 2003, Coleman et al. 2015). In particular, changes in taxa  
8 are comparatively less sensitive to environmental and anthropogenic selective pressures  
9 compared to traits, affecting the ability to detect the response of assemblages across short  
10 timeframes (e.g. Coleman et al. 2015, Dencker et al. 2017). Following the implementation of  
11 marine reserves, noticeable changes in taxa abundance and richness may take >5 years for  
12 targeted species and >15 years for indirect effects on other taxa (Babcock et al. 2010). In  
13 comparison, Coleman et al. (2015) compared 18 marine reserves of various ages against  
14 unprotected zones detecting consistent trait differences across the fish assemblage in four-  
15 year-old reserves, that were not detectable using taxa abundance alone. Additionally,  
16 anthropogenic and environmental pressures influence both taxonomic and trait diversity,  
17 however, the intensity and direction (e.g. positive, neutral or negative) of response varies  
18 between taxa (Claudet et al. 2010). More specifically, when a selective pressure causes a decline  
19 in some taxa with common traits amongst them, other taxa with very different common traits  
20 may increase in abundance (McKinney & Lockwood 1999, Wiegmann & Waller 2006, Mouillot  
21 et al. 2013). For example, fishing typically has the greatest impact on taxa at high trophic levels,  
22 associated with large maximum sizes and carnivorous diets, as opposed to smaller-bodied  
23 planktivores (Christensen et al. 2014).

1 Despite the advantages of trait analyses, its application is limited by the availability of trait  
2 information, inconsistencies of trait definition and choice, and measurement approaches used  
3 by researchers. Discrepancies in trait-based analyses have been extensively discussed in the  
4 literature (e.g. Violle et al. 2007, Costello et al. 2015, Degen et al. 2018). Traits can be chosen  
5 based on their perceived importance and relevance to specific research objectives, promoting  
6 the use of consistent traits across studies of particular areas of research. Such flexibility in trait  
7 choice has led to studies that only use subsets of traits as single or few trait categories (e.g.  
8 Olden et al. 2007, Eick & Thiel 2014), through to >50 traits (Doxa et al. 2016). In contrast, other  
9 studies do not preselect traits but instead include as much relevant trait information as possible  
10 that is available. This approach offers the best opportunity to understand ecological processes  
11 and response mechanisms (Bremner et al. 2006), by highlighting finer-scale trait differences  
12 between taxa (Petchey & Gaston 2006, Mouillot et al. 2013). However, compiling all relevant  
13 trait data can be costly and time-consuming, which should be considered in the planning stage  
14 of any study.

15 Ultimately, one of the objectives of trait-based ecology is trait 'generality' referring to the  
16 prediction of spatio-temporal patterns across a broad scope of taxa (i.e. taxonomic scope refers  
17 to the range of body plans and taxa considered for analysis), environments, and sites (Verberk  
18 et al. 2013). While standardised trait protocols have universalised approaches across terrestrial  
19 plants (Cornelissen et al. 2003, Perez-Harguindeguy et al. 2016) and invertebrates (Moretti et  
20 al. 2016), such protocols are not well developed for assessing marine taxonomic groups  
21 (Costello et al. 2015, Degen et al. 2018). Direct comparison of traits across marine organisms is  
22 hindered by trait irrelevance, where traits applicable to one particular group of taxa are not  
23 applicable to others (Costello et al. 2015, Beauchard et al. 2017). Trait irrelevance stems from  
24 the development of differing trait methodologies and definitions for specific taxonomic groups  
25 (Weiss & Ray 2019). However, a recent suggestion was proposed that broadening the

1 taxonomic scope and trait definitions across taxonomically diverse organisms will offer greater  
2 insights into community trait responses and spatio-temporal patterns (Weiss & Ray 2019).  
3 Trait-based studies across dissimilar marine species have been developed for benthic  
4 invertebrates (Bremner et al. 2006), plankton (Litchman et al. 2007), and recently developed  
5 for marine megafauna (Tavares et al. 2019).

6 Understanding how taxonomic scope and trait selection interact is an essential aspect for  
7 assessing ecosystem functioning, but any critical investigation of those dynamics in a marine  
8 system is lacking. Therefore, the main objective of this study was to evaluate the influence of  
9 taxonomic scope and trait selection on trait analysis by assessing marine assemblages across a  
10 small temporal (i.e. four years) and spatial (i.e. sites >3 kilometres apart) scale. Nektonic  
11 macrofauna were surveyed in 2015 and 2019 across interconnected bays of an inverse estuary  
12 system in southern Australia to assess measures of both taxonomic and trait diversity. The  
13 effect of taxonomic scope was investigated by comparing the traits of the nektonic assemblages  
14 comprised of fish and large, mobile macroinvertebrates (i.e. decapod crustaceans and  
15 cephalopods), against a commonly used marine indicator group (i.e. fish only). Within each  
16 assemblage group (i.e. fish only versus nekton), trait selection was assessed by comparing a  
17 restricted but commonly used set of three traits against a full set of 25 traits applicable to all  
18 sampled taxa. Overall, trait diversity was evaluated using four trait datasets; (1) fish only  
19 restricted traits, (2) fish only full traits, (3) nekton restricted traits, and (4) nekton full traits.  
20 This study provides the first assessment distinguishing how trait analyses are affected by  
21 taxonomic scope and trait selection, giving critical perspective for future marine monitoring  
22 programs.

## 1 2. MATERIALS & METHODS

### 2 2.1. Study site

3 The study was conducted in Coffin Bay, a multiple-use protected area located at the southern  
4 end of the Eyre Peninsula, situated within the temperate Eyre Yorke Block bioregion, South  
5 Australia (34°36' S, 135°24'E)(Fig. 1). Coffin Bay is a relatively small inverse estuary covering  
6 125 km<sup>2</sup> and consists of several interconnected shallow bays (Kämpf & Ellis 2015). As an  
7 inverse estuary, the bays have a significant salinity gradient that increases with distance from  
8 the estuary mouth (Simier et al. 2004, Kämpf & Ellis 2015). Flushing of the estuary primarily  
9 occurs in Port Douglas Bay, with the inner bays of Kellidie Bay, Mount Dutton Bay, and Yangie  
10 Bay exhibiting hypersaline conditions driven by surface heat fluxes. Mean daily temperatures  
11 range from 8.1 to 25.4°C, and annually the estuary receives ~500 mm of rainfall with pan  
12 evaporation of ~1500 mm on average ([bom.gov.au](http://bom.gov.au)). The estuary generally has shallow depth  
13 with 20% <1 m and the remaining 80% at a mean depth of ~3 m. Heterogenous and patchy  
14 habitats are found throughout the estuary, including seagrass, macroalgae, and unconsolidated  
15 sand (Saunders 2012).

16 Coffin Bay is a regional centre for oyster farming and tourism, especially popular with  
17 recreational fisheries (Ruth & Patten 2018) and the entire estuary is located within the  
18 multiple-use Thorny Passage Marine Park. More specifically, Coffin Bay consists of partially  
19 protected General Managed Use Zones, Habitat Protection Zones, and Special Purpose Areas  
20 where some marine activities are permitted, in addition to fully protected Sanctuary Zones  
21 which prohibit all forms of fishing but allows non-extractive activities  
22 ([environment.sa.gov.au/marineparks](http://environment.sa.gov.au/marineparks)). During this study, the Marine Park Zones in Coffin Bay  
23 were still young, with regulatory zones implemented in October 2014 (Bryars et al. 2016).

1 Thus, sample sites were allocated across different sections of Port Douglas Bay, Mount Dutton  
2 Bay and Kellidie Bay (Fig. 1), with higher regard to distance from the estuary mouth rather than  
3 zoning comparisons.

## 4 2.2. Sampling technique

5 The nekton assemblages were surveyed using benthic Baited Remote Underwater Video  
6 Stations (BRUVS). BRUVS are a commonly used method for monitoring aquatic macrofauna  
7 assemblages, especially fish, under a range of environmental conditions (Cappo et al. 2004,  
8 Gladstone et al. 2012). The advantages and disadvantages of BRUVS have been extensively  
9 discussed in the literature (Mallet & Pelletier 2014, Whitmarsh et al. 2017) with the main  
10 advantages including the ease of replication, relatively low cost, reduced risk to personnel, and  
11 the permanent visual record, facilitating additional analysis of previous surveys. BRUVS are also  
12 a non-destructive and non-extractive sampling method, making them ideal for sampling  
13 sensitive habitats or populations, and in marine protected areas where policy may limit some  
14 or all extractive methods (Cappo et al. 2003).

15 The camera system used in this study consisted of a single GoPro Hero7 set to record in 1080p  
16 at 60 frames per second with a wide field of view and mounted to a metal frame in alignment  
17 with the bait arm (see Clarke et al. 2019). The bait consisted of approximately 500 grams of  
18 minced pilchard (*Sardinops sagax*) in a plastic mesh basket suspended at the end of a 1.5 metre  
19 (long) PVC bait arm (Fig. S1.) The bait was crushed and thawed before deployment to maximise  
20 the dispersal of fish oil into the water column.

## 21 2.3. Sampling design

22 Sampling consisted of six replicate BRUVS deployments conducted at each of the five sites  
23 during the austral spring on 17<sup>th</sup>–18<sup>th</sup> of September 2015 and 20<sup>th</sup>–23<sup>rd</sup> of September 2019.

1 Sites were haphazardly distributed across the subsidiary bays (Fig. 1) with a total of 30 BRUVS  
2 deployments occurring in each of the two years. All simultaneous deployments were separated  
3 by a minimum distance of 250 metres to minimise the overlap of bait plumes and reduce the  
4 likelihood of organisms moving between replicates (Langlois et al. 2012). Surveys were  
5 conducted during daylight hours (08:00-17:00) with BRUVS deployed for a minimum soak time  
6 of 60 minutes.

#### 7 2.4. Image analysis

8 Video imagery was converted to .avi format using Xilisoft Video Converter Ultimate  
9 ([xilisoft.com](http://xilisoft.com)) and assessed using the software SeaGIS EventMeasure ([seagis.com.au](http://seagis.com.au)) which  
10 facilitated frame-by-frame playback and picture adjustment of low visibility conditions. Each  
11 video was assessed for a 60-minute bottom time duration commencing when the BRUVS landed  
12 on the seafloor. All macrofauna observed in the videos were identified to the lowest taxonomic  
13 level where possible. The relative abundance of each taxon per video was estimated using  
14 *MaxN*, a conservative estimate defined as the maximum number of individuals observed in a  
15 single frame (Cappo et al. 2003). The combined *MaxN* values across all nektonic taxa within a  
16 sample equated to the nekton abundance value. The number of different nektonic taxa  
17 identified within a sample equated to its nekton richness value.

#### 18 2.5. Trait composition

19 To assess the taxonomic scope, a narrow scope limited to fish only taxa, as fish are a common  
20 indicator group comprised of teleosts and elasmobranchs (32 taxa). This narrow taxonomic  
21 scope was compared against a broader scope of all nekton taxa including both fish and large  
22 macroinvertebrates (e.g. decapod crustaceans and cephalopods) (39 taxa). Macroinvertebrates  
23 are important indicators of ecological functioning in marine benthic environments (Bremner et  
24 al. 2003, Henriques et al. 2014). Additionally, while BRUVS mainly record fish, large

1 macroinvertebrates are reported in BRUVS surveys due to their attraction to bait (e.g. Peters et  
2 al. 2014, Clarke et al. 2019). However, the nekton assemblage in this study excluded marine  
3 mammals, birds, and other non-nektonic taxa (e.g. cnidarians, echinoderms) due to the rarity of  
4 those taxa and because BRUVS are unlikely to sample their relative abundance reliably.

5 Additionally, taxa were only included provided they could be identified to either species or  
6 genus level, with traits of the latter taxa representing an average from contributing species.

7 This reduced the total number of observed taxa for available trait analysis from 44 to 39.

8 The influence of trait selection was assessed by comparing a restricted set of three traits versus  
9 a full set of 25 traits using fish only and nekton assemblages. Trait information from the  
10 literature was used to compile taxa-trait matrices and traits were excluded when the  
11 information was unavailable for all taxa (e.g. age at maturity, maximum body weight) (see  
12 Supplementary Material, Table S1). Each trait was subdivided into various modalities  
13 representing the range of subcategories that could be expressed by the sampled taxa (Table S2).  
14 For example, the trait category salinity preference can be subdivided into the modalities;  
15 freshwater, brackish and marine. The extent to which each taxon expressed each modality was  
16 assigned a value using the 'fuzzy coding' procedure to account for interspecies variation within  
17 traits (Chevene et al. 1994).

18 Overall, the full set of 25 traits set consisted of 104 modalities in total, whereas the restricted  
19 trait set consisted of three traits subdivided among 21 modalities. The restricted trait set  
20 comprised the traits; maximum body length, trophic group and water column position. These  
21 three traits are commonly used and well-defined traits for evaluating assemblages of marine  
22 fish, with information available for the surveyed taxa (e.g. Stuart-Smith et al. 2013, Coleman et  
23 al. 2015, Stuart-Smith et al. 2018). The trait diversity of the fish and nekton assemblages was  
24 assessed using both the restricted and full trait sets, comprising four separate datasets for



1 comparison (i.e. fish restricted traits, fish full traits, nekton restricted traits and nekton full  
2 traits).

3 Sample-trait matrices for each of the four trait datasets were developed using the combined  
4 information of the taxa-sample and taxa-trait matrices. Trait modality values were community  
5 weighted by abundance using the *MaxN* values of each contributing taxon.

## 6 2.6. Statistical analysis

7 The two-factored statistical design of Year (2 levels, 2015 and 2019; fixed factor) and Site (5  
8 levels; random factor) was used to assess for differences in nekton taxa abundances, richness  
9 and assemblages, plus the four different trait datasets (i.e. fish only restricted traits, fish only  
10 full traits, nekton restricted traits and nekton full traits). Univariate total nekton abundance and  
11 richness were analysed using the two-factored statistical design in Permutational Analyses Of  
12 Variance (PERMANOVA) with a Euclidian resemblance matrix to test for differences between  
13 years and sites. Nekton assemblage, a multivariate measure of taxonomic diversity was  
14 transformed using dispersion weighting (by Site), to accommodate for the schooling nature of  
15 certain fish species (Clarke et al. 2006). Multivariate PERMANOVA based on Bray-Curtis  
16 similarities was performed on the same two-factored design, with 9999 permutations to detect  
17 differences at the  $p = <0.05$  level (Anderson 2001). Subsequently, pairwise tests were used to  
18 determine which pairs of levels contributed to significant differences in the overall test results.  
19 Significant spatial differences were visualised using Canonical Analysis of Principal Coordinates  
20 (CAP) based on Bray-Curtis similarities (9999 permutations). The similarity percentage routine  
21 (SIMPER) was used to assesses which taxa were responsible for contributing most to  
22 similarities within and dissimilarities between sites (Clarke et al. 2014).

1 Before multivariate analysis of traits, the redundant traits from each dataset were identified  
2 using Pearson Correlation tests and a correlation threshold of  $R^2 > 0.70$ . Trait redundancy  
3 refers to the correlation of individual or sets of trait modalities (McGill et al. 2006). From each  
4 correlated trait pair, the least ecologically relevant trait was removed from subsequent analysis.  
5 The Pearson Correlation test was repeated following the removal of each trait until correlation  
6 no longer occurred, reducing the number of traits from 25, to 20 and 21 traits in the full trait  
7 sets for the fish only and nekton assemblages, respectfully (Table S3).

8 Spatio-temporal patterns in each trait dataset were evaluated separately. Multivariate  
9 PERMANOVA using the two-factored design of Year and Site were conducted with dispersion  
10 weighting transformed trait data based upon Bray-Curtis similarities. The interaction of Year by  
11 Site was analysed using pairwise tests to determine which site contributed to differences  
12 between years. Where temporal differences were not significant, site data could be combined  
13 across years for spatial analysis. Subsequent pairwise tests were conducted where significant  
14 spatial and temporal differences were detected to determine which pairs of levels contributed  
15 to differences. Spatial and temporal differences were visualised using CAP analysis, and SIMPER  
16 analysis was used to identify the trait modalities contributing most to dissimilarities between  
17 years and sites. All analyses were conducted using PRIMER v7 software (Clarke et al. 2014) and  
18 the add-on module PERMANOVA+ (Anderson 2001)

## 1 3. RESULTS

### 2 3.1. Nekton assemblages in Coffin Bay

3 For all nekton across all years and sites, a total of 1,429 individuals from 39 taxa were recorded,  
4 consisting of teleosts (30 taxa), elasmobranchs (2 taxa), decapod crustaceans (5 crab taxa), and  
5 cephalopods (2 taxa) (Table S4). Several taxa could not be identified to species level due to low  
6 visibility, morphologically similar species (e.g. *Arripis georgianus* and *Arripis truttaceus*), and  
7 taxon that could only be recognised to genus level (e.g. Longsnout clingfish *Parvicrepis* sp 1).  
8 The most abundant taxa were Australian salmon (*Arripis* spp.) (320 individuals), weedy whiting  
9 (*Neoodax balteatus*) (319 individuals), and rough rock crabs (*Nectocarcinus integrifrons*) (157  
10 individuals), representing 53% of total abundance. The most ubiquitous taxa across all samples  
11 consisted of *Nec. integrifrons* (observed in 81.6% of replicates), *Arripis* spp. (56.6% of  
12 replicates) and the spider crab (*Leptomithrax gaimardii*) (61.6% of replicates).

### 13 3.2. Total nekton abundance and richness between sites

14 The total number of nekton taxa was lower in 2015 (27 taxa) compared to 2019 (36 taxa). Of  
15 the 44 taxa, 43.1% (19 taxa) were observed in both years, and those taxa accounted for 93.2%  
16 of total abundance across years. Nekton richness differed between sites (*Pseudo-F* = 3.41, *p* =  
17 0.017) and was driven by the low nekton richness at Kellidie Bay compared to most sites,  
18 except Point Longnose (Fig. 1.A, Table A1). Across all sites, nekton abundance was lower in  
19 2015 (639 individuals) compared to 2019 (790 individuals). However, PERMANOVA results did  
20 not detect significant differences by Year or Site, or an interaction of these factors (*p* = >0.19,  
21 Fig. 1.B, Table S5).

### 1 3.3. Overall spatio-temporal trends in measures of taxonomic and trait diversity

2 Assessment of the nekton assemblages and the fish only trait datasets did not reveal  
3 significant differences between 2015 and 2019 ( $p = >0.07$ , Table A2, Table S5). The nekton  
4 trait datasets, however, were significantly different between years ( $p = <0.048$ , Table A2), and  
5 only from the site Kellidie Bay ( $p = <0.042$ , Table A4). As there were no significant differences  
6 between 2015 and 2019 for the other four sites, they were combined across years to evaluate  
7 spatial patterns only. Significant differences between sites were detected using the nekton  
8 assemblages and the four trait datasets (Table 1).

9 Spatial separation between sites was greater for the nekton assemblage and fish only restricted  
10 trait dataset, with higher dissimilarity values from the latter for all pairwise comparisons  
11 except Mount Dutton versus Port Douglas Mid (Table A3, Fig. S3). The nekton trait datasets  
12 resulted in the least dissimilarity between sites (Table 1, Fig. S3). Across the four trait datasets,  
13 spatial dissimilarities were also generally lower when using the full trait set compared to the  
14 reduced trait set. Consistent spatial differences across years existed between Point Longnose  
15 versus both Mount Dutton and Port Douglas South (Table 1). Conversely, assemblages were  
16 consistently similar between the site pairs Point Longnose versus Port Douglas Mid, and Port  
17 Douglas South versus Mount Dutton.

### 18 3.4. Spatial patterns of nekton assemblages

19 Nekton assemblages combined across years significantly varied by Site ( $Pseudo-F = 3.79$ ,  $p =$   
20  $0.0001$ ) with pairwise dissimilarities between most sites (Table 1, Table A3). Significant spatial  
21 differences were detected from the CAP analysis (trace and delta  $p = 0.0001$ ) but allocation  
22 success was only 58.3%. Also, the split along the primary axis of the ordination plot mainly  
23 separated Point Longnose and Port Douglas Mid from all other sites. Dissimilarity values for the

1 nekton assemblages between sites were relatively high, ranging from 69% (Port Douglas Mid  
2 versus Point Longnose) to 85% (Kellidie Bay versus Point Longnose) (Table A1, Fig. S2).  
3 The distinction of Kellidie Bay to all other sites was driven by greater abundance of southern  
4 eagle rays (*Myliobatis tenuicaudatus*) and the presence of taxa exclusive to that site including  
5 spotted grubfish (*Parapercis ramsayi*) and Australian anchovy (*Engraulis australis*) (Fig. S2,  
6 Table S4). The taxa contributing to similarities between Mount Dutton and Port Douglas South  
7 included *Nec. integrifrons*, *Neo. balteatus* and *L. gaimardii* with the comparatively greater  
8 abundance of *Neo. balteatus* driving differences between other sites (Fig. 2, Fig. S2, Table S6).  
9 Dominant taxa across Port Douglas Mid and Point Longnose included *Nec. integrifrons*, the sand  
10 crab (*Ovalipes australiensis*) and King George whiting (*Sillaginodes punctatus*). Greater  
11 abundances of *S. punctatus*, were contributing most to differences between Port Douglas Mid  
12 and three other sites, excluding Point Longnose. (Fig. 2, Fig. S2, Table S6).

### 13 3.5. Spatio-temporal patterns of traits

14 For the trait differences between sites, pairwise comparisons determined that Kellidie Bay  
15 2015 samples were different from all other sites, except Point Longnose ( $t = 1.31$ ,  $p = 0.1024$ )  
16 and only from using the restricted trait set (Table S8). Similarly, Kellidie Bay in 2019 differed  
17 from all other sites, except Port Douglas South, but did so regardless of trait set ( $p = >0.25$ ,  
18 Table S8). These trends were further visualised by CAP analysis which detected significant  
19 differences between sites across trait datasets (trace  $p=0.001$ , Delta  $p \leq 0.0004$ )(Fig. 3). The  
20 primary and secondary axis generally split trait data from each site in the same manner as the  
21 CAP from the nekton assemblage (Fig. 2B). For the fish only trait datasets, allocation success  
22 ranged from 46.7% to 55.0%, with higher success using the restricted trait set. For the nekton  
23 trait datasets, allocation success was 48.3% for both trait sets (Fig. 3). Similarities within and  
24 between sites generally increased across the traits datasets with the addition of taxa, and traits

1 to a lesser extent (Table 2). Modalities associated with water column position, trophic group,  
2 defence structure, maximum body length, and tail structure explained most of the within site  
3 similarities and differences between sites (Table 2, Fig. 3).

### 4 3.6. Temporal differences in Kellidie Bay

5 Measures of taxonomic diversity did not significantly differ between years ( $p = >0.07$ , Table S5)  
6 and characterised Kellidie Bay as having relatively low taxa richness and abundance across  
7 both years (Fig. 1). Values were slightly higher on average for 2015 ( $14 \pm 17$  individuals,  $4 \pm 3$   
8 taxa) compared to 2019 ( $9 \pm 3$  individuals,  $4 \pm 2$  taxa). Trait differences were only detected from  
9 the nekton assemblages, indicating that the addition of macroinvertebrate trait data  
10 contributed to the significant temporal differences ( $p = <0.042$ , Table A4). Dissimilarity values  
11 of nekton trait diversity were relatively similar between the two years (Fig. 4), while within  
12 year variation was greater in 2015 (35.4%) compared to 2019 (65.6%) (Table 2). The SIMPER  
13 indicated taxa in Kellidie Bay across years were characterised by benthic habits, inferior  
14 mouths and unsociability (Table 2). Temporal differences were associated with increased  
15 abundance in 2019 of modalities including  $L_{\max}$  of  $>10$  cm, the absence of tail structures and  
16 unsociability (Fig. 4). Conversely, modalities that characterised 2015 including  $L_{\max}$  of 10 to 20  
17 cm and superior mouths were not as abundant (Fig. 4).

## 4. DISCUSSION

This study assessed spatio-temporal patterns of nekton assemblages surveyed from an inverse estuary by integrating measures of taxa (i.e. nekton and fish only) and traits (i.e. restricted and full trait sets). Both taxonomic scope and trait selection had some effect of trait analysis and the detection of spatio-temporal differences between the four trait datasets (fish only restricted traits; fish only full traits; nekton restricted traits; nekton full traits). Increasing the taxonomic scope reduced spatial dissimilarities in traits and detected Kellidie Bay as the only site to demonstrate a difference between survey years. The restricted and full traits sets showed similar spatio-temporal patterns within the fish and nekton assemblages.

### 4.1. Spatial patterns across years and the influence of taxonomic scope

In the Coffin Bay estuary, the different bays are characterised by variation in environmental parameters (e.g. flow, water physico-chemical properties and productivity)(Kämpf & Ellis 2015, Ruth & Patten 2018). Therefore, some degree of spatial dissimilarity in taxa and traits within Coffin Bay was expected. As indicated by Mouillot et al. (2007), local conditions exert selective pressure on the traits of estuarine assemblages through abiotic filtering. My findings support this, with dissimilarities in taxa and traits generally occurring in spatially-disconnected sites. Assemblages at the outermost site closest to the mouth of the estuary (Point Longnose) were consistently different to sites located >11 kilometres away in the upper reaches of the estuary (Mount Dutton and Kellidie Bay). Within estuaries, extremes in abiotic and biotic conditions are generally most pronounced with increasing distance from the estuary mouth (Eyre & Balls 1999, Akin et al. 2003). Subsequently, the contrasting selective pressures favour dissimilar taxa and traits adapted for differing conditions. At smaller spatial-scales, traits and taxa of assemblages are more similar due to overlapping selective pressures (Teichert et al. 2017), and

1 in my study assemblage dissimilarity was generally lowest from the comparison of adjacent  
2 sites, e.g. Point Longnose and Port Douglas Mid (<3 km). These results imply some degree of  
3 correlation in the spatial distribution of nektonic taxa and traits, regardless of taxonomic scope  
4 and trait selection.

5 Similar to other inverse estuaries, the taxa richness of Coffin Bay did not decrease linearly with  
6 distance from the estuary mouth (Whitfield et al. 2012). Nekton taxa richness was greater on  
7 average at Port Douglas Mid and Mount Dutton, and lowest at Kellidie Bay. In contrast to  
8 estuaries with significant inflows of freshwater, inverse estuaries support greater taxa richness  
9 due to the settlement of marine stenohaline species in addition to euryhaline species that are  
10 adapted to a range of salinity conditions (Whitfield et al. 2012, Henriques et al. 2017). While  
11 taxa richness of inverse estuaries is generally greater in the lower reaches, taxa distribution is  
12 determined by a combination of abiotic and biotic conditions (e.g. geographical position,  
13 habitat, trophic capacity) (Simier et al. 2004).

14 Dissimilarity values of traits within and between sites were greater when analysed using fish  
15 only compared to the nekton assemblages, indicating that teleosts and elasmobranchs  
16 contributed most to spatial dissimilarities, regardless of trait set. Compared to  
17 macroinvertebrates such as decapods, fish are generally characterised by greater trait diversity  
18 and greater dispersibility (Micheli & Halpern 2005, Henriques et al. 2014). The expression of a  
19 greater range of traits and dispersibility within the sampled fish assemblages likely contributed  
20 to greater spatial dissimilarity seen in my results. In comparison, macroinvertebrates are  
21 comparatively more sedentary and have less dispersal capacity (Henriques et al. 2014). While  
22 macroinvertebrates consisted of only 8 out of 39 taxa from the nekton assemblages, crabs were  
23 ubiquitous and expressed higher trait convergence, contributing to lower assemblage  
24 dissimilarity using the nekton traits. For the nekton trait datasets, modalities including benthic



1 habit, inferior mouth, and unsociability, characterised spatial patterns, and were dissimilar to  
2 the fish only trait datasets. The comparatively lower dispersibility and ecophysiological  
3 limitations of crabs likely promotes greater trait convergence as a response to abiotic and biotic  
4 filtering within the estuary system. (Wiens & Graham 2005). Nevertheless, despite their  
5 ubiquity within estuaries, intertidal crabs are responsive to spatial differences in  
6 environmental conditions (Vermeiren & Sheaves 2014). Subsequently, general spatial patterns  
7 could be detected regardless of taxonomic scope and trait set, but finer differences can be  
8 attributed to the trait differences of the included taxa.

9 With increasing spatial-scale, taxonomically different taxa are more likely to show similar  
10 patterns of spatial distribution (i.e. regional, continental, global) (Reich et al. 1997, Nekola &  
11 White 1999). Abiotic filtering has been demonstrated to drive trait selection in marine  
12 assemblage at large spatial scales enabling analyses using a wide taxonomic scope (Bremner et  
13 al. 2003, Violle et al. 2007). For example, multiple studies have highlighted the poleward shift of  
14 generalist fish and macroinvertebrates as a result of climatic change (e.g. Sunday et al. 2015,  
15 Frainer et al. 2017, McLean et al. 2019). However, at smaller scales, analyses of dissimilar taxa  
16 are more likely to produce contrasting outcomes (Paavola et al. 2006, Wolters et al. 2006). For  
17 instance, Pecuchet et al. (2018) compared marine copepods, demersal fish, and macro-infauna  
18 in the North Sea, concluding that spatial patterns did not correlate across taxa due to a  
19 decoupling of traits between strictly benthic and pelagic assemblages. In comparison, this  
20 present study assessed large, mobile macroinvertebrates and fish at shallow depths in a smaller  
21 study location, reducing the detection of strictly benthic and pelagic assemblages. Different  
22 responses between taxonomic groups can be caused by contrasting community assemblage  
23 processes, resource use and dispersibility, and has been demonstrated from cross-taxa studies  
24 in freshwater and terrestrial settings (e.g. Oertli et al. 2005, Flynn et al. 2009, Aubin et al. 2013).  
25 At relatively small spatial-scales such as the site-to-site comparison in the present study, the

1 separate analysis of taxonomically dissimilar groups will account for any associated deviations  
2 in trait expression and should be considered when designing future monitoring studies of  
3 marine assemblages.

#### 4 4.2. Temporal patterns between survey years

5 Estuaries are typically characterised by abiotic and biotic conditions that vary across a range of  
6 temporal scales (e.g. tides, seasons, years) (Elsdon & Gillanders 2006, Bricker et al. 2008). In  
7 turn, it is not unreasonable to expect such temporal variation to influence the assemblage  
8 composition. However, in the present study, I detected no differences in taxa and traits between  
9 2015 and 2019, except from the nekton trait datasets within one site, at Kellidie Bay. Long-term  
10 monitoring studies have indicated that while some taxa demonstrate seasonal and interannual  
11 variation, at large temporal-scales, estuary assemblages remain relatively consistent (Jackson &  
12 Jones 1999, Desmond et al. 2002). Stability in estuary assemblages can be maintained provided  
13 the absence of irregular disturbances (e.g. floods, eutrophication) (Jackson & Jones 1999, Simier  
14 et al. 2004). Thus, the results in this study would suggest that potentially except for Kellidie  
15 Bay, conditions have remained relatively similar within the austral spring season over a small  
16 temporal scale (i.e. four years). With additional monitoring that incorporates a range of  
17 temporal scale variation (e.g. tides, seasons, years) it would be possible to have a  
18 comprehensive understanding of the small-scale variation of the assemblage of Coffin Bay in  
19 the future.

20 Detected differences between years in traits were isolated to Kellidie Bay which is the  
21 innermost site and is the least influenced by the tidal flushing of shelf water (Kämpf & Ellis  
22 2015). Its relative isolation and geographic position cause the assemblage structure to be  
23 driven by localised ecosystem processes (e.g. salinity, productivity, temperature) (Ruth &  
24 Patten 2018). Temporal differences in Kellidie Bay were only detected using traits of the nekton

1 assemblage, regardless of trait set, indicating the contribution of sampled macroinvertebrates.  
2 Differences were driven by an increased abundance of traits associated with the rock crab *Nec.*  
3 *integrifrons* and smooth pebble crab (*Bellidilia laevis*), such as;  $L_{\max}$  of >10 cm, the absence of  
4 tail structures, unsociability, and the comparative decreased abundance of traits associated  
5 with *L. gaimardii*, a comparatively larger zoobenthivore crab species. These temporal  
6 differences were associated with greater within site similarity of nekton traits in 2019  
7 compared to 2015. An increase in trait similarity would indicate the homogenisation of traits  
8 (Olden & Rooney 2006) and therefore the non-random decline of taxa possessing unique traits  
9 in favour of taxa within similar, more common, winning traits (McKinney & Lockwood 1999,  
10 Wiegmann & Waller 2006). However, the taxa assemblage of Kellidie Bay did not significantly  
11 vary between years, indicating that temporal differences likely reflect natural fluctuations in  
12 taxa from small-scale variation. Regardless, the findings in this study highlighted the detection  
13 of a temporal difference using a broad taxonomic scope, regardless of trait set, even though the  
14 assessment was limited to two sampling occasions (i.e. 2015 and 2019).

#### 15 4.3. The influence of trait selection on trait analysis

16 Both the restricted and full trait sets produced relatively similar spatio-temporal patterns from  
17 the traits of the sampled assemblages. This observation supports the notion that the number of  
18 traits selected for analysis is less important than the traits themselves and their modalities  
19 (Petchey & Gaston 2006, Bremner 2008). To this extent, the trait modalities of maximum body  
20 length, water column position and trophic group were important in distinguishing the main  
21 spatio-temporal patterns across assemblages. The selection of fewer traits caused slightly  
22 greater dissimilarity within the fish only and nekton assemblages respectively, when compared  
23 to the full trait sets (Table 2, Table A1). This pattern was also observed by Bremner et al.  
24 (2006), whereby the subtraction of biomass-weighted traits reduced the similarity of benthic

1 invertebrates. The reduction of traits, however, also represents the loss of ecological  
2 information and capacity to determine finer trait differences. The full trait set identified  
3 additional trait categories that characterised spatio-temporal patterns, including the modalities  
4 of body shape, mouth position, defence structures and gregariousness. In future incorporating  
5 these additional traits into the restricted trait set may develop an optimal set of traits that  
6 provides more ecological information while minimising the resource input required to build a  
7 full trait database. This is particularly pertinent to the establishment of marine monitoring and  
8 assessment programs, such as those implemented globally as performance indicators of Marine  
9 Park Zones (e.g. Claudet et al. 2010, Stuart-Smith et al. 2013, Coleman et al. 2015).

10 While redundant traits were removed as a part of the methodology, individual modalities  
11 demonstrated high correlation, especially in the full trait sets. For example, the modalities of  
12 venomous spines, superior mouth and depressed body shape showed a high level of correlation  
13 from the fish only trait datasets due to shared expression of these attributes in the flatheads  
14 *Playcephalus bassensis* & *Playcephalus speculator* in particular. Greater trait redundancy in the  
15 full trait set could be attributed to its high number of modalities compared to the restricted trait  
16 set (104 versus 21 modalities) increasing the likelihood of redundancy to occur. Trait  
17 redundancy may potentially cause skewed results or numerical noise, if not identified and  
18 removed (McGill et al. 2006). The selection of specific modalities capable of delineating  
19 between species can overcome perceived redundancy between taxa, especially by using trait  
20 combinations over singular traits (e.g. guild or niche groups) (Simberloff 1991, Wilson 1999).  
21 However, generating unique combinations of traits for every taxon results in the correlation of  
22 trait diversity with taxonomic diversity (Naeem & Wright 2003) and the loss of generality in  
23 describing faunal assemblages from a trait perspective. Greater redundancy in trait-based  
24 studies is likely unavoidable due to the interaction of evolutionary and ecological linkages  
25 predisposing taxa to similar combinations of traits (Wiens & Graham 2005, Verberk et al. 2013).

1 However, selecting the right balance by using fewer, ecologically important traits instead of a  
2 full trait set in further studies would be the best means of minimising numerical noise  
3 associated with trait redundancy.

4 Trait-based analysis would appear sensitive to the resolution of modalities and the context to  
5 which they were developed. Trait resolution refers to the degree of detail used in describing the  
6 trait (i.e. the range and the number of modalities) (Da Silva et al. 2019). For example, the trait  
7 motility can be simplified into the modalities: mobile and immobile; or assessed at a greater  
8 resolution (e.g. freely motile, sessile, semi-mobile.). Conducting trait analysis at the maximum  
9 resolution offers the most precise and detailed approach, but is both costly and research-  
10 intensive, and therefore not feasible for most studies (Da Silva et al. 2019). Beyond the  
11 limitation of trait information, the uneven resolution of modalities used to describe the same  
12 trait hinders comparison within and across taxa (Costello et al. 2015). Several studies have  
13 focused on unifying synonymous traits for marine biota by proposing consistent definitions  
14 (e.g. Beauchard et al. 2017, Degen et al. 2018, Lam-Gordillo et al. 2020). Nevertheless, the  
15 absence of standardised modalities and variations in trait resolution will likely pose a  
16 significant challenge for comparative studies and developing trait datasets for years to come.  
17 This challenge is further complicated by the context in which modalities are developed and  
18 their application or lack thereof across a range of taxa, environments and sites. For example,  
19 modalities commonly associated with Australian reef fish (e.g. browsing herbivores, cleaners,  
20 excavators) were initially chosen to assess trophic groups (Stuart-Smith et al. 2013, Stuart-  
21 Smith et al. 2018). However, these reef-specific modalities were not useful for the sampled  
22 assemblage due to comparatively less trophic and habitat (e.g. seagrass, algae, bare soft  
23 sediment) specialisation in Coffin Bay. This trend also conforms to the latitudinal distribution of  
24 fish, with greater niche breadth in temperate biomes compared to the polar and tropic regions  
25 (Sunday et al. 2011) and higher omnivory of fish in inverse estuaries (Henriques et al. 2017).

1 While the influence of trait resolution is outside the scope of the present study, an emphasis on  
2 the selection of well-defined, ecologically-relevant traits across taxa would appear to be the  
3 best route for achieving generality in trait-based ecology based on evidence from this study.  
4 Such an approach would be particularly useful for ongoing monitoring of ecosystem functioning  
5 and bioindicators, such as Marine Park performance programs.

## 6 5. CONCLUSIONS

7 The increasing intensity of anthropogenic and natural pressures as well as the complexity of  
8 marine assemblage responses necessitates the use of integrative monitoring strategies.  
9 Evaluation of trait diversity enables the interpretation of spatio-temporal patterns across  
10 dissimilar taxa, complimenting the assessment of taxonomic diversity. Overall, this study  
11 assessed the potential limitations and advantages of trait-based approaches regarding the  
12 taxonomic scope and trait selection across marine nektonic assemblages. The results suggest  
13 that broadening taxonomic scope across a greater proportion of the nekton assemblage is  
14 useful in establishing a baseline understanding of spatio-temporal patterns. However,  
15 interpretation of small-scale trait variation should rely on a narrow taxonomic scope across a  
16 range of taxa to account for variable responses from dissimilar taxa that cannot be represented  
17 by a whole-of-assemblage or bioindicator approaches. Furthermore, the results indicate that  
18 selecting well-defined, ecologically-informative traits derived from the specific assemblage and  
19 ecosystem of focus offers an efficient strategy for monitoring marine assemblages. I encourage  
20 future research to utilise this initial drill-down approach to isolate useful trait sets and reduce  
21 the resource intensity associated with ongoing ecosystem monitoring while maximising the  
22 practical use of trait-based approaches over the long-term.

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## 1 IV. Tables

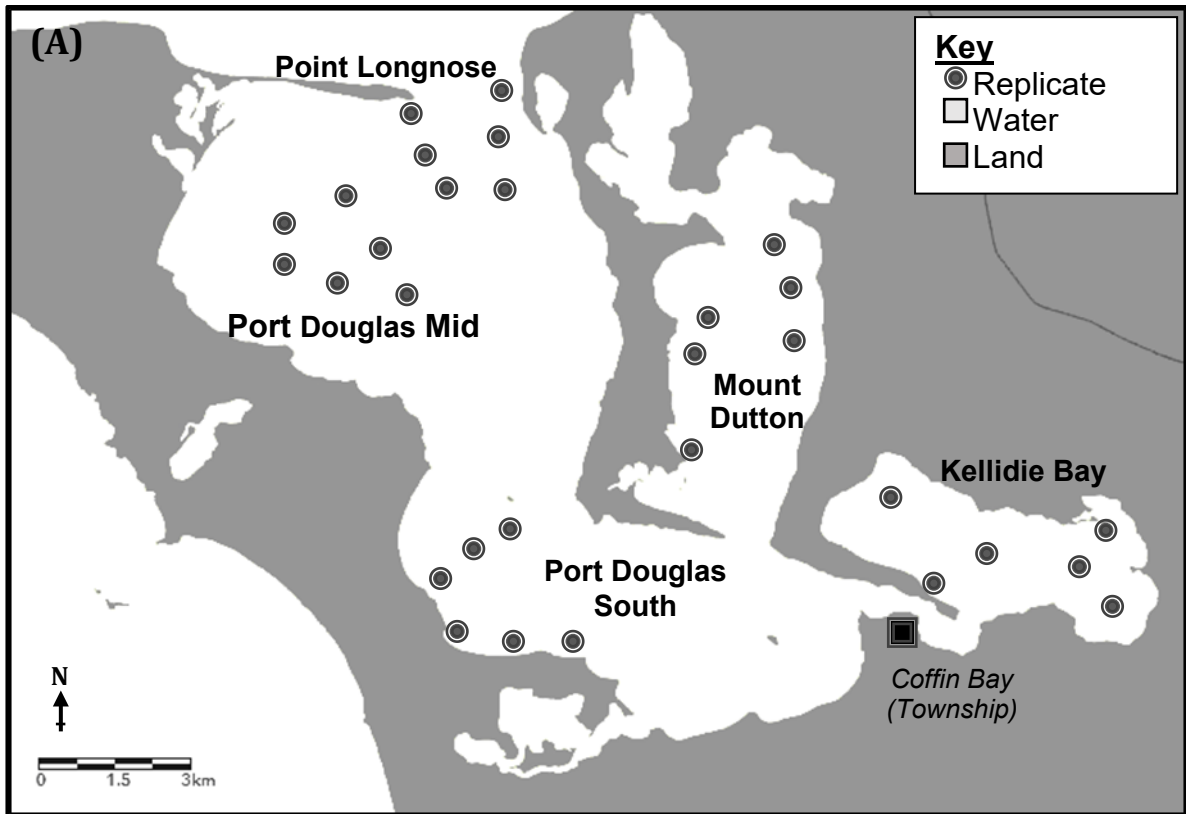
2 Table 1. Pairwise PERMANOVA results from the measures of taxa assemblage (Table A1) and  
 3 traits (Table A3). Kellidie Bay comparisons for nekton assemblage excluded due the significant  
 4 interaction of the factors Year and Site, denoted as (n/a). Sites compared consisted of Kellidie  
 5 Bay (KB), Mount Dutton (MD), Port Douglas South (PDS), Port Douglas Mid (PDM) and Point  
 6 Longnose (PL). Significant pairwise differences denoted \*, \*\*, \*\*\*, \*\*\*\* respectively for  $p$ -values  
 7 <0.05, <0.01, < 0.001, <0.0001.

8 9 10 11 12 13	Sites	<u>Taxa</u>	<u>Traits</u>			
		Nekton assemblage	Fish only		Nekton	
			<i>Restricted</i>	<i>Full</i>	<i>Restricted</i>	<i>Full</i>
	KB & MD	***	***	**	n/a	n/a
	KB & PDS	*	*	*	n/a	n/a
	KB & PDM	****	****	***	n/a	n/a
	KB & PL	****	***	*	n/a	n/a
	MD & PDS	-	-	-	-	-
	MD & PDM	**	*	-	-	-
	MD & PL	****	**	**	**	****
	PDS & PDM	***	**	*	*	-
	PDS & PL	***	**	*	**	**
	PDM & PL	-	-	-	-	-

1 Table 2. Summary of within site SIMPER results for the factor Site across years, except the  
 2 results from the nekton trait datasets due to an interaction of Year and Site for Kellidie Bay.  
 3 Numbers in red show the % similarity within site, while the black numbers indicate the number  
 4 of modalities contributing to 75% of similarity. The listed modalities represent the 5 modalities  
 5 that contributed to the largest similarities within sites or were in the top 75% of contributors.

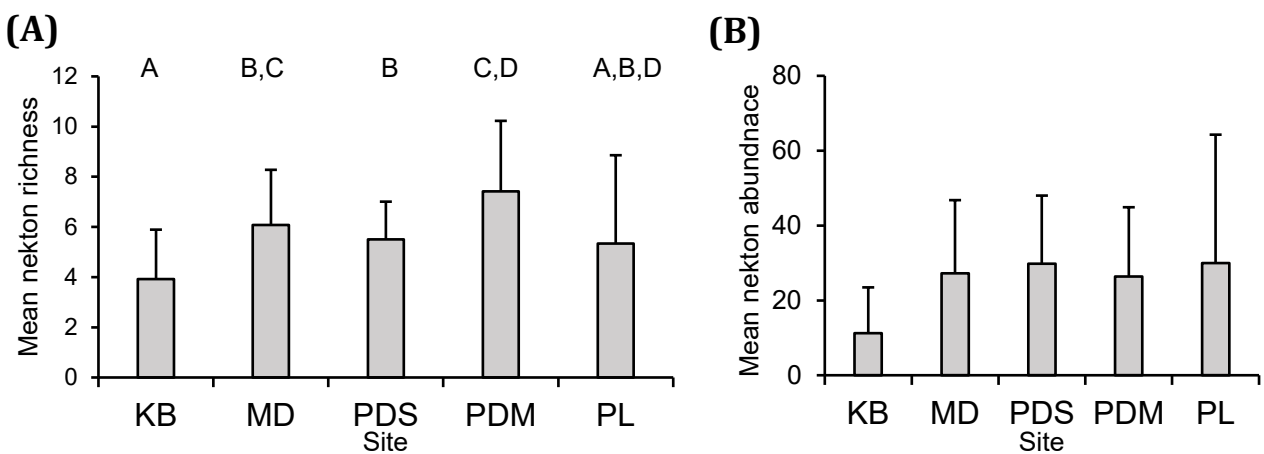
<b>Sites:</b>	<b>Fish only assemblage</b>				<b>Nekton assemblage</b>			
	<i>Restricted traits</i>		<i>Full traits</i>		<i>Restricted traits</i>		<i>Full traits</i>	
<i>Mount Dutton</i>	35.0%	4	38.5%	23	48.3%	5	50%	26
	Zoobenthivore		Zoobenthivore		Benthic		Inferior mouth	
	L <sub>max</sub> 10 to 20		DepthM 20 to 30		Zoobenthivore		Benthic	
	Demersal		Non-targeted		Omnivore-herbivore		Exoskeleton	
	L <sub>max</sub> 70 to 80		L <sub>max</sub> 10 to 20 cm		L <sub>max</sub> 10 to 20 cm		Marine	
			Subtropical		L <sub>max</sub> <10 cm		Zoobenthivore	
<i>Port Douglas South</i>	23.3%	5	30.7%	25	43%	5	49%	29
	L <sub>max</sub> 10 to 20 cm		Fusiform		Benthic		Inferior mouth	
	Macrocarivore		Subtropical		L <sub>max</sub> 10 to 20 cm		Marine	
	Zoobenthivore		Brackish		Zoobenthivore		Benthic	
	Demersal		Temperate		Omnivore-herbivore		Exoskeleton	
	L <sub>max</sub> 50 to 60 cm		Oviparous		L <sub>max</sub> <10 cm		Bony carapaces	
<i>Port Douglas Mid</i>	41.1%	4	44.39%	22	52%	5	55%	26
	L <sub>max</sub> 70 to 80 cm		L <sub>max</sub> 70 to 80 cm		Benthic		Benthic	
	Benthic		Superior mouth		Zoobenthivore		Inferior mouth	
	L <sub>max</sub> 80 to 90 cm		Venomous spines		L <sub>max</sub> 70 to 80 cm		unsociable	
	Zoobenthivore		Depressed		L <sub>max</sub> <10 cm		Exoskeleton	
			Unsociable		Omnivore-herbivore		Bony carapaces	
<i>Point Longnose</i>	22.6%	2	27.90%	12	46.4%	4	52%	18
	Benthic		Venomous spines		Benthic		Unsociable	
	L <sub>max</sub> 80 to 90 cm		Depressed		L <sub>max</sub> 10 to 20 cm		Benthic	
			Truncated		L <sub>max</sub> <10 cm		Inferior mouth	
			Superior mouth		Zoobenthivore		Bony carapaces	
							Tail absent	
<i>Kellidie Bay</i>	18.4%	4	22.7%	20				
	L <sub>max</sub> 100< cm		Ovoviviparous					
	L <sub>max</sub> 10 to 20 cm		Tail - bare					
	Macrocarivore		Venomous spines					
	Zoobenthivore		Depressed					
			Inferior mouth					
<i>Kellidie Bay 2015</i>					36%	3	35%	20
					Benthic		Inferior mouth	
					L <sub>max</sub> 10 to 20 cm		Benthic	
					Zoobenthivore		DepthM 50<	
							L <sub>max</sub> 10 to 20 cm	
							Exoskeleton	
<i>Kellidie Bay 2019</i>					65%	3	66.2%	14
					L <sub>max</sub> <10 cm		Inferior mouth	
					Benthic		unsociable	
					Omnivore-herbivore		Bony carapaces	
							Tail absent	
							L <sub>max</sub> <10 cm	

1 V. Figures

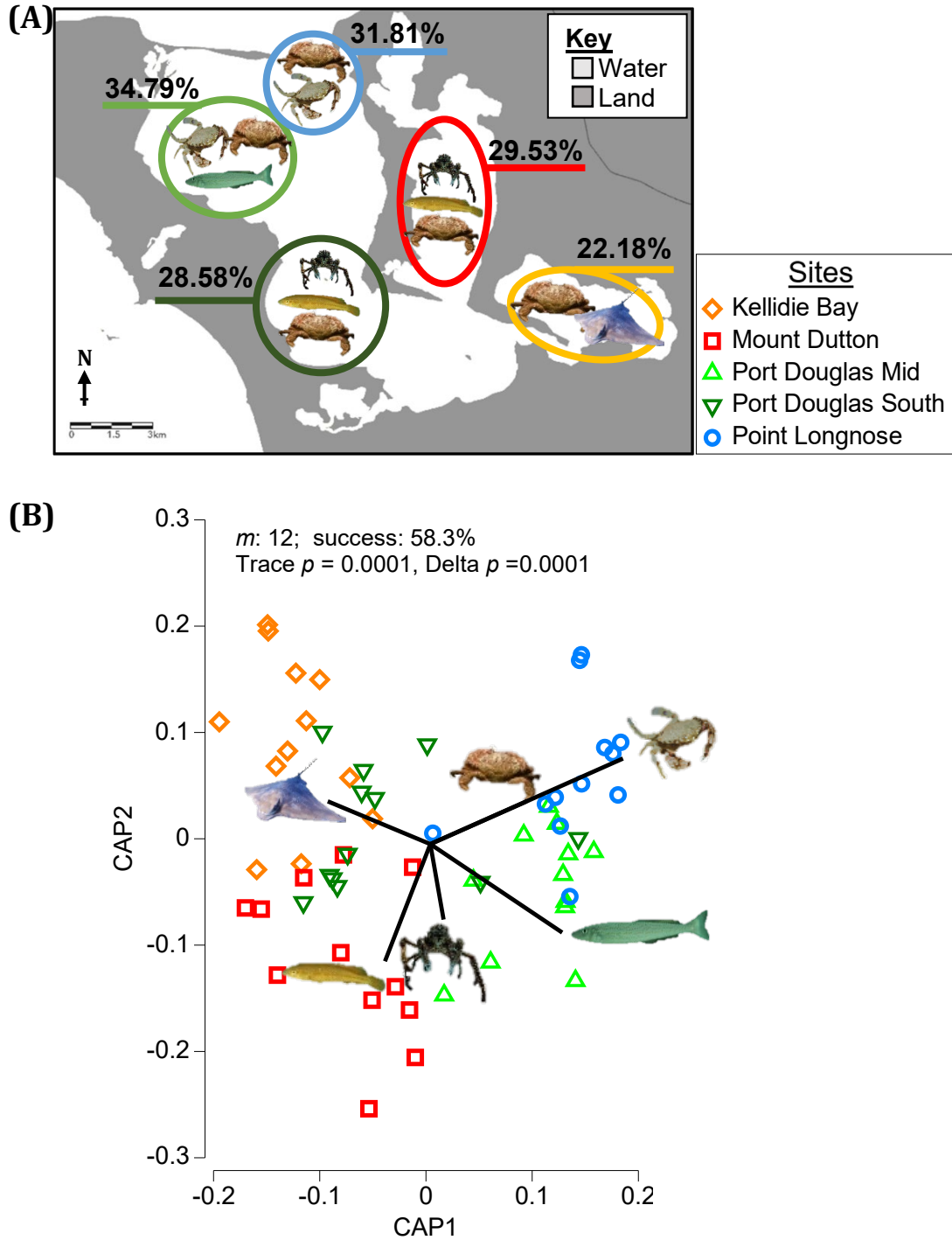


2 Fig. 1. Location of sample replicates with reference to the five sites surveyed using baited  
 3 remote underwater video stations in 2015 and 2019 within the Coffin Bay estuary, South  
 4 Australia.

5  
6  
7

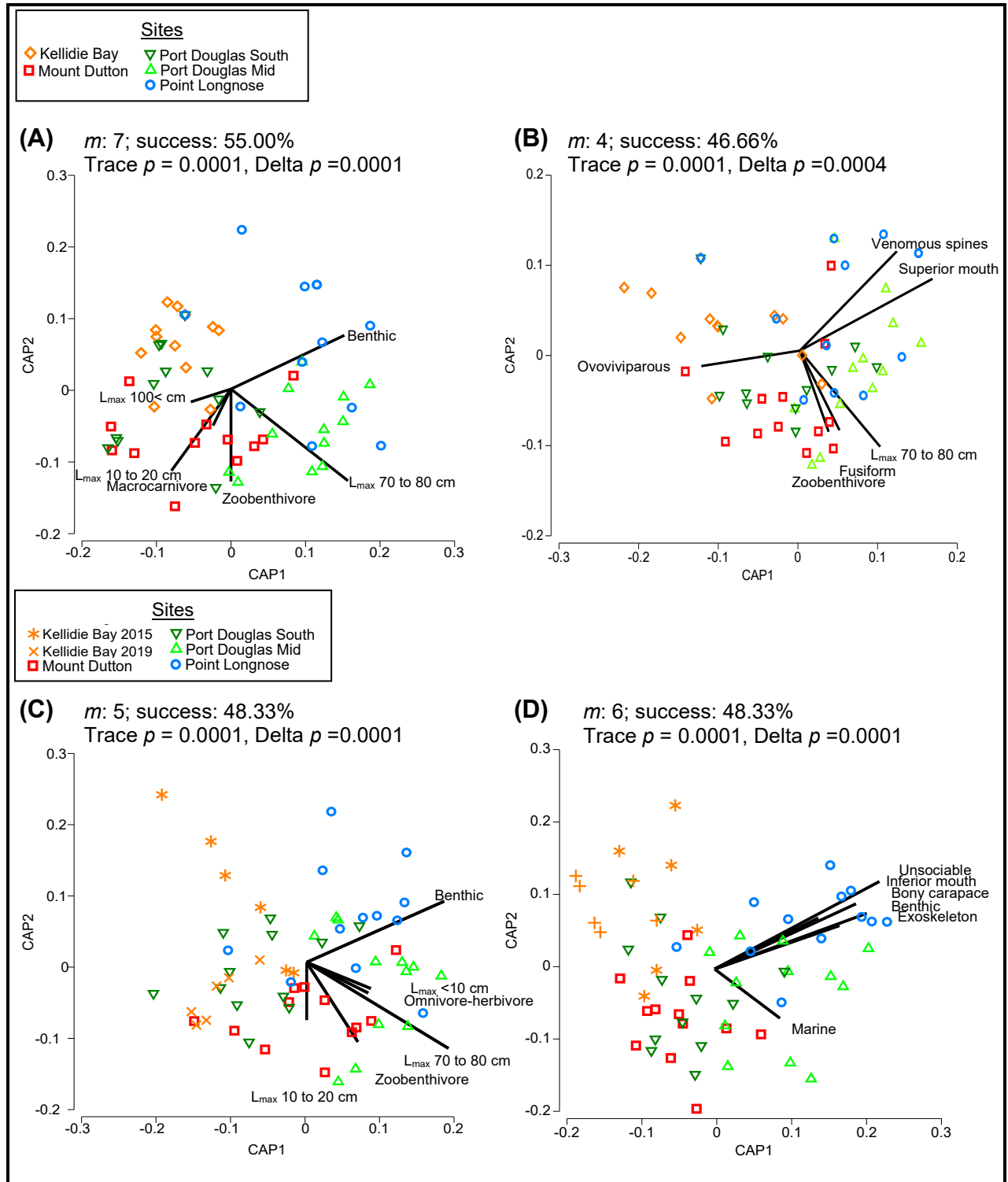


8 Fig. 1. Mean (A) nekton richness (+SD) and (B) abundance (+SD), by the factor Site across 2015  
 9 and 2019. Pairwise similarities ( $p > 0.05$ ) denoted by letter pairings, no significant differences  
 10 were detected between sites for nekton abundance. Sites consisted of Kellidie Bay (KB), Mount  
 11 Dutton (MD), Port Douglas South (PDS), Port Douglas Mid (PDM), and Point Longnose (PL).



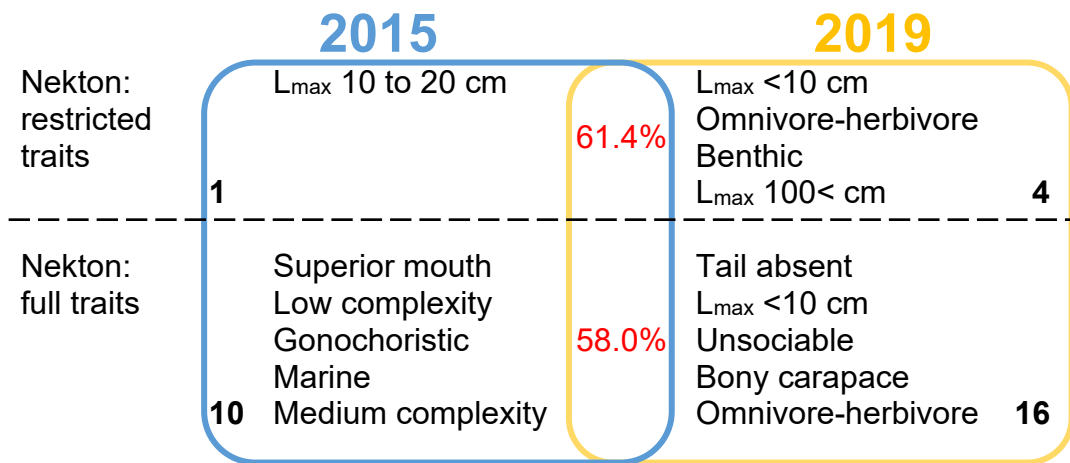
1 Fig. 2. Taxa pictograms (Table S4) represent the taxa that contributed most to the average site  
 2 similarity as identified from SIMPER analysis (Table S6). **(A)** a map of Coffin Bay with the values  
 3 indicating average similarity within each site. **(B)** Constrained-ordination plot (CAP) showing  
 4 the first two PCO axes for the factor site.  $m$ = number of axes used, significant values for the tests  
 5 also shown. The length and angle vectors of the overlays represent the strength and direction of  
 6 correlations of the taxa that contributed most to similarity.

1



2 Fig. 3. Constrained-ordination plot (CAP) showing the first two PCO axes for the factor Site, of  
 3 fish only (A) restricted trait dataset, and (B) full trait dataset; and nekton (C) restricted trait  
 4 dataset, and (D) full trait dataset.  $m$ = number of axes used, significant values for the tests also  
 5 shown. Kellidie Bay 2015 and 2019 results shown for nekton trait datasets due to interaction of  
 6 Year and Site. The length and angle vectors of the overlays represent the strength and direction  
 7 of correlations of the modalities that contributed most to similarity within groups according to  
 8 SIMPER analysis (Table 2).





1

2 Fig. 4. Venn diagram displaying SIMPER results for the interaction of Year and Site for Kellidie  
 3 Bay using the nekton trait datasets. Numbers within the overlapping area in red show the %  
 4 dissimilarity between years, while the black numbers indicate the number of traits with a  
 5 higher average abundance at the respective year. The listed modalities represent the top five  
 6 contributors to the largest dissimilarities between years or were in the top 75% of contributors.  
 7 They are ordered with the top modality having highest % contribution to the dissimilarity  
 8 between years. Kellidie Bay was the only site to show significant differences between years, and  
 9 fish assemblage trait data was excluded as a significant interaction was not detected (see Table  
 10 A2).

## VI. Appendices

Table A1. Pairwise PERMANOVA results for nekton richness and nekton assemblage between sites, dissimilarity values from SIMPER also shown for the latter measure. Nekton abundance not shown as significant differences by the factor Site not detected. Sites consisted of Kellidie Bay (KB), Mount Dutton (MD), Port Douglas South (PDS), Port Douglas Mid (PDM) and Point Longnose (PL). **Bold values ( $p = <0.05$ ).**

Perms:	<b>Nekton richness</b>		<b>Nekton assemblage</b>		
	9921-9949		9921-9949		
<b>Groups</b>	<i>t</i>	<i>p</i> -value	<i>t</i>	<i>p</i> -value	Dissimilarity (%)
KB & MD	2.57	<b>0.0167</b>	1.86	<b>0.0007</b>	79.7
KB & PDS	2.14	<b>0.0484</b>	1.43	<b>0.0358</b>	77.0
KB & PDM	4.16	<b>0.0006</b>	2.43	<b>0.0001</b>	77.0
KB & PL	1.18	0.2600	2.36	<b>0.0001</b>	85.3
MD & PDS	0.78	0.4475	1.32	0.0959	73.3
MD & PDM	1.58	0.1284	1.75	<b>0.0044</b>	73.0
MD & PL	0.62	0.5470	2.44	<b>0.0001</b>	82.6
PDS & PDM	2.57	<b>0.0190</b>	1.99	<b>0.0009</b>	76.5
PDS & PL	0.15	0.9049	2.09	<b>0.0005</b>	79.8
PDM & PL	1.73	0.1008	1.35	0.1105	69.0

Table A2. PERMANOVA results from the trait data for each of the trait datasets. **Bold values ( $p = <0.05$ ).**

<b>Trait dataset</b>	<b>Source</b>	<b>df</b>	<b>MS</b>	<b>Pseudo-F</b>	<b><i>p</i>-value</b>	
<i>Fish only restricted traits</i>	Year	1	1761.3	0.80	0.5825	
	Site	4	6484.6	3.90	<b>0.0001</b>	
	Perms: 5329-9912.	Year x Site	4	2210.6	1.33	0.1485
	Residuals	50	1662.5			
	Total	59				
<i>Fish only full traits</i>	Year	1	1734.7	0.71	0.6390	
	Site	4	6094.7	2.81	<b>0.0002</b>	
	Perms: 5321-9907	Year x Site	4	2460.2	1.14	0.2968
	Residuals	50	2167.6			
	Total	59				
<i>Nekton restricted traits</i>	Year	1	2757.5	1.36	0.2876	
	Site	4	4067.5	3.37	<b>0.0001</b>	
	Perms: 5300-9906.	Year x Site	4	2024.0	1.69	<b>0.0334</b>
	Residuals	50	1200.7			
	Total	59				
<i>Nekton full traits</i>	Year	1	1522.0	0.75	0.5731	
	Site	4	4686.1	3.65	<b>0.0001</b>	
	Perms: 5295-9905	Year x Site	4	2035.8	1.58	<b>0.0475</b>
	Residuals	50	1284.9			
	Total	59				

Table A3. Pairwise PERMANOVA results of trait composition from each of the trait datasets for the factor site, as well as dissimilarity values from SIMPER. Sites compared consisted of Kellidie Bay (KB), Mount Dutton (MD), Port Douglas South (PDS), Port Douglas Mid (PDM) and Point Longnose (PL). Kellidie Bay comparisons for nekton assemblage excluded due to differences within year and site. **Bold values ( $p = <0.05$ ).**

<b>Fish only trait datasets</b>						
Permutations:	<i>Restricted traits</i>			<i>Full traits</i>		
	9930-9957			9938-9950		
<b>Groups</b>	<i>t</i>	<i>p-value</i>	<i>Dissimilarity (%)</i>	<i>t</i>	<i>p-value</i>	<i>Dissimilarity (%)</i>
KB & MD	2.35	<b>0.0007</b>	81.1	1.9172	<b>0.0044</b>	76.5
KB & PDM	3.02	<b>0.0001</b>	84.8	2.2692	<b>0.0004</b>	77.0
KB & PDS	1.82	<b>0.0130</b>	84.7	1.7446	<b>0.0144</b>	80.5
KB & PL	2.08	<b>0.0005</b>	88.1	1.6645	<b>0.0148</b>	81.4
MD & PDM	1.75	<b>0.0127</b>	67.8	1.4031	0.0890	61.3
MD & PDS	1.33	0.1289	75.3	1.0825	0.2907	66.7
MD & PL	2.07	<b>0.0033</b>	83.2	1.8145	<b>0.0083</b>	75.3
PDM & PDS	2.10	<b>0.0011</b>	78.6	1.6749	<b>0.0156</b>	68.0
PDM & PL	1.29	0.1496	70.2	1.2116	0.1814	65.5
PDS & PL	1.81	<b>0.0074</b>	86.9	1.6435	<b>0.0240</b>	78.3

<b>Nekton trait datasets</b>						
Permutations:	<i>Restricted traits</i>			<i>Full traits</i>		
	9930-9957			9938-9950		
<b>Groups</b>	<i>t</i>	<i>p-value</i>	<i>Dissimilarity (%)</i>	<i>t</i>	<i>p-value</i>	<i>Dissimilarity (%)</i>
MD & PDM	1.41	0.0791	52.7	1.44	0.0711	51.0
MD & PDS	1.02	0.3841	54.8	0.85	0.5885	50.9
MD & PL	1.98	<b>0.0026</b>	59.3	2.35	<b>0.0001</b>	59.2
PDM & PDS	1.76	<b>0.0170</b>	57.9	1.46	0.0798	51.3
PDM & PL	1.24	0.1800	52.0	1.35	0.1140	48.1
PDS & PL	1.84	<b>0.0084</b>	60.9	2.18	<b>0.0018</b>	57.7

Table A4. Results of pairwise PERMANOVA results for the interaction of the factors year and site showing comparison between years using the four trait datasets. **Bold values ( $p = <0.05$ ).**

	<b>Nekton trait datasets</b>				<b>Fish only trait datasets</b>			
	<i>Restricted traits</i>		<i>Full traits</i>		<i>Restricted traits</i>		<i>Full traits</i>	
	461-462		462		336-462		336-462	
<b>Site</b>	<i>t</i>	<i>p-value</i>	<i>t</i>	<i>p-value</i>	<i>t</i>	<i>p-value</i>	<i>t</i>	<i>p-value</i>
Kellidie Bay	1.91	<b>0.0203</b>	1.58	<b>0.0416</b>	1.48	0.0531	1.12	0.2489
Mount Dutton	1.26	0.1679	1.12	0.2353	0.82	0.6681	0.58	0.9270
Port Douglas South	1.47	0.1393	1.19	0.2410	1.17	0.2630	1.06	0.3388
Port Douglas Mid	0.95	0.4606	1.13	0.2745	1.12	0.2718	1.25	0.1833
Point Longnose	1.00	0.3704	0.99	0.3822	1.07	0.3306	1.06	0.3152

## VII. Author Guidelines

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- meet ethics guidelines (i.e. institutional, national and international guidelines concerning the use of animals in research, sampling of endangered species, and ethics in publication). All conflicts of interest must be declared.

If the manuscript was previously submitted to a publication outlet, this must be disclosed and a rationale for its current submission provided. It is the expectation that such submissions incorporate any previous recommendations and address any reviewer concerns prior to submission to any Inter-Research (IR) journal. Submissions of manuscripts that have been archived as preprint (defined as the manuscript version initially submitted to a publication outlet for review, i.e. not yet peer-reviewed) in an online depository are allowed (see <http://www.int-res.com/journals/open-access/> for details) but such deposits must be disclosed in the cover letter upon submission. Take note of any restrictions in the license agreement of the preprint archive that may affect or limit your desired IR publication model (e.g. by depositing a manuscript in a preprint archive you may be required to publish it with Open Access). Permission to re-use any previously published material must have been obtained by the authors from the copyright holders. Submitting a manuscript implies agreement to IR terms of publication related to [Open Access](#), [copyright](#) and manuscript processing. Please submit your manuscript using the **online manuscript submission system** (click on the appropriate journal):

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In the unlikely event that you have problems, please email the submission to the **editorial office** of the journal (click on the appropriate journal):

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The submission must contain 2 separate files:

- a cover letter (see 'Cover Letter' tab for details)
- the manuscript, which must:
  - be correctly formatted to match journal style (see 'Manuscript' tab for details)
  - be in one file (it includes all text, with tables, figures and their captions at the end)
  - include page numbers and line numbers throughout (restart line numbering on each page; do not use 'continuous' line numbering)
  - be smaller than 5 MB (for accepted manuscripts, higher-resolution figures can be provided later)

**Appendices:** supporting material not longer than 2 printed pages may be published at the end of the main article. Figures, tables and equations should be numbered A1, A2, A3, etc. Longer materials or those not suitable for printing may be published as electronic supplements (see below).

**Electronic supplements:** material unsuitable for inclusion within the article (overlong tables, mathematical derivations, video clips, computer code, etc.) may be published on the Inter-Research website as an electronic supplement (linked to the article and abstract page). This material will not be copyedited, typeset, or checked for accuracy; responsibility for its content and presentation rests with the author(s). Figures, tables and equations should be numbered S1, S2, S3, etc.; if references are used, the supplement must contain its own complete Literature Cited section.

## Manuscript Structure

### 1. Manuscript length and structure

The target lengths for the different manuscript types (Research Article, Note, Review, Comment, Reply Comment and Opinion Piece) are listed in 'Author guidelines'.

Manuscripts should be structured as follows:

- Title page (title, author list, author affiliations, corresponding author email, running page head, abstract, key words)
- Main text (see below)
- Acknowledgements
- Literature cited
- Tables (with legends)
- Figures (with legends)
- Appendices (length: up to 2 printed pages; longer materials should be submitted as online supplementary materials in a separate file)

Main text:

- **Research Articles** and **Notes** should follow the IMRAD format (Introduction, Materials & Methods, Results, Discussion and an optional Conclusions section). Note that separate Results and Discussion sections are strongly preferred, but exceptions are possible if the manuscript's content warrants a combined Results & Discussion section.
- **Reviews, Comments, Reply Comments** and **Opinion Pieces** may deviate from the IMRAD format as necessary.

### 2. Title page

**Title:** The title should be concise and informative, i.e. summarizing either the subject or the most important findings of the study rather than merely the hypothesis addressed. It should have around 100 characters (ca. 15 words), and 150 characters at most (including spaces). Avoid 'A', 'An', 'The', 'On', etc. at the beginning. Avoid questions in the title.

Provide a **running page head** with 3 to 6 words; e.g. 'Detection of shrimp WSSV'.

**Authors and addresses:** If a manuscript has several authors from different institutions:

- use superscript numerals for identification;
- provide the address of each author's institution, identifying any present address(es) if applicable. Include zip or postal code but not street address or box number;
- use an asterisk (\*) to refer to a footnote that identifies the single corresponding author and provide her/his e-mail.

**Abstract:** Limit length to 250 words. Provide concise information on your work, its significance and its principal results. Avoid literature cites, series of data, or meaningless clauses such as 'the results are discussed'.

**Key words:** Supply 3 to 8 key words, listed in order of importance.

### 3. Text

Please number all pages and restart line numbering on each page (important: do not use 'continuous' line numbering), 12 point font, double spacing and numbered sections. Manuscripts that do not use correct English grammar, spelling and punctuation will be returned to authors without review; if you are not a native English speaker, you should have the text edited by someone who is, before submitting your manuscript. You may also wish to consult a 'How to' book such as Day & Gastel (2011; How to write and publish a scientific paper, 7th edn. Greenwood Press, Santa Barbara, CA).

**Section headings:** Main sections (IMRAD) should be numbered '1. INTRODUCTION', '2. MATERIALS & METHODS', etc. Subsections should be numbered as e.g. '2.1. Study site', '2.2. Sample collection', etc. Avoid going beyond third-level subsections (e.g. 3.1.1.).

**Verbosity:** Please eliminate verbiage; example:

- Verbose – 'The speed was chosen because past studies by Miller (1995) and Smith (1998) have shown this to be slightly greater than the maximum sustained swimming speed.'
- Not verbose – 'The speed is slightly greater than the maximum sustained swimming speed (Miller 1995, Smith 1998).'
- Verbose – 'It has been shown that boat noise affects whale behaviour (Smith 1994).'
- Not verbose – 'Boat noise influences whale behaviour (Smith 1994).'

**Genus and species names** must be in italics; write the genus name in full at first mention in each section (Abstract, Introduction, Materials and Methods, Results, Discussion) and abbreviate whenever mentioned again in the same section. When referring to a species, do not use the genus name alone, unless you have previously defined it that way; be precise when using 'sp.' (singular) and 'spp.' (plural).

At first mention in a section – 'The filter feeding of blue mussels *Mytilus edulis* was examined'.

After first mention in a section – 'Filter feeding rates of *M. edulis* increased with increasing temperature.' **Abbreviations:** Define abbreviations and acronyms in the Abstract and at first mention in the main text, and thereafter use only the abbreviation / acronym.

**Equations and units:** Use standard SI units. Relations or concentrations (e.g. mg per l) must be given as 'mg l<sup>-1</sup>' (not mg/l). Variables are usually italicised (except for Greek letters). Italicisation should be consistent in normal, superscript and subscripted text. Example of proper spacing: 'p < 0.05, r<sup>2</sup> = 0.879' (not 'p<0.05, r<sup>2</sup>=0.879'); but: 'we studied organisms of size <0.5 μm'

**Figures and tables:** Figures, tables, and their captions should be self-explanatory; e.g. abbreviations and acronyms must be defined here. For table footnotes, use superscripted lower case letters; asterisks can be used to indicate statistical significance (must be defined in the legend). Please consult '[Figures](#)' for details on figure preparation.

**Sequence data:** Full sequence information is required when molecular methods are used. The sequences of novel primers must be given. Novel nucleotide or protein sequences must be deposited in the GenBank, EMBL or DDBJ databases and an accession number obtained.

**Conservation Evidence:** If your study is testing for an intervention, please check the existing evidence for your intervention at [www.conservationevidence.com](http://www.conservationevidence.com). State whether or not relevant evidence is available there, and if so, briefly summarise it in your Introduction. Otherwise, search for individual studies testing the action, and summarise any relevant evidence. If Conservation Evidence does not yet cover the topic and no individual studies exist, please state this; you may briefly reference other relevant literature, but this is not essential.

**Ocean acidification data reporting:** When presenting methods and results reporting ocean acidification the '[Guide to best practices for ocean acidification research and data reporting](#)' must be followed. Specifics for reporting ocean acidification data in scientific journals are outlined in [Annex 1 of the 2015 addendum](#).

### 4. Acknowledgement section

Declare all sources of funding of the study. In addition, you may wish to acknowledge any assistance you received from anyone not listed as author. Include this section before your Literature Cited.

### 5. References

All references cited in the text must be listed in the Literature Cited section, and all listed literature must appear in the text, using Harvard (Name-Year) referencing style. Citing references as 'in press' implies that the article has been accepted for publication; if pagination information is not available yet, the DOI should be included in the citation in the Literature Cited section. Unpublished results and submitted articles should be cited as: author's name unpub. data (e.g. N. Smith unpubl. data) in the text only.

**a. Within the text**

2 authors: use '&' between last names

3 or more authors: use the first author's last name followed by 'et al.' (not italicized and not separated by a comma)

If the same first author published multiple papers in the same year and the within-text citations would look identical, distinguish these citations with a lower case letter (a, b, c, etc.) after the year.

Multiple citations within a single bracket: separate cites with a comma (not a semi-colon). Sort multiple cites chronologically from oldest to newest and if several cites are from the same year, sort them alphabetically.

Examples:

(Smith & Miller 1965, Ahmed 1968, Miller et al. 2000a)

(Burns 2000, Miller et al. 2000a,b, Quinn 2000, Barni in press)

**b. Literature Cited section**

Format required for citing literature (examples):

**Periodicals:** Use standard abbreviations according to 'BIOSIS Serial Sources' or use the style for your selected journal in a reference managing software. A list of over 30000 journal names and BIOSIS abbreviations can be found [here](#). In addition, Endnote users may download styles for IR journals in this [zip file](#) for import into reference managing software.

- Dempster T, Holmer M (2009) Introductory editorial. *Aquacult Environ Interact* 1:1-5

**Books:** Write the title of the book in lower case, and give the publisher and place of publication. In the case of book series, give the series editor as well. Example:

- Hanski I (2005) The shrinking world: ecological consequences of habitat loss. In: Kinne O (ed) *Excellence in ecology*, Book 14. International Ecology Institute, Oldendorf/Luhe

**Papers from books, conference reports, symposium proceedings, etc.:** Give the title of the chapter, the editor(s) and title of the volume, the publisher and place of the publisher (not the location where the conference was held), and the pages of the chapter. The date cited must be the year of publication (not the year in which the conference was held). Example:

- West TL, Amrose WG (1992) Abiotic and biotic effects on population dynamics of oligohaline benthic invertebrates. In: Colombo G, Ferrari I, Ceccherelli VU, Rossi R (eds) *Marine eutrophication and population dynamics*. Proc 25th Eur Mar Biol Symp. Olsen & Olsen, Fredensburg, p 189-194

**Dissertations:** Write the title in lower case, the type of thesis / dissertation (e.g. MS / MSc / PhD), and give the university and its location. Example:

- Eve TM (2001) *Chemistry and chemical ecology of Indo-Pacific gorgonians*. PhD dissertation, University of California, San Diego, CA

**Websites:** Permanent databases such as FishBase, GenBank, or climatological sources may be included in the Literature Cited list; the access date must be given. URLs for printed publications also available online may be included with their citations.

Example:

- Froese F, Pauly D (2009) FishBase. [www.fishbase.org](http://www.fishbase.org) (accessed 13 Jan 2013)  
Other website references should only be cited in the body text.

**6. Final checklist**

Please cross-check your manuscript using this list. Consult recent IR publications as a general guide for formatting:

- Include page numbers and line numbers (restart on each page)
- Ensure that abbreviations are defined at first mention in the abstract, main manuscript Included text and figure/table legends, and that the legends are informative
- Use periods instead of commas as decimal signs
- Correctly present your statistical results (e.g. include two sets of degrees of freedom for ANOVA results and significance/p-values of regressions)
- Cite all of the references in the text and vice versa
- Correctly label your figure axes with a title and a unit where applicable
- Create legible figures: i.e. large enough font size (at least 10 pt) with sufficient resolution for pdf viewing
- Prepare the manuscript (text, figures and tables) as a single file