



Temporal stability in a protected and isolated fish community within marine parks surrounding Lord Howe Island



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ABSTRACT

Remote oceanic islands often display high levels of biodiversity and endemism, making them important locations for marine parks aimed at conserving biodiversity. To determine whether marine parks are reaching conservation objectives requires consistent assessments of their effectiveness through time. Lord Howe Island and Balls Pyramid are World Heritage listed remote oceanic islands in the Tasman Sea that support a diverse assemblage of fishes including many endemic and protected species. To conserve the region's unique marine biodiversity, state and Commonwealth marine parks including no-take zones and partially protected zones open to line fishing were established. After approximately 5, 9 and 13 years of protection of shelf habitat we tested for changes in the marine park's fish assemblage across management zones through time using baited remote underwater video systems (BRUVs). We detected no difference in total fish abundance, diversity, or assemblage composition between management zone types. The relative abundance of targeted carangids, yellowtail kingfish and silver trevally were 2 and 1.6 times greater in no-take zones than partially protected zones respectively, however, the substantial variation in their abundances among locations and sites meant that these differences were not statistically significant. No clear difference in the relative abundance of endemic, near-endemic and protected species were observed between management zone types. Generally, the abundance and diversity of fishes varied most among locations, sites and sampling years. The overall lack of difference in the fish assemblage between management zone types and its stability through time suggests current anthropogenic threats are relatively minor, and the marine park's condition is reasonably healthy. Future surveys of the marine park's fish assemblage will be valuable to test for body-size differences between zone types and to monitor trends in condition, particularly in response to possible changes in the number, frequency and intensity of anthropogenic threats.

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1. Introduction

Remote oceanic islands represent areas of global biological significance as they often support disproportionate levels of biodiversity, including many endemic species (Allen, 2008; Edgar et al., 2004; Roberts et al., 2002). Biodiversity associated with small remote oceanic islands is also more susceptible to stochastic natural disturbances and anthropogenic threats as species often have restricted ranges and low abundances making them more vulnerable to impacts (Kier et al., 2009). Consequently, it is critical that remote oceanic islands receive appropriate conservation management to ensure adequate protection of their unique

biodiversity and maintenance of ecosystem function (Edgar et al., 2010, 2008).

Marine parks have become an important tool to manage anthropogenic threats to biodiversity (Gell and Roberts, 2003; Halpern, 2003) and may be particularly useful in protecting areas of global biological significance, such as remote oceanic islands. 'No-take' marine reserves, where all forms of fishing and development are prohibited and the less restrictive 'partially protected areas', are commonly used to protect vulnerable habitats and local biodiversity (Kelaher et al., 2014). To determine whether this management tool meets conservation objectives often requires ongoing monitoring involving spatial and/or temporal comparisons among marine park zones (Gerber et al., 2005; Pomeroy et al., 2005). Ideally, assessments of marine park effectiveness should include a comparison before and after the establishment

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of the marine park. However, in the absence of this information monitoring marine parks through time is essential to build a contemporary ecological baseline to assess any future change related to marine park zoning (Glasby, 1997; Kelaher et al., 2014). Given the vulnerability of marine biodiversity associated with remote oceanic islands, long-term monitoring data of these systems are incredibly valuable, providing evidence to inform policy makers and managers regarding management practices.

Lord Howe Island and the nearby Balls Pyramid are remote oceanic islands with unique biodiversity and natural history (Edgar et al., 2010; Roberts et al., 2002). The islands are located 600 km east of Port Macquarie, NSW, Australia, at a latitude of 31°50'S in the Tasman Sea. They are geographically positioned on the Tasman Front; the oceanographic boundary between tropical and temperate water masses (Nilsson and Cresswell, 1980). As a result, the region has a unique composition of tropical, subtropical and temperate marine biota, including the southernmost coral reef co-existing with abundant and diverse temperate macro-algal communities (Edgar et al., 2010; Linklater et al., 2019). Owing to the islands isolation, the region also supports relatively high levels of endemism among algae, fishes and marine invertebrates (Allender and Kraft, 1983; Baird et al., 2017; Edgar et al., 2010; Hobbs et al., 2009; Kraft, 2000; Krug et al., 2018; Nimbs et al., 2020; Ponder et al., 2000). In acknowledgement of these biological attributes, the Lord Howe Island Group received UNESCO World Heritage listing in 1982 (Environment Australia, 2000).

To protect and conserve Lord Howe Island's marine biodiversity, the NSW government proclaimed the Lord Howe Island Marine Park (LHIMP) in 1999 encompassing state waters (<3 nm from land) (Marine Estate Management Act 2014; Jordan et al., 2016) and in 2000 the Lord Howe Island Marine Park (Commonwealth waters) was proclaimed by the federal government in the adjacent Commonwealth waters (3–12 nm) (National Parks and Wildlife Conservation Act 1975). In 2013, the Commonwealth Lord Howe Marine Park (LHMP) was proclaimed (Environment Protection and Biodiversity Conservation Act 1999), which extended the area protected in Commonwealth waters by about 20 times. To manage human activities on shelf habitats, multiple marine park management zones were established in the state and Commonwealth waters. These included sanctuary zones in the LHIMP and national park zones in the LHMP, which are no-take zones (IUCN Protected Area Category II) that prohibit extractive activities. Both marine parks also include various partially protected areas (IUCN Protected Area Category IV) where some forms of fishing are permitted. In the LHIMP, the partially protected 'habitat protection zones' allow charter boat operations and recreational line fishing but no spearfishing or any form of commercial fishing (Kelaher et al., 2014). In the LHMP, the 'recreational use zone' allows recreational fishing but no charter fishing, commercial fishing or spearfishing. In contrast, the LHMP's habitat protection zones do allow these fishing methods along with some methods of commercial fishing under authorisation (details available at: <https://parksaustralia.gov.au/marine/parks/temperate-east/lord-howe/>). An exception is the habitat protection zone (Lord Howe) of the LHMP, which also prohibits spearfishing. Enforcement of zoning regulations first came into effect in the state and Commonwealth waters in 2004 and 2002, respectively.

The LHIMP and LHMP comprises a rich assemblage of fishes, with more than 490 species documented in its waters, most of which inhabit shallow inshore areas (Allen and Paxton, 1974; Allen et al., 1976; Davis et al., 2018; Francis, 1991; Francis, 1993; Francis and Randall, 1993; Parker, 1993). Most species are tropical with broad ranges, however, total biomass of fishes is heavily skewed towards temperate species (Edgar et al., 2010) and approximately 4% of the inshore fishes are endemic to the Lord

Howe Island and Norfolk Island region (Allen et al., 1976). One study has examined the effectiveness of the LHIMP management zones in safeguarding the region's fish assemblage but focussed on shallow-water inshore habitats only two years after the parks' establishment (Edgar et al., 2010). With the exception of Rees et al. (2018b), which examined LHIMP and LHMP zoning on the abundance of the carangid, *Seriola lalandi*, no research has evaluated long-term zoning effects on fish assemblages occupying the extensive shelf habitat (20–50 m) of Lord Howe Island and Balls Pyramid. Therefore, the effect of the LHIMP and LHMP zoning and general changes in the whole demersal fish assemblage through time in this habitat type remains unknown. This is despite the shelf habitat being the most extensive habitat type protected in state waters of the LHIMP.

This study aimed to assess changes in the spatial and temporal patterns of demersal fish assemblages in no-take zones (NTZs) and partially protected areas (PPAs) on shelf habitat in the LHIMP and LHMP. Our study surveyed fish assemblages after approximately 5, 9 and 13 years of the marine parks' establishment. We tested the general null hypotheses that there would be: 1) no difference in species composition and abundance between NTZs and PPAs; and 2) that any differences in the abundance and diversity of fish in NTZs compared with PPAs would be consistent through time. We were also interested in temporal trends in the abundance of key fished and endemic species, as they may indicate whether these species are being adequately conserved or whether any additional management actions may be required. Another key objective of the study was to provide a contemporary baseline for fish assemblages on shelf habitats in the Lord Howe Island region from which future changes can be quantified.

2. Methods

2.1. Study region and fish assemblage

Sampling was carried out in the NSW Lord Howe Island Marine Park (LHIMP: within 3 nm of land) and the adjacent Commonwealth Lord Howe Marine Park (LHMP: >3 nm from land) (Fig. 1). The LHIMP and LHMP fish assemblage comprises species of special importance, such as *Coris bulbifrons* and *Epinephelus daemeli*, which are listed as 'vulnerable' and 'near threatened' on the IUCN red list, respectively (Choat and Pollard, 2010; Pollard and Sadovy, 2018). Under the NSW Fisheries Management Act 1994, three species of fish; *E. daemeli*, *Chaetodontoplus ballinae* and *Girella cyanea* are protected. Several species from the fish assemblage are targeted by recreational fishers and charter boat fishing operations. The predominant target species are *Seriola lalandi* and *Pseudocaranx dentex*, which are caught and sold locally by charter boat operators to restaurants on the island (effectively the sole providers of fresh fish to the island's local and tourist population) (Figueira and Hunt, 2012). To a lesser extent fishers target *Lethrinus* spp., *G. cyanea* and *C. bulbifrons* as well as seasonal pelagic fishes. Fishing activity is likely to result in by-catch of certain species; most notably *Carcharhinus galapagensis* that often deplete hooked catch (Robbins et al., 2011). No commercial fishing is allowed in the state waters of the LHIMP. Some commercial fishing is permitted in the Habitat Protection Zones of the LHMP, however, the target species are predominantly highly mobile pelagic fishes (e.g. tuna) as part of the Eastern Tuna and Billfish Fishery and the Southern Bluefin Tuna fishery. The Southern and Eastern Scalefish and Shark Fishery is not permitted to operate within 25 nautical miles of Lord Howe Island and Balls Pyramid (AFMA, 2018).

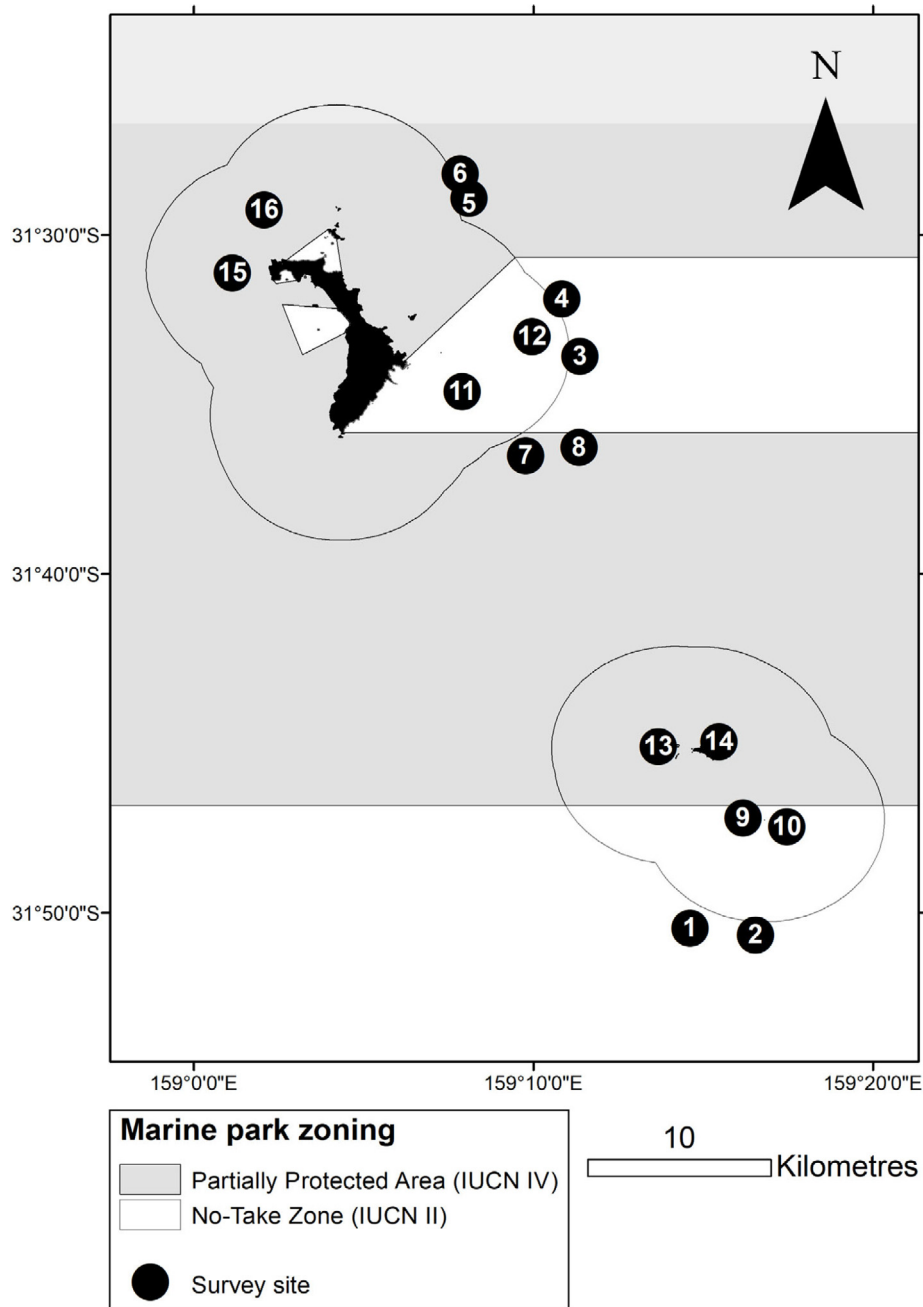


Fig. 1. A map of survey sites (black circles) in the state Lord Howe Island Marine Park (LHIMP: <3 nautical miles of land) and the Commonwealth Lord Howe Island Marine Park (LHMP: >3 nautical miles from land). The Lord Howe Island shelf is in the north and the Balls Pyramid shelf to the south. The 3 nautical mile line is displayed around Lord Howe Island and Balls Pyramid. Regions in white represent no-take zones (NTZs) while regions in grey, partially protected areas (PPAs).

2.2. Survey design and data collection

Fish assemblages were surveyed using baited remote underwater video systems (BRUVs). Each BRUV contained a Canon HG21 video camera within an underwater camera housing constructed by SeaGIS Pty (www.seagis.com.au). Sixteen sites were sampled on the Lord Howe Island and Balls Pyramid shelves comprising coral reef, relict reef, rubble and rock habitat between the depth of 25 and 50 m (Linklater et al., 2019). Eight sites were in the LHIMP and eight sites in the LHMP, with an even sampling effort between NTZs and PPAs (n = 8 per zone). At each site, 4 BRUVs were deployed at least 150 m apart for a minimum of 35 min to ensure a 30 min sample. Previous studies have indicated that a 30 min deployment provides a representative sample

of fish assemblages at this latitude (Harasti et al., 2015). Each site was sampled in 2009, 2013 and 2017. Sampling occurred between the 10th to 19th of November in 2009, the 22nd to 30th April in 2013 and the 19th of October to 18th of December in 2017. For the 2009 sampling, bait consisted of 1 kg of crushed pilchards (*Sardinops sagax*); a highly effective bait (Wraith et al., 2013). Due to a limited supply of bait, the same kilogramme of bait was re-used for up to 4 BRUV deployments. In 2013 and 2017, bait consisted of a fresh 500 g of crushed pilchards for each BRUV deployment.

Footage from each BRUV was analysed in the laboratory using EventMeasure software (www.seagis.com.au). For each deployment, species richness and relative abundance (MaxN) was recorded. Species richness was the number of species of fish observed during the each BRUV deployment. The relative abundance

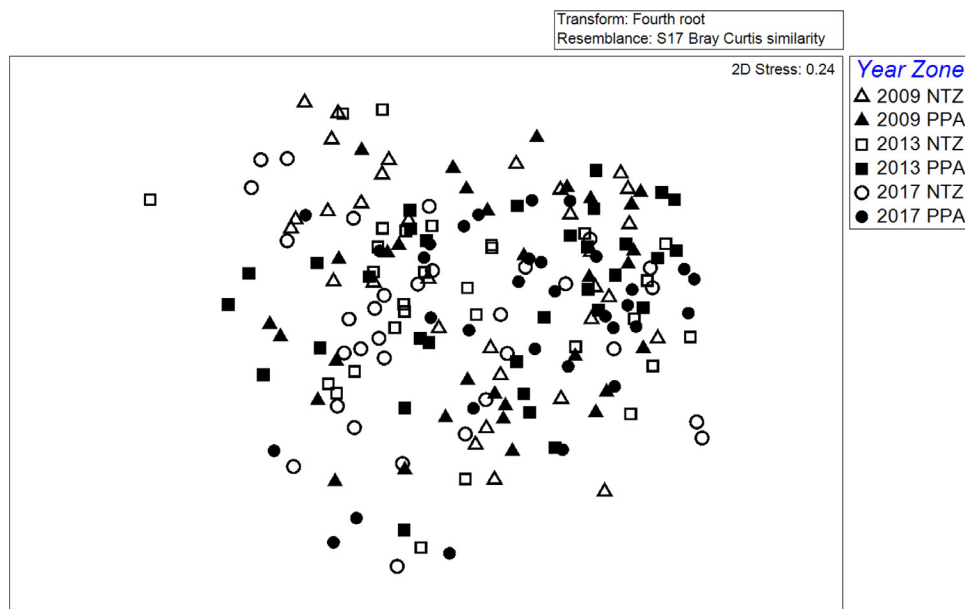


Fig. 2. Non-metric multidimensional scaling (nMDS) ordination of Lord Howe Island fish assemblage. Points closer together in ordination space represent sites with more similar species compositions.

of fishes, MaxN, was the maximum number individuals of one species viewed at any one time during the sample (Parker and DeMartini, 1995). MaxN values for individual species were then summed to generate total relative abundance, Total MaxN, for each sample.

2.3. Statistical analysis

Multivariate and univariate PERMANOVA analyses (Anderson, 2001; Clarke, 1993) were carried out with the PRIMER-E v7 package using type III sums of squares with 9999 permutations. Multivariate differences in fish assemblages between management zones were tested using a 4 factor PERMANOVA on Bray–Curtis dissimilarity values calculated from fourth root transformed data. The factors were year (3 levels and random), zone (2 levels and fixed; NTZ and PPA), location (4 levels nested within zone and random) and site (2 levels nested within location and random). Non-metric multidimensional scaling (nMDS) was used to generate two-dimensional ordinations to visualise variation in the fish assemblage. Univariate analyses to examine differences in Total MaxN, species richness and the abundance of key species were tested using 4 factor PERMANOVA's with the factors as previously described for the multivariate analyses. All univariate analyses were completed using Euclidian distance of raw data to create similarity matrices.

Key species examined included those that were common, fished or caught as by-catch by fishers and endemic, near endemic or protected fishes under the NSW Fisheries Management Act 1994. Common species were those recorded on >50% of deployments across all years (*Chaetodontoplus conspicillatus*, *Coris picta*, *Pseudolabrus luculentus*, *Sufflamen fraenatum* and *Thamnaconus analis*). Fished species were *Lethrinus nebulosus*, *Pseudocaranx dentex* and *Seriola lalandi* (Figueira and Hunt, 2012). Galapagos whaler sharks: *Carcharhinus galapagensis* were also included in this category as they are often caught as by-catch and usually released alive by charter fishing operators (Figueira and Hunt, 2012). Endemic and near endemic species included *Amphichaetodon howensis*, *Genicanthus semicinctus*, *Scorpaena cardinalis* and *Coris bulbifrons*. A number of endemic, near endemic and protected species displayed patchy distributions with low abundances making robust statistical analyses difficult. For these

Table 1

Results of a permutational multivariate analysis of variance (PERMANOVA) comparing demersal fish assemblages between zones using Bray–Curtis similarity measures following fourth root transformations. Factors were: Year (Ye, random with 3 levels: 2009, 2013 and 2017), Zone (Zo, fixed with 2 levels: NTZ and PPA), Location (Lo, random with 4 levels nested in zone) and Site (Si, random with 2 levels nested in location). Values in bold indicate statistical significance at $\alpha = 0.05$.

Source	df	SS	MS	Pseudo-F	P(perm)
Ye	2	11 401	5 701	2.33	0.006
Zo	1	7 697	7 697	0.70	0.845
Lo(Zo)	6	69 903	11 651	2.18	< 0.001
YexZo	2	866	2 933	1.20	0.282
Si(Lo(Zo))	8	30 834	3 854	1.86	0.001
YexLo(Zo)	12	29 371	2 448	1.18	0.156
YexSi(Lo(Zo))	16	33 217	2 076	1.21	0.050
Res	141	241 260	1 711		
Total	188	429 410			

species; *Chaetodon tricinctus*, *Chaetodontoplus ballinae*, *Epinephelus daemeli* and *Girella cyanea*, patterns between management zones were described. Post hoc pairwise comparisons were made on terms of interest in the model that were statistically significant in the main PERMANOVA analysis. Monte Carlo random draws were used to obtain correct P-values where sufficient permutations (<50) were not available in pair wise analyses (Anderson et al., 2008). Following PERMANOVA, post-hoc pooling of lower order terms was performed if $P > 0.25$, to increase the power of the main tests (Underwood, 1997). Plots were created using the “ggplot2” package (Wickham, 2016) in R statistical computing language (R Core Team, 2020).

3. Results

In total 10,050 individuals from 134 species were recorded from BRUV deployments in 2009, 2013 and 2017. No differences were detected in fish assemblages between NTZs and PPAs (Fig. 2, Table 1). The major difference in the fish assemblage was among locations followed by sampling times and sites (Fig. 2, Table 1). Similarly, there was no difference in total relative abundance of fishes nor species richness between NTZs and PPAs. However, there were strong differences in total relative abundance and

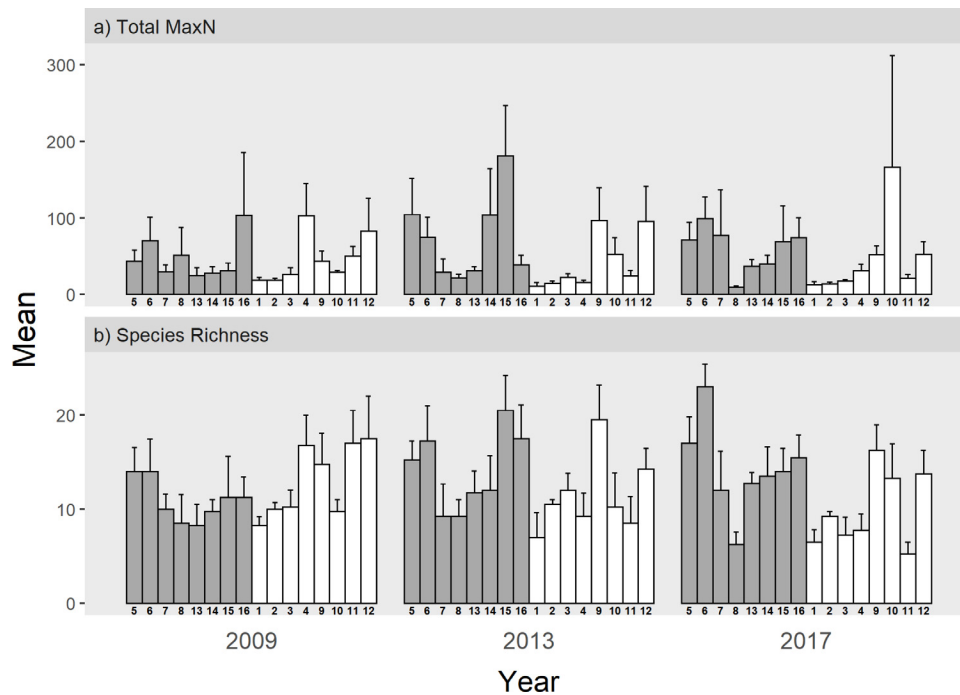


Fig. 3. Mean (\pm SE) total relative abundance and species richness between zones in 2009, 2013 and 2017 ($n = 4$). Shaded bars represent partially protected areas (PPAs) and clear bars represent no-take zones (NTZs).

Table 2

Results of a PERMANOVA comparing (a) total MaxN and (b) species richness between zones using Euclidian distance. Factors were as listed in Table 3.1. Values in bold indicate statistical significance at $\alpha = 0.05$. Data stemming from pooling procedures outlined in Underwood (1997) referred to 'Pooled'.

Source	df	SS	MS	Pseudo-F	P(perm)	Source	df	SS	MS	Pseudo-F	P(perm)
(a) Total MaxN						(b) Species richness					
Ye	2	3352	1 676	0.43	0.674	Ye	2	22	11	0.25	0.776
Zo	1	11 110	11 110	0.89	0.521	Zo	1	125	125	0.44	0.822
Lo(Zo)	6	80059	13 343	2.69	0.021	Lo(Zo)	6	1220	203	2.27	0.005
YexZo	2	7104.6	3 552	0.90	0.430	YexZo	2	365	182	4.23	0.059
Si(Lo(Zo))	8	28 084	3 511	0.53	0.824	Si(Lo(Zo))	8	472	59	2.09	0.042
YexLo(Zo)	12	47 094	3 925	0.59	0.821	YexLo(Zo)	12	518	43	1.53	0.115
YexSi(Lo(Zo))	16	105 710	6 607	1.31	0.181	Pooled	157	4426	28		
Res	141	711 100	5 043			Total	188	7158			
Total	188	993 790									

species richness among locations (Fig. 3a, b; Table 2a, b). Generally, the locations including site 15 and 16, and site 9 and 10 had the greatest total relative abundance through time. The highest species richness was generally recorded at sites 5, 6, 9, 12, 15 and 16 across the three sampling years.

The abundance of common species: *Chaetodontoplus conspicillatus*, *Coris picta* and *Pseudolabrus luculentus* were not influenced by zone type (Fig. 4a, b, c; Table 3a, b, c). In general, abundances were highly variable among years at the site level. The abundance of *Sufflamen fraenatum* and *Thamnaconus analis* differed among years but was dependent on zoning. In NTZs, the abundance of *S. fraenatum* was greater in 2013 compared to 2009 and 2017. In contrast, the abundance of *S. fraenatum* in PPAs was lower in 2009 compared to 2013 and 2017 (Fig. 4d, Table 3d). The abundance of *T. analis* was greater in 2009 compared to 2013 and 2017 inside NTZs, while in PPAs their abundance was greater in 2017 compared to 2013 (Fig. 4e, Table 3e).

The abundance of fished species: *Lethrinus nebulosus*, *Pseudocaranx dentex*, *Seriola lalandi* and by-catch species: *Carcharhinus galapagensis* did not differ between NTZs and PPAs (Fig. 5, Table 4). For the abundance of *C. galapagensis*, strong differences among locations and sampling times were observed. *C. galapagensis* were significantly more abundant in 2017 than in 2013 or 2009 (Fig. 5a; Table 4a). The abundance of *L. nebulosus* differed

among sites and sampling times (Fig. 5b, Table 4b) with no clear pattern being obvious. Clear differences in the abundance of carangids; *P. dentex* and *S. lalandi* was observed among locations and sites (Fig. 5c, d; Table 4c, d). Although not statistically significant, there was a 1.6 times greater number of *P. dentex* in NTZs compared to PPAs. This difference was due to three NTZ sites (9, 10 and 11) consistently recording higher abundances of *P. dentex* (Fig. 5c). Similarly, there was 2 times more *S. lalandi* individuals recorded in NTZs compared to PPAs, primarily driven by high abundances at site 9 and 10 across each sampling time (Fig. 5d).

The abundance of endemic or near endemic species: *Amphichaetodon howensis* and *Genicanthus semicinctus* did not differ between management zones (Fig. 6a, b; Table 5a, b). The abundance of *A. howensis* was highly variable through space and time while the abundance of *G. semicinctus* differed strongly among locations. Generally, higher abundances of *G. semicinctus* were observed at sites 5, 6, 9 and 12. No individuals of *G. semicinctus* were observed at site 1, 2 and 8 across all sampling times. The endemic *Coris bulbifrons* differed among years but only in PPAs, where in 2017 and 2013 there was a greater abundance compared to 2009 (Fig. 6c; Table 5c). There was a trend for more *C. bulbifrons* in NTZs than PPAs in 2009, however this was not statistically significant. Clear differences in the abundance of *C. bulbifrons* were observed

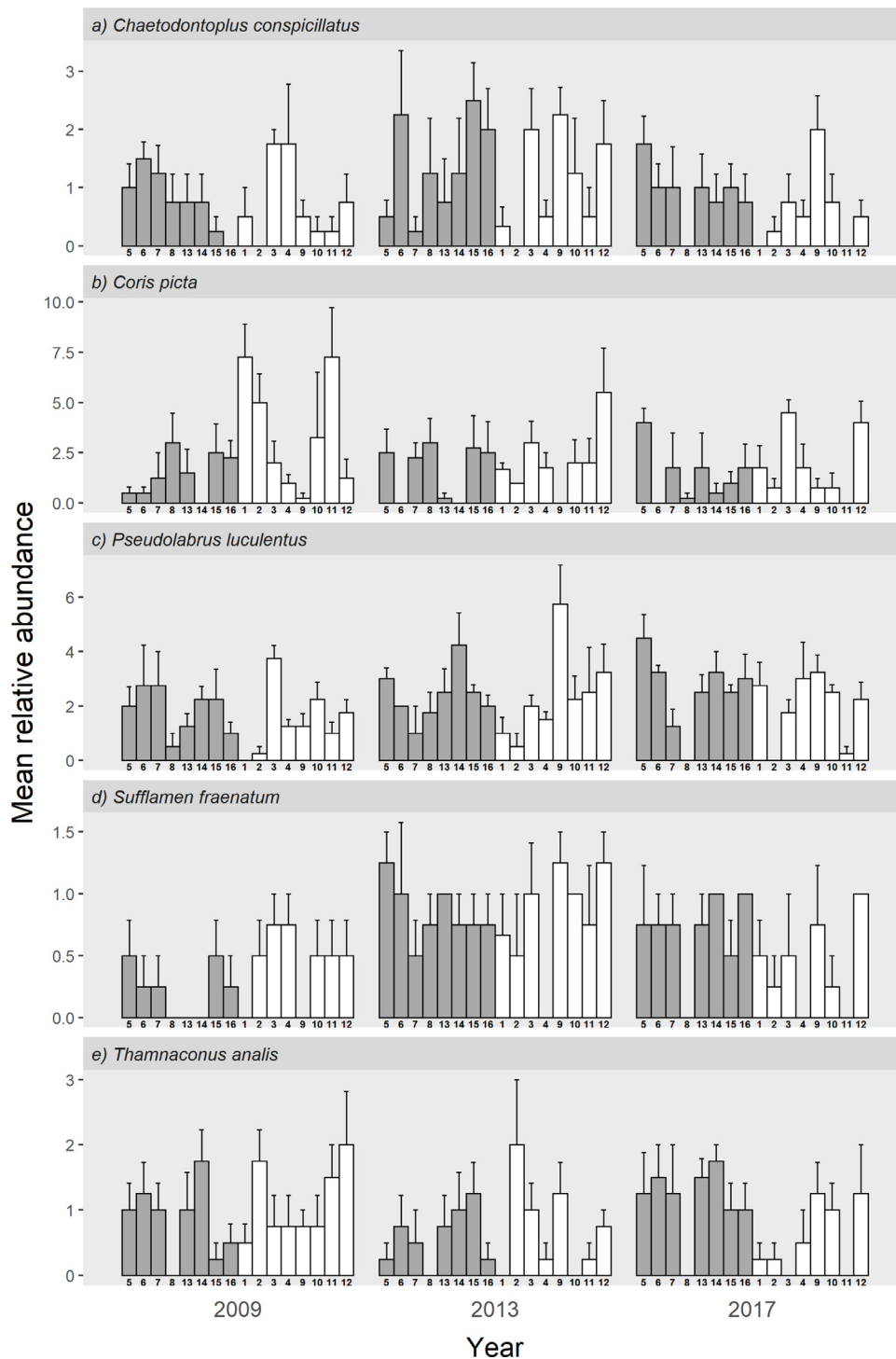


Fig. 4. Mean (\pm SE) relative abundance of common species; (a) *Chaetodontoplus conspicillatus*, (b) *Coris picta*, (c) *Pseudolabrus luculentus*, (d) *Sufflamen fraenatum* and (e) *Thamnaconus analis* between zones in 2009, 2013 and 2017 ($n = 4$). Shaded bars represent partially protected areas (PPAs) and clear bars represent no-take zones (NTZs).

among locations, with generally higher abundances recorded at site 16 while no individuals were recorded at sites 1, 2, and 8 throughout the study. Similarly, there was a significant difference in the abundance of *Scorpaena cardinalis* among years but only in PPAs, with a greater abundance observed in 2009 compared to 2013 and 2017 (Fig. 6d, Table 5d).

Other endemic, near endemic and protected species displayed low abundances and patchy distributions among replicates, sites,

locations and zones. The abundance of *Chaetodon tricinctus* appears to be stable between years as individuals were observed at 5 sites in 2009, 6 sites in 2013 and 9 sites in 2017 (Fig. 7a). *Chaetodontoplus ballinae*, exhibited a distinct pattern in their spatial distribution. With the exception of one individual observed at site 10 in 2017, all other recordings were at one location (site 1 and 2) across all survey years (Fig. 7b). The number of individuals of the protected *E. daemelii* varied among sampling years, with 10 individuals observed in 2009 compared to 6 individuals in

Table 3

Results of a PERMANOVA comparing the abundance of common species; (a) *Chaetodontoplus conspicillatus*, (b) *Coris picta*, (c) *Pseudolabrus luculentus*, (d) *Sufflamen fraenatum* and (e) *Thamnaconus analis* between zones using Euclidian distance. Factors are the same as those listed in Table 3.1. Values in bold indicate statistical significance at $\alpha = 0.05$. Data stemming from pooling procedures outlined in Underwood (1997) referred to 'Pooled'.

Source	df	SS	MS	Pseudo-F	P(perm)	Source	df	SS	MS	Pseudo-F	P(perm)
(a) <i>C. conspicillatus</i>						(b) <i>C. picta</i>					
Ye	2	8.6	4.3	1.95	0.189	Ye	2	23.3	11.7	1.01	0.395
Zo	1	2.1	2.1	1.20	0.377	Zo	1	41.7	41.7	1.89	0.226
Lo(Zo)	6	20.1	3.4	1.20	0.082	Lo(Zo)	6	94.2	15.7	1.25	0.329
YexZo	2	0.6	0.3	0.13	0.880	YexZo	2	24.9	12.5	1.08	0.372
Si(Lo(Zo))	8	12.1	1.5	1.37	0.217	Si(Lo(Zo))	8	78.1	9.8	0.91	0.492
YexLo(Zo)	12	26.5	2.2	1.99	0.027	YexLo(Zo)	12	138.2	11.5	1.07	0.441
Pooled	157	173.9	1.1			YexSi(Lo(Zo))	16	172.8	10.8	1.99	0.018
Total	188	244.7				Res	141	764.7	5.4		
						Total	188	1346.9			
(c) <i>P. luculentus</i>						(d) <i>S. fraenatum</i>					
Ye	2	18.8	9.4	2.20	0.154	Ye	2	7.8	3.9	13.24	0.000
Zo	1	5.2	5.2	0.58	0.713	Zo	1	0.0	0.0	0.24	0.564
Lo(Zo)	6	91.6	15.3	2.14	0.052	Lo(Zo)	6	2.6	0.4	0.96	0.506
YexZo	2	2.3	1.1	0.27	0.765	YexZo	2	2.0	1.0	3.38	0.035
Si(Lo(Zo))	8	37.9	4.7	1.18	0.372	Si(Lo(Zo))	8	3.6	0.5	1.54	0.148
YexLo(Zo)	12	51.4	4.3	1.06	0.427	Pooled	169	50.0	0.5		
YexSi(Lo(Zo))	16	64.5	4.0	1.84	0.030	Total	188	66.4			
Res	141	309.5	2.2			Pairwise comparison: NTZ: 2009 = 2017 < 2013, PPA: 2017 = 2013 > 2009					
Total	188	583.9									
(e) <i>T. analis</i>											
Ye	2	4.1	2.1	2.86	0.062						
Zo	1	0.5	0.5	0.24	0.547						
Lo(Zo)	6	11.6	1.9	0.95	0.524						
YexZo	2	6.1	3.1	4.28	0.016						
Si(Lo(Zo))	8	16.4	2.1	2.85	0.005						
Pooled	169	121.5	0.7								
Total	188	160.5									
Pairwise comparison: NTZ: 2009 > 2013 = 2017, PPA: 2017 > 2013; 2009 = 2013 = 2017											

Table 4

Results of a PERMANOVA comparing the abundance of fished and by-catch species; (a) *Carcharhinus galapagensis*, (b) *Lethrinus nebulosus*, (c) *Pseudocaranx dentex* and (d) *Seriola lalandi* between zones using Euclidian distance. Factors are the same as those listed in Table 3.1. Values in bold indicate statistical significance at $\alpha = 0.05$. Data stemming from pooling procedures outlined in Underwood (1997) referred to 'Pooled'.

Source	df	SS	MS	Pseudo-F	P(perm)	Source	df	SS	MS	Pseudo-F	P(perm)
(a) <i>C. galapagensis</i>						(b) <i>L. nebulosus</i>					
Ye	2	69.9	34.9	4.34	0.016	Ye	2	1.5	0.8	1.48	0.271
Zo	1	7.1	7.1	0.27	0.539	Zo	1	0.2	0.2	0.34	0.896
Lo(Zo)	6	285.3	47.5	4.50	0.020	Lo(Zo)	6	10.8	1.8	1.53	0.184
YexZo	2	16.6	8.3	1.03	0.363	YexZo	2	0.4	0.2	0.39	0.688
Si(Lo(Zo))	8	84.5	10.6	1.31	0.235	Si(Lo(Zo))	8	9.3	1.2	1.54	0.215
Pooled	169	1360.2	8.0			YexLo(Zo)	12	6.1	0.5	0.67	0.776
Total	188	1809.9				YexSi(Lo(Zo))	16	12.2	0.8	1.76	0.039
						Res	141	61.0	0.4		
						Total	188	101.7			
(c) <i>P. dentex</i>						(d) <i>S. lalandi</i>					
Ye	2	11.9	5.9	1.26	0.330	Ye	2	0.8	0.4	0.07	0.957
Zo	1	7.7	7.7	0.43	0.827	Zo	1	17.7	17.7	0.61	0.337
Lo(Zo)	6	139.3	23.2	1.46	0.043	Lo(Zo)	6	227.5	37.9	1.99	0.081
YexZo	2	11.3	5.6	1.19	0.350	YexZo	2	2.0	1.0	0.16	0.887
Si(Lo(Zo))	8	110.6	13.8	3.70	0.001	Si(Lo(Zo))	8	152.5	19.1	3.09	0.001
YexLo(Zo)	12	56.8	4.7	1.27	0.228	Pooled	169	1041.7	6.2		
Pooled	157	586.0	3.7			Total	188	1445.5			
Total	188	926.4									

2013 and 2017 (Fig. 7c). A decline in the number of protected *G. cyanea* was also apparent over survey years, with 30 individuals observed in 2009 and just 7 individuals in 2013 and 2017 (Fig. 7d). The highest abundances of *G. cyanea* observed across all sampling years were at the PPA location containing site 5 and 6 (Fig. 7d).

4. Discussion

The effects of no-take marine reserves in protecting coral and temperate reef fish assemblages has been well documented in

the literature (Goetze et al., 2021; Guidetti et al., 2014; Lester et al., 2009). The current study, provides a rare example of an assessment of potential ecological change in fish assemblages between no-take zones (NTZs) and partially protected areas (PPAs) in a remote oceanic setting, where human pressures are relatively minimal (Cinner et al., 2018). In our study we identified no clear changes in the fish assemblage related to NTZ protection through time. Rather, most variation in the abundance and diversity of fishes was observed among sampling years, locations and sites. The lack of difference between marine park zones contrasts with many international studies that have demonstrated substantial

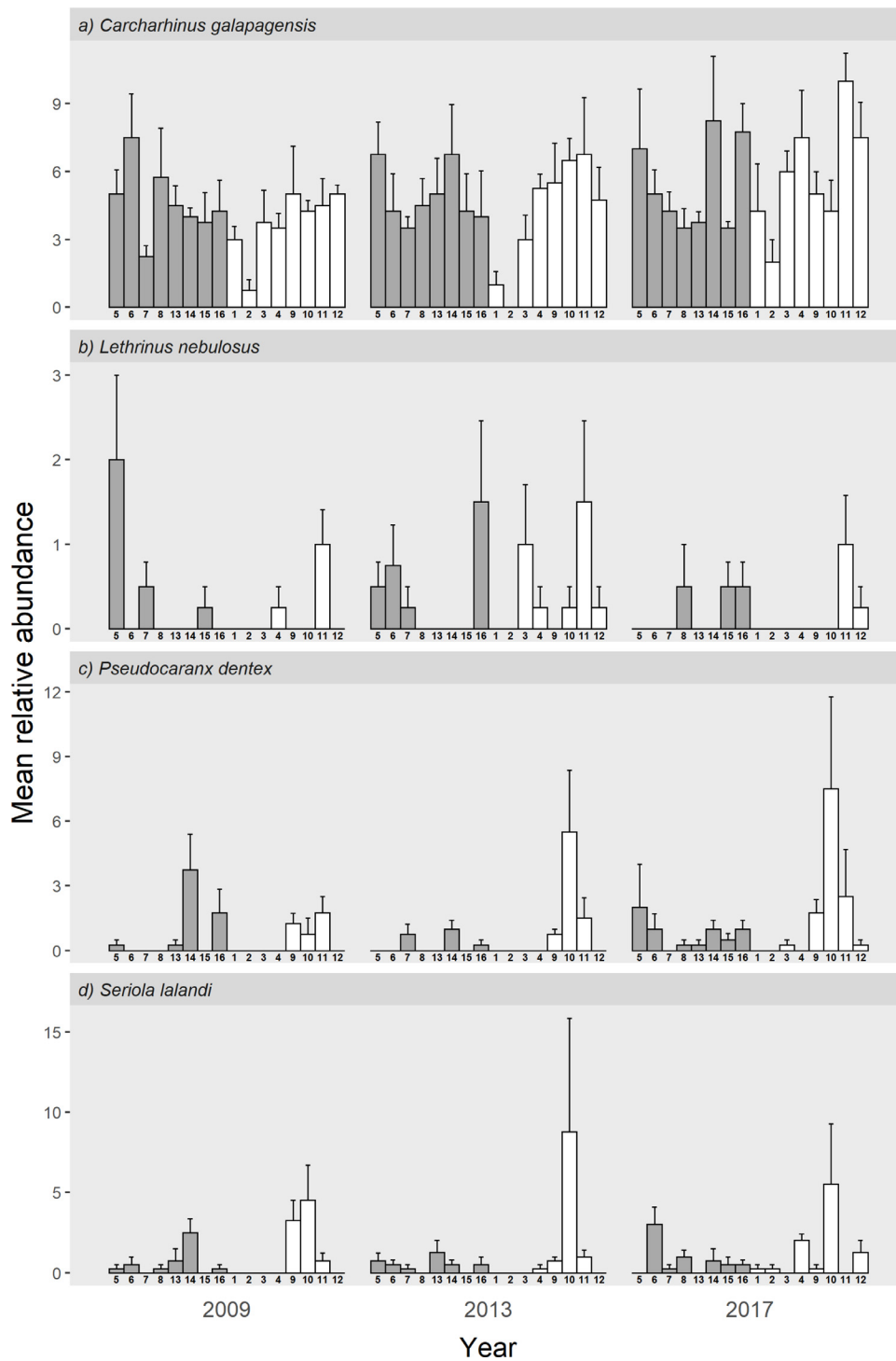


Fig. 5. Mean (\pm SE) abundance of fished and by-catch species; (a) *Carcharhinus galapagensis*, (b) *Lethrinus nebulosus*, (c) *Pseudocaranx dentex* and (d) *Seriola lalandi* between zones in 2009, 2013 and 2017 ($n = 4$). Shaded bars represent partially protected areas (PPAs) and clear bars represent no-take zones (NTZs).

differences in the assemblage of fishes in reef habitats within NTZs and zones open to fishing (Babcock et al., 2010; Lester et al., 2009; Russ et al., 2008; Sciberras et al., 2013, 2015). No clear change in the fish assemblage in NTZs may appear unexpected, considering that LHIMP and LHMP zones are relatively large in size (CAPAD, 2018), old in age (>10 years), remote, and well enforced; all of which are key criteria for successful NTZs (Edgar et al., 2014). However, the lack of a clear difference between management zones is most likely due to the relatively healthy

condition of the marine park’s environment and relatively minor human impacts in the region.

The abundance of the targeted carangids, *Seriola lalandi* and *Pseudocaranx dentex* was 2 and 1.6 times greater in NTZs than PPAs respectively, however, these differences were not statistically significant. This was unexpected, as both species are caught in relatively high numbers for the local restaurant trade (Figueira and Hunt, 2012). There are several possible explanations for the lack of difference between zone types. First, the levels of fishing within the marine parks PPAs (which excludes several forms of

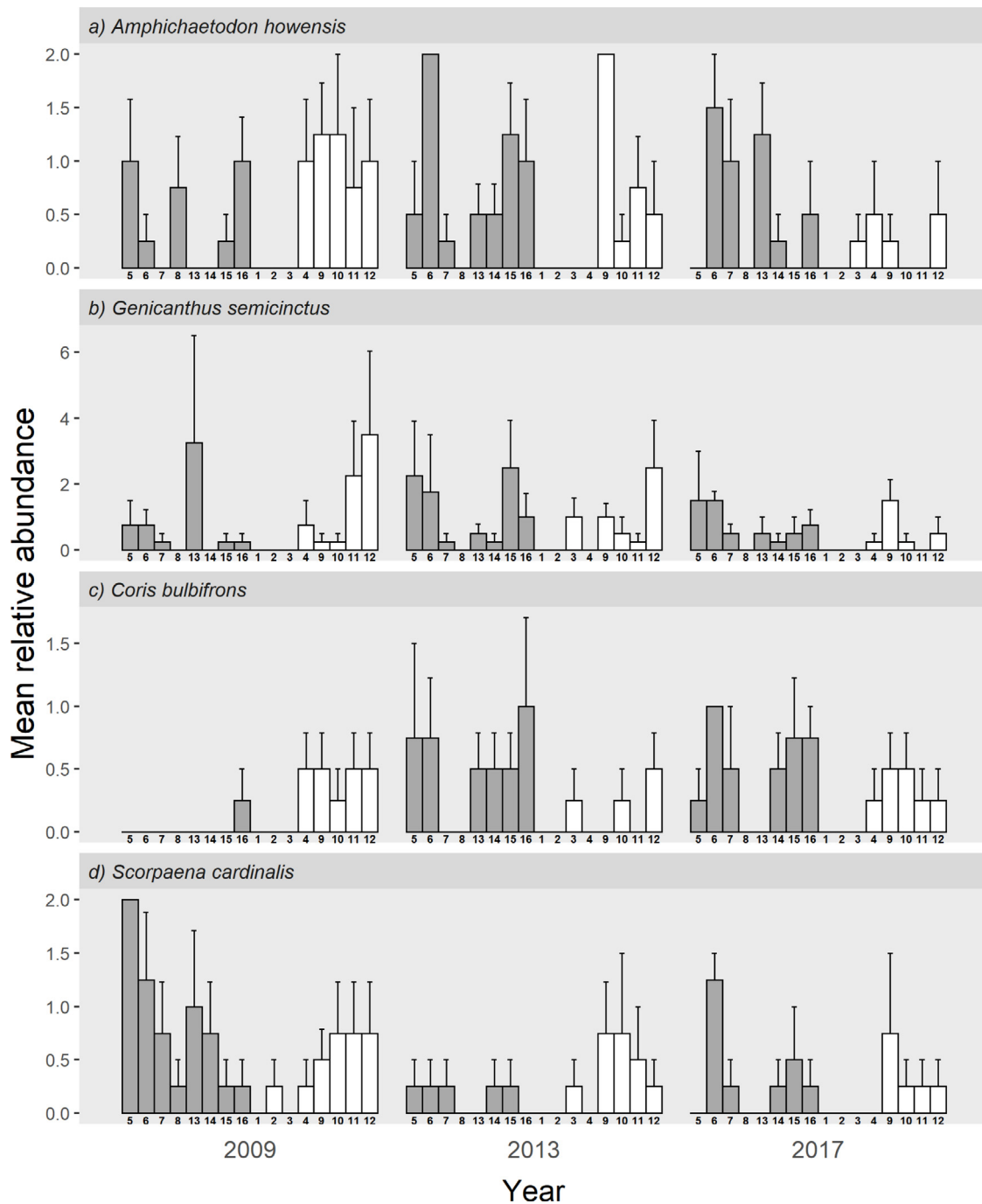


Fig. 6. Mean (\pm SE) relative abundance of endemic, near endemic and protected species; (a) *Amphichaetodon howensis*, (b) *Genicanthus semicinctus*, (c) *Coris bulbifrons* and (d) *Scorpaena cardinalis* between zones in 2009, 2013 and 2017 (n = 4). Shaded bars represent partially protected areas (PPAs) and clear bars represent no-take zones (NTZs).

commercial fishing) may be of a low enough intensity to have no significant effects on the abundances of these fishes. Second, the NTZs in the region may not be an appropriate size to encompass the movement patterns on these species, which may lead to exposure to fishing pressure in adjacent PPAs. Alternatively, the substantial variation in their abundance among locations can make it difficult to detect even large effects of marine park zoning. It appears that this variation may be attributable to differences in habitat structure among the sites (within each of the zone types) and its effect on the abundance of carangids. Rees et al. (2018b) found the abundance of *S. lalandi* was substantially

greater in NTZs compared to PPAs, but only on reefs displaying high structural complexity. It is highly likely that a similar pattern would be observed for *P. dentex*, as their abundances were consistently high at the same locations as *S. lalandi*. Future surveys in these marine parks should closely monitor carangid numbers to see whether effect sizes between NTZs and PPAs grow through time and to apply acoustic telemetry techniques to better understand their movement patterns in relation to zone boundaries.

No clear difference in the abundance of the carcharhinid shark: *Carcharhinus galapagensis* was observed between NTZs and PPAs. As *C. galapagensis* is often incidentally caught as by-catch this

Table 5

Results of a PERMANOVA comparing the abundance of endemic, near endemic and protected species; (a) *Amphichaetodon howensis*, (b) *Genicanthus semicinctus*, (c) *Coris bulbifrons* and (d) *Scorpaena cardinalis* between zones using Euclidian distance. Factors are the same as those listed in Table 3.1. Values in bold indicate statistical significance at $\alpha = 0.05$. Data stemming from pooling procedures outlined in Underwood (1997) referred to 'Pooled'.

Source	df	SS	MS	Pseudo-F	P(perm)	Source	df	SS	MS	Pseudo-F	P(perm)
(a) <i>A. howensis</i>						(b) <i>G. semicinctus</i>					
Ye	2	1.6	0.8	0.86	0.455	Ye	2	4.5	2.2	0.58	0.581
Zo	1	1.0	1.0	0.48	0.790	Zo	1	1.8	1.8	0.59	0.713
Lo(Zo)	6	12.9	2.1	1.61	0.147	Lo(Zo)	6	47.0	7.8	1.58	0.034
YexZo	2	3.8	1.9	2.04	0.176	YexZo	2	3.5	1.8	0.46	0.655
Si(Lo(Zo))	8	8.8	1.1	1.00	0.480	Si(Lo(Zo))	8	24.0	3.0	1.01	0.438
YexLo(Zo)	12	11.1	0.9	0.85	0.617	YexLo(Zo)	12	46.4	3.9	1.30	0.216
YexSi(Lo(Zo))	16	17.5	1.1	2.07	0.014	Pooled	157	466.2	3.0		
Res	141	74.5	0.5			Total	188	593.7			
Total	188	131.2									
(c) <i>C. bulbifrons</i>						(d) <i>S. cardinalis</i>					
Ye	2	1.3	0.6	2.46	0.091	Ye	2	5.7	2.8	6.76	0.002
Zo	1	0.8	0.8	0.40	0.426	Zo	1	0.7	0.7	0.36	0.456
Lo(Zo)	6	4.9	0.8	3.18	0.005	Lo(Zo)	6	11.1	1.8	4.42	0.001
YexZo	2	3.5	1.8	6.86	0.001	YexZo	2	2.5	1.3	3.00	0.048
Pooled	177	45.4	0.3			Pooled	177	74.0	0.4		
Total	188	55.7				Total	188	94.1			
Pairwise comparison: NTZ: 2009 = 2013 = 2017, PPA: 2017 = 2013 > 2009						Pairwise comparison: NTZ: 2009 = 2013 = 2017, PPA: 2017 = 2013 < 2009					

finding may indicate that the current level of fishing in the LHIMP and LHMP may not be resulting in a measurable effect on this species. It is worth noting however, that a fast swimming mobile shark species, such as this, is expected to be capable of moving large distances. Consequently, the size of the NTZs may not be large enough to adequately protect this species from incidental by-catch mortality. Furthermore, considering the expected mobility of *C. galapagensis*, results on spatial comparisons between management zones need to be interpreted with caution as relative abundance estimates for this species may not be independent. There is also the possibility that *C. galapagensis* abundance estimates are influenced by the presence of boats, as depredation of fishing catch by *C. galapagensis* is an issue in the region (Mitchell et al., 2018a,b). Further research on the movement patterns of *C. galapagensis* is required to determine whether the NTZs are of sufficient size to encompass their home range and to better understand their possible movements among simultaneously deployed BRUVs and behaviour towards boats (Mitchell et al., 2021).

We note that *C. galapagensis* were the most prevalent species across the LHIMP and LHMP being recorded on 96% of deployments. In comparison to marine parks at similar latitudes on mainland Australia (Solitary Islands and Port Stephens-Great Lakes Marine Parks) (Malcolm et al., 2007) and globally (MacNeil et al., 2020), the relative abundance and commonality of this carcharhinid shark appears much higher in this location compared to others. Anecdotal evidence from local fishers and tourism operators suggests that the number of *C. galapagensis* has increased in recent decades. Our findings provide support for this observation, with the abundance of *C. galapagensis* significantly increasing through time with a greater abundance recorded in 2017 (mean MaxN = 5.6) compared to 2013 (mean MaxN = 4.7) and 2009 (mean MaxN = 4.2). This is a promising finding given the global decline in shark numbers and their important trophic position in marine ecosystems (Dulvy et al., 2014; Speed et al., 2019; Stevens et al., 2000). However, additional research is required to validate their abundances given the potential for inflated counts due to BRUV spacing and possible attraction to boats.

Another key finding from the study was the discrete and consistent differences in the abundance of certain species among locations during each sampling period. The protected *Girella cyanea*, were recorded in relatively high abundances at only one PPA

location (site 5 and 6) through time. The result is likely to be driven by this location's shallower water and proximity to Lord Howe Island, as *G. cyanea* appear to be common in nearshore waters of the LHIMP (Edgar et al., 2010). The protected Ballina angelfish; *Chaetodontoplus ballinae*, also exhibited strong patterns in their spatial distribution, with individuals being recorded at one location in the Balls Pyramid NTZ across all years. The presence of *C. ballinae* at this location is again likely to be related to depth, with sites at this location approximately 10 m deeper compared to other locations. This observation confirms those by Speare et al. (2004) who recorded 12 individuals of *C. ballinae* on the deeper margins of the Lord Howe Island and Balls pyramid shelf (27–100 m) using BRUVs and towed video surveys. Therefore, it is likely that this species may be more common than previously thought and these observations highlight the advantages of using remote survey techniques to sample biological assemblages at depths greater than those generally surveyed by conventional survey methods, such as SCUBA (Fetterplace et al., 2018). Discrete and consistent differences among locations over time are important considerations for the conservation management of the LHIMP and LHMP, as it highlights the locations and their habitats that are representing and protecting biodiversity.

Most endemic, near endemic and protected species examined in this study displayed similar abundances between management zones and across time. Surprisingly, the abundance of *Coris bulbifrons* increased in PPAs from 10 individuals in 2009 to 22 individuals in 2017. This is a promising finding given their restricted range, low abundances and their targeting by fishers in nearshore environments of Lord Howe Island (although catch and release is often practiced). Genetic research has indicated that there are relatively high levels of contemporary gene flow between the populations in the LHIMP to the surrounding Elizabeth and Middleton Reefs situated in the LHMP (van der Meer et al., 2015). The abundance of *Scorpaena cardinalis* remained stable in NTZs over time but decreased in PPAs, which was unexpected as *S. cardinalis* is unlikely to be heavily targeted by fishers.

The abundance of two protected species; *Epinephelus daemeli* and *Girella cyanea* displayed a general declining trend between 2009, 2013 and 2017. However, both species were recorded in very low numbers making accurate assessments of their abundance through time difficult. Nevertheless, highlighting general trends in the abundance of protected species is important, particularly for *E. daemeli* as their numbers have been significantly

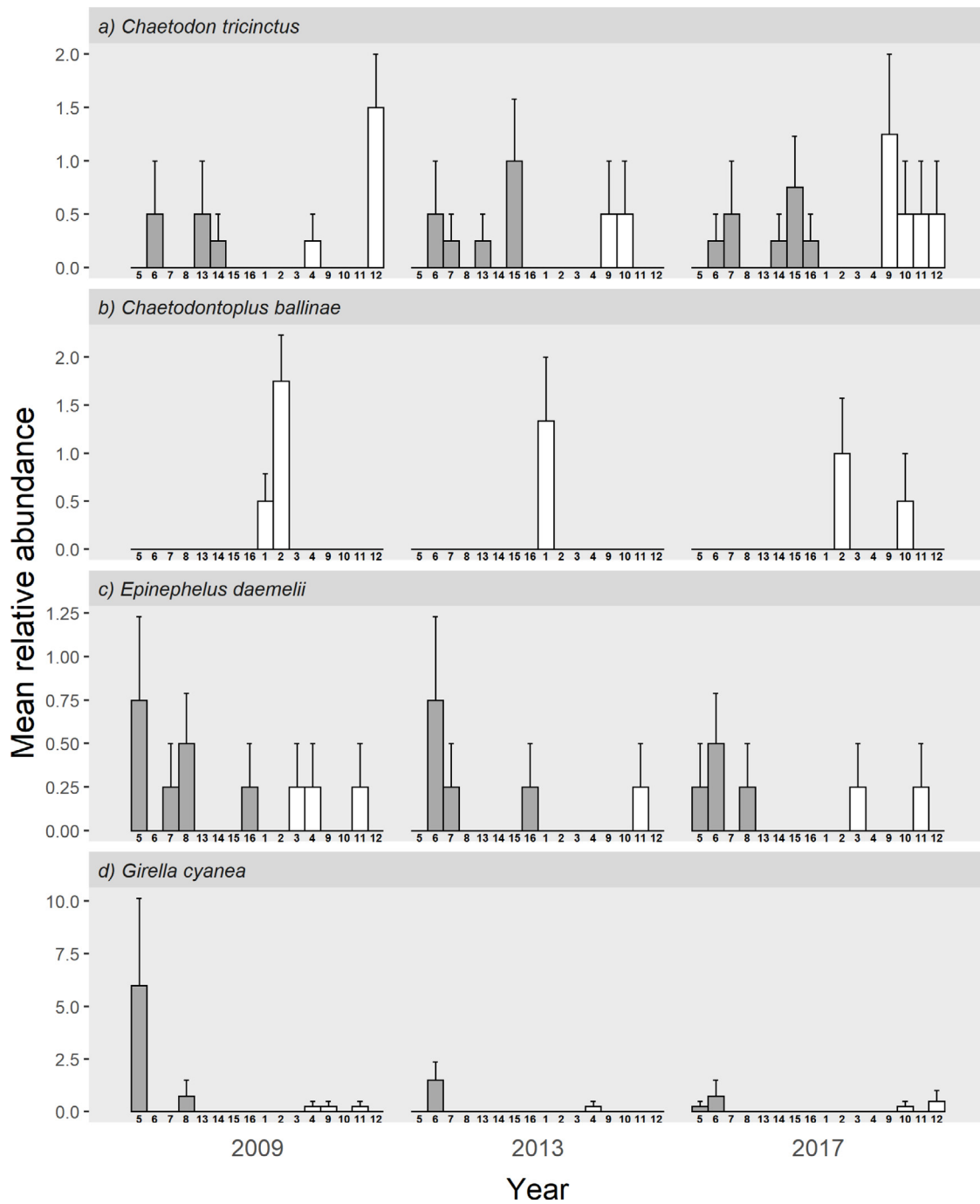


Fig. 7. Mean (\pm SE) abundance of endemic, near endemic and protected species; (a) *Chaetodon tricinctus*, (b) *Chaetodontoplus ballinae*, (c) *Epinephelus daemeli*, and (d) *Girella cyanea* between zones in 2009, 2013 and 2017 ($n = 4$). Shaded bars represent partially protected areas (PPAs) and clear bars represent no-take zones (NTZs).

reduced in Lord Howe Island and mainland Australia due to historic overfishing (Harasti et al., 2014; Pogonoski et al., 2002). Similarly, recent surveys of *E. daemeli* at Elizabeth and Middleton Reefs within the LHMP (Commonwealth waters) have also reported declines in the number of sightings between 2013 and 2018 (Edgar et al., 2018). Further research using BRUVs and a continued targeted monitoring program (Harasti et al., 2014; Harasti and Malcolm, 2013) is required to determine whether the declining trend through time observed in this study is genuine. Interestingly, the distribution of *E. daemeli* was exclusively restricted to the Lord Howe Island shelf and all individuals observed

were adults. Previous research has shown that *E. daemeli* larvae recruit into intertidal and shallow subtidal reef habitat then migrate onto deeper reefs with age (Francis et al., 2016; Harasti et al., 2014). This may explain their absence on the Balls Pyramid shelf where intertidal habitat is limited, and possibly highlights the importance of Lord Howe Island’s lagoon and nearshore habitats as nursery areas for *E. daemeli*, although juveniles were not observed in intertidal pools in a recent study (Davis et al., 2018). Previous research has demonstrated the pronounced effect that seascape connectivity of nursery and adult habitats can have on the abundance of certain fishes (Rees et al., 2018a). Further research in the Lord Howe Island region is required

to better understand the ontogenetic migration of *E. daemeli* from nearshore to offshore shelf habitats. Although there was a striking decrease in the abundance of *G. cyanea*, it is likely that this pattern was mostly driven by their schooling behaviour and patchy distribution in deep habitats, as this species is much more common in nearshore habitats (Davis et al., 2018; Edgar et al., 2010; Hobbs et al., 2009). However, complementary data from shallower habitats would be beneficial in future surveys to better assess the spatial and temporal trends of this species.

The temporal differences observed in the Lord Howe Island fish assemblages may not be indicative of changes in response to anthropogenic threats but rather natural variability or discrepancies in our sampling method among years. For example, the 2009 sampling was completed in November where the average sea temperature is 21 °C compared to 23 °C degrees in April and 20 – 22.5 °C in October to December when the 2013 and 2017 sampling were undertaken (Allen et al., 1976). This is likely to impact the composition of tropical, subtropical and temperate species within the assemblage. There were also differences in the amount of bait and degree of bait replenishment between the 2009 and later surveys that may have influenced the observed changes in the fish assemblage between the sampling periods. Although, differences in bait volume have been shown to have limited impact on BRUV data (Hardinge et al., 2013). Despite the disparities in our sampling time and method, consistent patterns among locations for certain species suggests that any discrepancies, caused by methodological variations, had a minimal impact on the temporal patterns we observed. Consequently, changes in species abundances are more probably due to natural fluctuations in species abundances, for example from variation in successful recruitment among years. Such cyclic patterns in species abundances have been observed over a 12-year period in an Australian mainland marine park at a similar latitude (Malcolm et al., 2015). We encourage ongoing future BRUV monitoring in the LHIMP and LHMP, using standardised sampling methodology, at consistent time-frequencies (e.g. every 4-5 years) to help disentangle zoning effects from sampling artefacts and natural variability.

A number of modifications to the LHIMP and LHMP monitoring program could be introduced that are likely to provide benefits to the ongoing management of these marine parks. First, future surveys should aim to use stereo-BRUVs, which can provide body-size data in a non-destructive and cost effective manner that is comparable to fisheries-dependent methods (Langlois et al., 2012, 2015). As fishing often removes larger-bodied individuals from populations (Jackson et al., 2001), assessments of no-take zone effectiveness incorporating body-size metrics are more likely to be sensitive to fishing effects than assessments only using count data (Claudet et al., 2010; Bosch et al., 2021). Without body-size data there is a possibility that fishing effects may have gone undetected in this study. Second, future assessments of the marine parks would benefit from an external reference location, which would provide an opportunity to test whether both NTZs and PPAs provide benefits relative to areas outside the marine park boundaries (see Knott et al., 2021). Third, the use of spatially balanced sampling designs that incorporates the 16 long-term monitoring sites (Foster et al., 2017) and generates random survey sites across the study region would provide a more representative picture of the fish assemblage across the Lord Howe Island and Balls Pyramid shelf. A spatially balanced sampling design for future surveys would also provide the opportunity to better explore fish-habitat relationships and build spatially-explicit species distribution models to assist with the ongoing management of the marine park (Rees et al., 2021).

5. Conclusions

Overall, there were no clear changes in the fish assemblage, diversity, total abundance and abundance of key species between no-take zones (NTZs) and partially protected areas (PPAs) within the LHIMP and LHMP. This is likely to be a result of the relatively pristine environment and minimal anthropogenic threats that exist currently and prior to the establishment of the marine park. We note, however, that our assessment did not examine differences in body-size or biomass across zone types, which may be more sensitive to anthropogenic threats in the region. Many species, including some targeted, endemic, near endemic and protected species displayed consistent patterns of abundances between zones across the three sampling years, suggesting that shelf fish assemblages are relatively stable in the LHIMP and LHMP through time. With possible increases in human pressures within the region (e.g. climate change, tourism operations and fishing) our study provides an important contemporary baseline from which to monitor potential future change in the marine park's fish assemblage. These monitoring data will aid policy-makers and managers by providing an indication of the ecological responses of fish populations to conservation and fisheries management actions.

CRedit authorship contribution statement

M.J. Rees: Conceptualization, Data curation, Formal analysis, Investigation, Methodology, Project administration, Writing – original draft, Writing – review & editing. **N.A. Knott:** Conceptualization, Data curation, Investigation, Methodology, Project administration, Resources, Supervision, Writing – original draft, Writing – review & editing, Funding acquisition. **T.R. Davis:** Data curation, Investigation, Methodology, Project administration, Resources, Writing – review & editing. **A.R. Davis:** Conceptualization, Project administration, Resources, Supervision, Writing – original draft, Writing – review & editing, Funding acquisition. **S. Gudge:** Data curation, Investigation, Resources, Methodology, Writing – review & editing, Funding acquisition, Project administration. **J.M. Neilson:** Data curation, Methodology, Investigation, Resources, Visualization, Writing – review & editing, Project administration. **L.C. Fetterplace:** Formal analysis, Investigation, Writing – review & editing, Visualization. **A. Jordan:** Conceptualization, Methodology, Funding acquisition, Project administration, Resources, Supervision, Writing – review & editing.

Declaration of competing interest

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

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References

- AFMA, 2018. Southern and Eastern Scalegfish and Shark Fishery management arrangements booklet 2018. Australian Fisheries Management Authority, Canberra.
- Allen, G.R., 2008. Conservation hotspots of biodiversity and endemism for Indo-Pacific coral reef fishes. *Aquat. Conserv. Mar. Freshw. Ecosyst.* 18, 541–556.
- Allen, G.R., Hoese, D.F., Paxton, J.R., 1976. Annotated checklist of the fishes of Lord Howe Island.
- Allen, G., Paxton, J., 1974. A tropical outpost in the Pacific. *Aust. Natl. Hist.* 18, 50–55.
- Allender, B., Kraft, G., 1983. The marine algae of Lord Howe Island (NSW): The dictyotales and Cutleriales (Phaeophyta). *Brunonia* 6, 73–130.
- Anderson, M.J., 2001. Permutation tests for univariate or multivariate analysis of variance and regression. *Can. J. Fish. Aquat. Sci.* 58, 626–639.
- Anderson, M., Gorley, R.N., Clarke, R.K., 2008. *Permanova+ for primer: Guide to software and statistical methods.*
- Babcock, R.C., Shears, N.T., Alcalá, A.C., Barrett, N.S., Edgar, G.J., Lafferty, K.D., McClanahan, T.R., Russ, G.R., 2010. Decadal trends in marine reserves reveal differential rates of change in direct and indirect effects. *Proc. Natl. Acad. Sci. USA* 107, 18256–18261.
- Baird, A.H., Hoogenboom, M.O., Huang, D., 2017. *Cyphastrea salae*, a new species of hard coral from Lord Howe island, Australia (Scleractinia, Merulinidae). *ZooKeys* 662.
- Bosch, N.E., Monk, J., Goetze, J., Wilson, S., Babcock, R.C., Barrett, N., Clough, J., Currey-Randall, L.M., Fairclough, D.V., Fisher, R., Gibbons, B.A., 2021. Effects of human footprint and biophysical factors on the body-size structure of fished marine species. *Conserv. Biol.* <http://dx.doi.org/10.1111/cobi.13807>.
- Collaborative Australian Protected Areas Database (CAPAD), 2018. Commonwealth of Australia 2019. Accessed 13/04/2021.
- Choat, J.H., Pollard, D., 2010. *Coris bulbifrons*. In: The IUCN Red List of Threatened Species 2010. e.T187392A8522703. <http://dx.doi.org/10.2305/IUCN.UK.2010-4.RLTS.T187392A8522703.en>.
- Cinner, J.E., Maire, E., Huchery, C., MacNeil, M.A., Graham, N.A., Mora, C., McClanahan, T.R., Barnes, M.L., Kittinger, J.N., Hicks, C.C., D'agata, S., 2018. Gravity of human impacts mediates coral reef conservation gains. *Proc. Natl. Acad. Sci.* 115 (27), E6116–E6125.
- Clarke, K.R., 1993. Non-parametric multivariate analyses of changes in community structure. *Aust. J. Ecol.* 18, 117–143.
- Claudet, J., Osenberg, C.W., Domenici, P., Badalamenti, F., Milazzo, M., Falcón, J.M., Bertocci, I., Benedetti-Cecchi, L., García-Charton, J.A., Goñi, R., Borg, J.A., 2010. Marine reserves: fish life history and ecological traits matter. *Ecol. Appl.* 20 (3), 830–839.
- Davis, T.R., Larkin, M.F., Harasti, D., 2018. Application of non-destructive methods for assessing rock pool fish assemblages on Lord Howe Island, Australia. *Reg. Stud. Mar. Sci.* 24, 251–259.
- Dulvy, N.K., Fowler, S.L., Musick, J.A., Cavanagh, R.D., Kyne, P.M., Harrison, L.R., Carlson, J.K., Davidson, L.N., Fordham, S.V., Francis, M.P., Edgar, G.J., Banks, S., Farina, J.M., Calvopina, M., Martinez, C., 2004. Regional biogeography of shallow reef fish and macro-invertebrate communities in the galapagos archipelago. *J. Biogeogr.* 31, 1107–1124.
- Edgar, G., Ceccarelli, D., Stuart-Smith, R., Cooper, A., 2018. Biodiversity Surveys of the Elizabeth and Middleton Reefs Marine National Park Reserve, 2013 and 2018. Reef Life Survey Foundation Incorporated.
- Edgar, G.J., Davey, A., Kelly, G., Mawbey, R.B., Parsons, K., 2010. Biogeographical and ecological context for managing threats to coral and rocky reef communities in the Lord Howe Island Marine Park, south-western Pacific. *Aquat. Conserv.-Mar. Freshw. Ecosyst.* 20, 378–396.
- Edgar, G.J., Langhammer, P.F., Allen, G., Brooks, T.M., Brodie, J., Crosse, W., De Silva, N., Fishpool, L.D.C., Foster, M.N., Knox, D.H., McCosker, J.E., McManus, R., Millar, A.J.K., Mugo, R., 2008. Key biodiversity areas as globally significant target sites for the conservation of marine biological diversity. *Aquat. Conserv.-Mar. Freshw. Ecosyst.* 18, 969–983.
- Edgar, G.J., Stuart-Smith, R.D., Willis, T.J., Kininmonth, S., Baker, S.C., Banks, S., Barrett, N.S., Becerro, M.A., Bernard, A.T.F., Berkhout, J., Buxton, C.D., Campbell, S.J., Cooper, A.T., Davey, M., Edgar, S.C., Foerster, G., Galvan, D.E., Irigoyen, A.J., Kushner, D.J., Moura, R., Parnell, P.E., Shears, N.T., Soler, G., Strain, E.M.A., Thomson, R.J., 2014. Global conservation outcomes depend on marine protected areas with five key features. *Nature* 506, 216–+.
- Environment Australia, 2000. Lord Howe Island Marine Park Proposal. Environment Australia, Marine Protected Area Section, Canberra.
- Fetterplace, L.C., Turnbull, J.W., Knott, N.A., Hardy, N.A., 2018. The devil in the deep: Expanding the known habitat of a rare and protected fish. *Eur. J. Ecol.* 4, 22–29.
- Figueira, W., Hunt, B., 2012. Lord Howe Island Charter Fisher Report: 2004–2012. Prepared for the Lord Howe Island Marine Park.
- Foster, S.D., Hosack, G.R., Lawrence, E., Przeslawski, R., Hedge, P., Caley, M.J., Barrett, N.S., Williams, A., Li, J., Lynch, T., Dambacher, J.M., Sweatman, H.P.A., Hayes, K.R., 2017. Spatially balanced designs that incorporate legacy sites. *Methods Ecol. Evol.* 8, 1433–1442.
- Francis, M.P., 1991. Additions to the fish faunas of Lord Howe, Norfolk, and Kermadec Islands, Southwest Pacific Ocean. *Pac. Sci.* 45, 204–220.
- Francis, M.P., 1993. Checklist of the coastal fishes of Lord Howe, Norfolk, and Kermadec Islands, southwest Pacific Ocean. *Pac. Sci.* 47 (2), 136–170.
- Francis, M.P., Harasti, D., Malcolm, H.A., 2016. Surviving under pressure and protection: a review of the biology, ecology and population status of the highly vulnerable grouper *Epinephelus Daemeli*. *Mar. Freshw. Res.* 67, 1215–1228.
- Francis, M.P., Randall, J.E., 1993. Further additions to the fish faunas of Lord Howe and Norfolk Islands, Southwest Pacific Ocean. *Pac. Sci.* 47, 118.
- Gell, F.R., Roberts, C.M., 2003. Benefits beyond boundaries: the fishery effects of marine reserves. *Trends Ecol. Evol.* 18, 448–455.
- Gerber, L.R., Beger, M., McCarthy, M.A., Possingham, H.P., 2005. A theory for optimal monitoring of marine reserves. *Ecol. Lett.* 8, 829–837.
- Glasby, T.M., 1997. Analysing data from post-impact studies using asymmetrical analyses of variance: A case study of epibiota on marinas. *Aust. J. Ecol.* 22, 448–459.
- Goetze, J.S., Wilson, S., Radford, B., Fisher, R., Langlois, T.J., Monk, J., Knott, N.A., Malcolm, H., Currey-Randall, L.M., Ierodiaconou, D., 2021. Increased connectivity and depth improve the effectiveness of marine reserves. *Global Change Biol.* 27, 3432–3447.
- Guidetti, P., Baiata, P., Ballesteros, E., Di Franco, A., Hereu, B., Macpherson, E., Micheli, F., Pais, A., Panzalis, P., Rosenberg, A.A., Zabala, M., Sala, E., 2014. Large-scale assessment of mediterranean Marine Protected Areas effects on fish assemblages. *PLoS One* 9.
- Halpern, B.S., 2003. The impact of marine reserves: Do reserves work and does reserve size matter? *Ecol. Appl.* 13, S117–S137.
- Harasti, D., Gallen, C., Malcolm, H., Tegart, P., Hughes, B., 2014. Where are the little ones: distribution and abundance of the threatened serranid *Epinephelus daemeli* (Gunther, 1876) in intertidal habitats in New South Wales, Australia. *J. Appl. Ichthyol.* 30, 1007–1015.
- Harasti, D., Malcolm, H., 2013. Distribution, relative abundance and size composition of the threatened serranid *Epinephelus daemeli* in New South Wales, Australia. *J. Fish Biol.* 83, 378–395.
- Harasti, D., Malcolm, H., Gallen, C., Coleman, M.A., Jordan, A., Knott, N.A., 2015. Appropriate set times to represent patterns of rocky reef fishes using baited video. *J. Exp. Mar. Biol. Ecol.* 463, 173–180.
- Hardinge, J., Harvey, E.S., Saunders, B.J., Newman, S.J., 2013. A little bait goes a long way: The influence of bait quantity on a temperate fish assemblage sampled using stereo-BRUVs. *J. Exp. Mar. Biol. Ecol.* 449, 250–260.
- Hobbs, J., Neilson, J., Gilligan, J., 2009. Distribution, Abundance, Habitat Association and Extinction Risk of Marine Fishes Endemic to the Lord Howe Island Region. Report to Lord Howe Island Marine Park, 37.
- Jackson, J.B., Kirby, M.X., Berger, W.H., Bjorndal, K.A., Botsford, L.W., Bourque, B.J., Bradbury, R.H., Cooke, R., Erlanson, J., Estes, J.A., Hughes, T.P., 2001. Historical overfishing and the recent collapse of coastal ecosystems. *Science* 293 (5530), 629–637.
- Jordan, A., Fairfull, S., Creese, B., 2016. Managing threats to the marine estate in new south Wales (Australia) to maximise community wellbeing. *J. Coast. Res.* 64, 2–646.
- Kelaher, B.P., Coleman, M.A., Broad, A., Rees, M.J., Jordan, A., Davis, A.R., 2014. Changes in fish assemblages following the establishment of a network of no-take marine reserves and partially-protected areas. *PLoS One* 9.
- Kier, G., Kreft, H., Lee, T.M., Jetz, W., Ibsch, P.L., Nowicki, C., Mutke, J., Barthlott, W., 2009. A global assessment of endemism and species richness across island and mainland regions. *Proc. Natl. Acad. Sci.* 106, 9322–9327.
- Knott, N.A., Williams, J., Harasti, D., Malcolm, H.A., Coleman, M.A., Kelaher, B.P., Rees, M.J., Schultz, A., Jordan, A., 2021. A coherent, representative, and bioregional marine reserve network shows consistent change in rocky reef fish assemblages. *Ecosphere* 12, e03447.
- Kraft, G.T., 2000. Marine and estuarine benthic green algae (Chlorophyta) of Lord Howe Island, south-western Pacific. *Aust. Syst. Bot.* 13, 509–648.
- Krug, P.J., Berriman, J.S., Valdés, Á., 2018. Phylogenetic systematics of the shelled sea slug genus *Oxynoe* Rafinesque, 1814 (Heterobranchia: Sacoglossa), with integrative descriptions of seven new species. *Invertebrate Syst.* 32, 950–1003.
- Langlois, T.J., Fitzpatrick, B.R., Fairclough, D.V., Wakefield, C.B., Hesp, S.A., McLean, D.L., Harvey, E.S., Meeuwij, J.J., 2012. Similarities between line fishing and baited stereo-video estimations of length-frequency: novel application of kernel density estimates. *PLoS One* 7 (11), e45973.
- Langlois, T.J., Newman, S.J., Cappo, M., Harvey, E.S., Rome, B.M., Skepper, C.L., Wakefield, C.B., 2015. Length selectivity of commercial fish traps assessed from in situ comparisons with stereo-video: is there evidence of sampling bias? *Fish. Res.* 161, 145–155.
- Lester, S.E., Halpern, B.S., Grorud-Colvert, K., Lubchenco, J., Ruttenberg, B.I., Gaines, S.D., Airame, S., Warner, R.R., 2009. Biological effects within no-take marine reserves: a global synthesis. *Mar. Ecol. Prog. Ser.* 384, 33–46.
- Linklater, M., Jordan, A.R., Carroll, A.G., Neilson, J., Gudge, S., Brooke, B.P., Nichol, S.L., Hamylton, S.M., Woodroffe, C.D., 2019. Mesophotic corals on the subtropical shelves of Lord Howe Island and Balls Pyramid, south-western Pacific Ocean. *Mar. Freshw. Res.* 70, 43–61.

- MacNeil, M.A., Chapman, D.D., Heupel, M., Simpfendorfer, C.A., Heithaus, M., Meekan, M., Harvey, E., Goetze, J., Kiszka, J., Bond, M.E., Currey-Randall, L.M., Speed, C.W., Sherman, C.S., Rees, M.J., Udyawer, V., Flowers, K.L., Clementi, G., Valentin-Albanese, J., Gorham, T., Adam, M.S., Ali, K., Pina-Amargós, F., Angulo-Valdés, J.A., Asher, J., Barcia, L.G., Beaufort, O., Benjamin, C., Bernard, A.T.F., Berumen, M.L., Bierwagen, S., Bonnema, E., Bown, R.M.K., Bradley, D., Brooks, E., Brown, J.J., Buddo, D., Burke, P., Cáceres, C., Cardeñosa, D., Carrier, J.C., Caselle, J.E., Charloo, V., Claverie, T., Clua, E., Cochran, J.E.M., Cook, N., Cramp, J., D'Alberty, B., de Graaf, M., Dornhege, M., Estep, A., Fanovich, L., Farabaugh, N.F., Fernando, D., Flam, A.L., Floros, C., Fourqurean, V., Garla, R., Gastrich, K., George, L., Graham, R., Guttridge, T., Hardenstine, R.S., Heck, S., Henderson, A.C., Hertler, H., Hueter, R., Johnson, M., Jupiter, S., Kasana, D., Kessel, S.T., Kiilu, B., Kirata, T., Kuguru, B., Kyne, F., Langlois, T., Lédée, E.J.L., Lindfield, S., Luna-Acosta, A., Maggs, J., Manjaji-Matsumoto, B.M., Marshall, A., Matich, P., McCombs, E., McLean, D., Meggs, L., Moore, S., Mukherji, S., Murray, R., Kaimuddin, M., Newman, S.J., Nogués, J., Obota, C., O'Shea, O., Osuka, K., Papastamatiou, Y.P., Perera, N., Peterson, B., Pozzo, A., Prasetyo, A., Quamar, L.M.S., Quinlan, J., Ruiz-Abierno, A., Sala, E., Samoily, M., Schärer-Umpierre, M., Schlaff, A., Simpson, N., Smith, A.N.H., Sparks, L., Tanna, A., Torres, R., Travers, M.J., Bergmann, M., van Zinnicq, Vigliola, L., Ward, J., Watts, A.M., Wen, C., Whitman, E., Wirsing, A.J., Wothke, A., Zarza-González, E., Cinner, J.E., 2020. Global status and conservation potential of reef sharks. *Nature* 583, 801–806.
- Malcolm, H.A., Gladstone, W., Lindfield, S., Wraith, J., Lynch, T.P., 2007. Spatial and temporal variation in reef fish assemblages of marine parks in New South Wales, Australia - baited video observations. *Mar. Ecol. Prog. Ser.* 350, 277–290.
- Malcolm, H.A., Schultz, A.L., Sachs, P., Johnstone, N., Jordan, A., 2015. Decadal changes in the abundance and length of snapper (*Chrysophrys auratus*) in subtropical marine sanctuaries. *PLoS One* 10.
- van der Meer, M.H.D., Berumen, M.L., Hobbs, J.P.A., van Herwerden, L., 2015. Population connectivity and the effectiveness of marine protected areas to protect vulnerable, exploited and endemic coral reef fishes at an endemic hotspot. *Coral Reefs* 34, 393–402.
- Mitchell, J.D., Camilieri-Asch, V., Jaine, F.R., Peddemors, V.M., Langlois, T.J., 2021. Galapagos shark movement patterns and interactions with fishing vessels in the marine parks surrounding Lord Howe Island. Report to Parks Australia.
- Mitchell, J.D., McLean, D.L., Collin, S.P., Langlois, T.J., 2018a. Shark depredation in commercial and recreational fisheries. *Rev. Fish Biol. Fish.* 28 (4), 715–748.
- Mitchell, J.D., McLean, D.L., Collin, S.P., Taylor, S., Jackson, G., Fisher, R., Langlois, T.J., 2018b. Quantifying shark depredation in a recreational fishery in the Ningaloo Marine Park and Exmouth Gulf, Western Australia. *Mar. Ecol. Prog. Ser.* 587, 141–157.
- Nilsson, C., Cresswell, G., 1980. The formation and evolution of east Australian current warm-core eddies. *Prog. Oceanogr.* 9, 133–183.
- Nimbs, M.J., Hutton, I., Davis, T.R., Larkin, M.F., Smith, S.D., 2020. The heterobranch sea slugs of Lord Howe Island, NSW, Australia (Mollusca: Gastropoda). *Proc. R. Soc. Vic.* 132, 12–41.
- Parker, P., 1993. Lord Howe Island Marine Reserve: the final stages of planning. *Natl. Parks J.* 37, 1–15.
- Parker, D., DeMartini, E., 1995. Evaluation of a video camera technique for indexing abundances of juvenile pink snapper, *Pristipomoides filamentosus*, and other Hawaiian insular shelf fishes. *Fish. Bull.* 93, 67–77.
- Pogonoski, J.J., Paxton, J.R., Pollard, D.A., 2002. Conservation overview and action plan for Australian threatened and potentially threatened marine and estuarine fishes. *Environ. Aust.*
- Pollard, D.A., Sadovy, Y., 2018. *Epinephelus daemeli*. In: The IUCN Red List of Threatened Species 2018. eT61337A100465433. <http://dx.doi.org/10.2305/IUCN.UK.2018-2.RLTS.T61337A100465433.en>.
- Pomeroy, R.S., Watson, L.M., Parks, J.E., Cid, G.A., 2005. How is your MPA doing? A methodology for evaluating the management effectiveness of marine protected areas. *Ocean Coast. Manag.* 48, 485–502.
- Ponder, W.F., Loch, I., Berents, P., 2000. An Assessment of the Marine Invertebrate Fauna of the Lord Howe Island Shelf. Report prepared for Environment Australia, Australian Museum, Sydney.
- R Core Team, 2020. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria, (2020). Retrieved from <https://www.R-project.org/>.
- Rees, M.J., Knott, N.A., Davis, A.R., 2018a. Habitat and seascape patterns drive spatial variability in temperate fish assemblages: implications for marine protected areas. *Mar. Ecol. Prog. Ser.* 607, 171–186.
- Rees, M.J., Knott, N.A., Hing, M.L., Hammond, M., Williams, J., Neilson, J., Swadling, D.S., Jordan, A., 2021. Habitat and humans predict the distribution of juvenile and adult snapper (Sparidae: *Chrysophrys auratus*) along Australia's most populated coastline. *Estuar. Coast. Shelf Sci.*
- Rees, M.J., Knott, N.A., Neilson, J., Linklater, M., Osterloh, I., Jordan, A., Davis, A.R., 2018b. Accounting for habitat structural complexity improves the assessment of performance in no-take marine reserves. *Biol. Cons.* 224, 100–110.
- Robbins, W.D., Peddemors, V.M., Kennelly, S.J., 2011. Assessment of permanent magnets and electropositive metals to reduce the line-based capture of Galapagos sharks, *Carcharhinus galapagensis*. *Fish. Res.* 109, 100–106.
- Roberts, C.M., McClean, C.J., Veron, J.E., Hawkins, J.P., Allen, G.R., McAllister, D.E., Mittermeier, C.G., Schueler, F.W., Spalding, M., Wells, F., Vynne, C., Werner, T.B., 2002. Marine biodiversity hotspots and conservation priorities for tropical reefs. *Science* 295, 1280–1284.
- Russ, G.R., Cheal, A.J., Dolman, A.M., Emslie, M.J., Evans, R.D., Miller, I., Sweatman, H., Williamson, D.H., 2008. Rapid increase in fish numbers follows creation of world's largest marine reserve network. *Curr. Biol.* 18, R514–R515.
- Sciberras, M., Jenkins, S.R., Kaiser, M.J., Hawkins, S.J., Pullin, A.S., 2013. Evaluating the biological effectiveness of fully and partially protected marine areas. *Environ. Evid.* 2, 4.
- Sciberras, M., Jenkins, S.R., Mant, R., Kaiser, M.J., Hawkins, S.J., Pullin, A.S., 2015. Evaluating the relative conservation value of fully and partially protected marine areas. *Fish. Fish.* 16, 58–77.
- Speare, P., Cappel, M., Rees, M., Brownlie, J., Oxley, W., 2004. Deeper Water Fish and Benthic Surveys in the Lord Howe Island Marine Park (Commonwealth Waters). The Australian Institute of Marine Science, pp. 1–18.
- Speed, C.W., Rees, M.J., Cure, K., Vaughan, B., Meekan, M.G., 2019. Protection from illegal fishing and shark recovery restructures mesopredatory fish communities on a coral reef. *Ecol. Evol.* 9, 10553–10566.
- Stevens, J., Bonfil, R., Dulvy, N., Walker, P., 2000. The effects of fishing on sharks, rays, and chimaeras (chondrichthyans), and the implications for marine ecosystems. *ICES J. Mar. Sci.: J. Cons.* 57, 476–494.
- Underwood, A.J., 1997. Experiments in Ecology: Their Logical Design and Interpretation using Analysis of Variance. Cambridge University Press.
- Wickham, H., 2016. *Ggplot2: Elegant Graphics for Data Analysis*. Springer.
- Wraith, J., Lynch, T., Minchinton, T.E., Broad, A., Davis, A.R., 2013. Bait type affects fish assemblages and feeding guilds observed at baited remote underwater video stations. *Mar. Ecol. Prog. Ser.* 477, 189–199.