

Reef-scale partitioning of cryptobenthic fish assemblages across the Great Barrier Reef, Australia

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ABSTRACT: Onshore to offshore gradients in marine assemblages have been well documented on coral reefs, with most studies showing a distinct separation between onshore and offshore locations. Here we use enclosed anaesthetic sampling of small, cryptobenthic reef fishes to assess changes in assemblage composition across the Great Barrier Reef continental shelf. The cryptobenthic fishes exhibited fine-scale partitioning across the shelf. Three dominant species of goby accounted for over 55% of all fishes collected, with 1 species characterising each of the 3 key shelf positions: inner-, mid- and outer-shelf. Multivariate analyses of assemblage composition revealed further separation of reefs within the inner- and mid-shelf positions, highlighting the exceptional sensitivity of cryptobenthic reef fish assemblages to shelf position, with a progressive separation of individual reef assemblages with distance from the shore. These among-reef patterns contrast markedly with other reef fish taxa which invariably show 2 broad assemblages across the continental shelf (inner- vs. a composite mid- and outer-shelf community). As a result of this exceptional sensitivity to environmental conditions, cryptobenthic reef fish communities may represent good subjects for high-resolution monitoring of disturbances on coral reefs.

KEY WORDS: Community structure · Habitat selectivity · Sediment · Resilience · Connectivity · Self-recruitment

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INTRODUCTION

Environmental gradients often drive shifts in assemblage composition across ecosystems. On coral reefs, proximity to shore is associated with a variety of environmental gradients (e.g. sediment inputs, wave action and salinity) and has considerable effects on the structure of biological assemblages. The wide continental shelf of the Great Barrier Reef (GBR) has proved an ideal system for studying how proximity to shore influences coral reef organisms, and studies of algal, sponge, coral and fish have revealed high levels of community structure (Done 1982, Wilkinson & Cheshire 1989, Hoey & Bellwood 2008, Wismer et al. 2009).

While the literature almost ubiquitously refers to 3 shelf positions, based on distance from shore

(the inner-shelf, mid-shelf and outer-shelf; e.g. Done 1982, Russ 1984a), most studies of cross-shelf gradients of reef assemblages (regardless of taxonomy) report only 2 discrete taxonomic or functional assemblages across the continental shelf, e.g. inner- versus mid- and outer-shelf (Williams 1982, Williams & Hatcher 1983, Russ 1984a,b, Wilkinson & Cheshire 1988, Newman & Williams 1996). To date, only small groups of highly responsive taxa (e.g. subfamilial taxa of fishes with specialised feeding modes) have displayed 3 different communities across the shelf (e.g. Hoey & Bellwood 2008, Hoey et al. 2013).

Of all fish assemblages, perhaps the most responsive, yet most frequently overlooked, are cryptobenthic reef fishes. These fishes, under 50 mm in length, are highly abundant and diverse on coral reefs (Ackerman & Bellwood 2000); however, little is known

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about their distributions and the consequent implications for coral reef ecosystem function (Depczynski et al. 2007).

Cryptobenthic fishes have a close association with the benthos and provide crucial energetic links between the benthos and nekton on coral reefs. These functions are driven by the exceptional growth rates and mortality of cryptobenthic reef fishes which underpin many trophic pathways (Depczynski & Bellwood 2003, 2005, Winterbottom & Southcott 2008, Winterbottom et al. 2011). They are, in many respects, the 'powerhouse' of reef ecosystems, sensu Depczynski et al. (2007). Cryptobenthic fishes, therefore, offer a unique perspective on the effects of environmental gradients on both coral reef ecosystem structure and function. It is well known that cryptobenthic reef fishes show partitioning between microhabitats within reefs (Munday et al. 1997, Herler et al. 2011, Ahmadi et al. 2012a,b, Tornabene et al. 2013), but the patterns at broader, biogeographic scales are less well understood.

Our aim, therefore, was to examine the distribution and abundance of cryptobenthic reef fish species across the continental shelf of the northern GBR, characterising the reef fish faunas, to contrast the observed patterns with those previously described for other coral reef taxa. Due to their low mobility, strong habitat preferences (Depczynski & Bellwood 2004, González-Cabello & Bellwood 2009), and high sensitivity to changes in habitat structure (Bellwood et al. 2006, 2012, Pratchett et al. 2008), we hypothesised that cryptobenthic fishes were likely to exhibit considerable among-reef variation in assemblage composition. We therefore assessed a single, common habitat type, to examine broad cross-shelf patterns in the distribution of cryptobenthic fishes across the GBR continental shelf.

MATERIALS AND METHODS

Study sites

To examine cross-shelf variation in the assemblage structure of small cryptobenthic reef fishes, 60 samples were collected across the continental shelf of the northern GBR. Six reefs were visited; 2 from each of the 3 standard shelf positions: inner-, mid- and outer-shelf reefs (Fig. 1). The inner-shelf reefs (14–17 km from the coast) were Linnet Reef and Martin Reef; mid-shelf reefs (30–32 km) were Lizard Island and North Direction; and outer-shelf reefs (45–50 km) Hicks Reef and Day Reef. Ten samples were obtained from

each reef (in January; the Austral summer). Samples were collected from back reef rubble conglomerates at a depth of 2 to 4 m, and sample locations were separated by at least 20 m. Back reef rubble conglomerates were selected as the sampling habitat due to their widespread availability, consistent composition and structural complexity, and their suitability for cryptobenthic fishes (Depczynski & Bellwood 2004).

Collecting techniques

Small cryptobenthic reef fishes were collected using an enclosed clove-oil sampling technique (Ackerman & Bellwood 2002). A fine mesh net, 3.2 × 1 m (w × h) was arranged in a circle to delineate a 0.8 m² sampling area and to prevent the escape of any fishes. 0.50 to 0.75 l of a 5:1 ethanol:clove oil solution was then sprayed into the sampling area to anaesthetise all fishes within. After 1 min, 3 divers began a 20 min systematic search for anaesthetised fishes. Specimens were placed in an ice-water slurry, then identified to species (wherever possible) following Lachner & Karnella (1980), Myers (1991), Randall et al. (1997) and Randall (2005), with additional identifications by H. K. Larson (Museum and Art Gallery of the Northern Territory, Australia, pers. comm.).

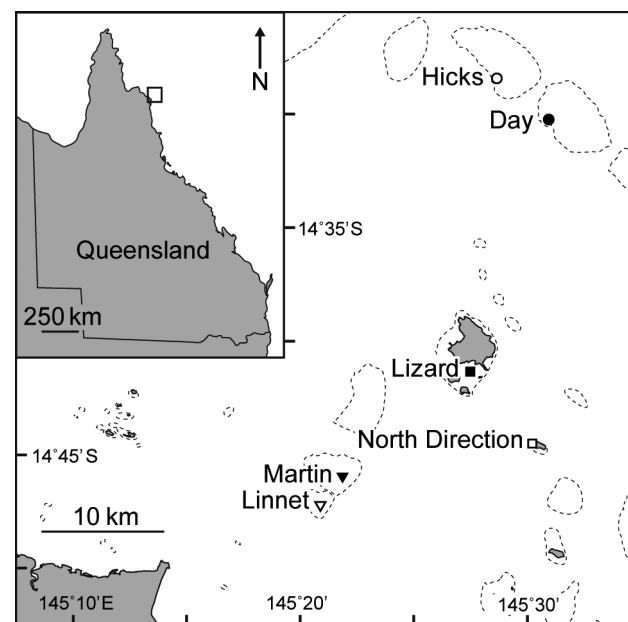


Fig. 1. Map of sampling locations across the continental shelf of the northern Great Barrier Reef. Inner-shelf: Linnet and Martin Reefs; mid-shelf: Lizard Island and North Direction Reefs; outer-shelf: Hicks and Day Reefs. Inlaid map indicates position of site map in relation to Queensland, Australia

Data analysis

Differences in the composition of cryptobenthic fish assemblages among reefs ($n = 10$ per reef), were visualised using a non-metric multidimensional scaling analysis (nMDS) and a canonical analysis of principal components (CAP). The nMDS was chosen as its unconstrained ordination allows visualisation of broad patterns in community structure, while the constrained ordination in the CAP is used to test the hypothesis that cryptobenthic fish communities differ among reefs. Both multivariate tests were performed using Bray-Curtis and chi-square distance matrices of non-standardised, $\log(x + 1)$ transformed abundance data of all species. The 2 dissimilarity measures highlight different properties of the cryptobenthic fish assemblage. Bray-Curtis accounts for the relative abundance of species revealing differences in assemblage structure, whereas chi-squared distance is not influenced by abundance; instead, it emphasises differences in assemblage composition (Anderson & Willis 2003, Willis & Anderson 2003). Vectors on all ordinations were calculated using a multiple correlation model. Finally, to test for differences in the assemblages among reefs, 1-way PERMANOVAs were performed using the same data prior to pairwise analyses to identify significant clusters. Assumptions of homogeneity of dispersions were tested using permutational analyses of multivariate dispersions (PERMDISPs) for all PERMANOVAs. All multivariate analyses were conducted in PRIMER6 with PERMANOVA+.

RESULTS

A total of 1472 specimens of 79 species in 17 families was collected (total mean density [\pm SE]: 30.7 ± 3.9 ind. m^{-2} ; see species list in Appendix 1). The Gobiidae (25 species) and Pomacentridae (13 species) had the highest species richness at all sites. Fish density was likewise dominated by gobies (22.7 ± 3.4 ind. m^{-2} ; 73.9% of individuals) and pomacentrids (2.3 ± 0.7 ind. m^{-2} ; 7.3% of individuals). The remaining 15 reef fish families comprised just 18.8% of all individuals (5.8 ± 0.7 ind. m^{-2}).

Only 3 species (all in the Gobiidae) accounted for 55.9% of all specimens collected (Fig. 2; no other species accounted for more than 4.3% of total specimens). The relative abundance of these 3 species is more remarkable given their highly uneven distributions across the continental shelf. Indeed, each of the 3 standard shelf positions was characterised by just

one of these key species (Fig. 3). On inner-shelf reefs, *Asterropteryx semipunctata* accounted for 58.0% of all specimens collected (15.2 ± 1.5 ind. m^{-2}). Mid-shelf reefs were dominated by *Eviota queenslandica* (32.3% specimens, 12.7 ± 1.7 ind. m^{-2}), and outer-shelf reefs by *E. variola* (51.7% specimens, 13.7 ± 2.0 ind. m^{-2} ; Fig. 2).

Assessment of the entire cryptobenthic reef fish assemblage revealed finer distinctions across the continental shelf. Using a Bray-Curtis dissimilarity

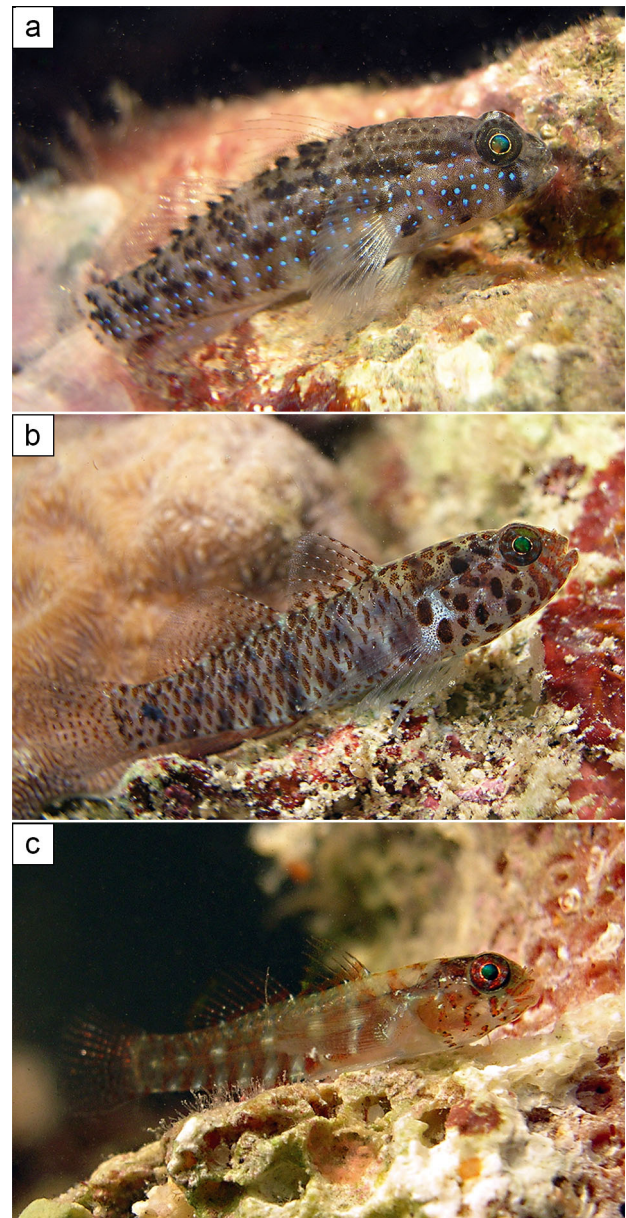


Fig. 2. The 3 key species which accounted for 55.9% of all species collected. (a) *Asterropteryx semipunctata* (21.1 mm total length [TL]), (b) *Eviota queenslandica* (16.2 mm TL) and (c) *E. variola* (12.3 mm TL). Photographs by Alonso González-Cabello

matrix to compare the relative abundance of species within assemblages, both the nMDS (Fig. 4) and CAP (Fig. 5; $\delta^2 = 0.980$, $p = 0.0001$) revealed a general pattern of shifting assemblage structure across the shelf. There was little or no overlap between reefs, except for the 2 outer-shelf reefs which overlapped almost entirely (Figs. 4 & 5). In both ordinations, the vectors revealed that the 3 key species — *A. semipunctata*, *E. queenslandica* and *E. variola* — played an important role in separating the locations. However, small suites of less abundant species helped to distinguish each of the inner- and mid-shelf reefs from each other (Figs. 4b & 5). The results of the PERMANOVA (Pseudo- $F_{5,54} = 16.074$, permutation based p using unrestricted permutation of raw data [$p_{(perm)}$] = 0.0001) and non-significant result of the PERMDISP highlight these fine-scale assemblage differences, with the pairwise analysis identifying 5 groupings from the 6 reefs; all reefs were statistically independent except for the 2 outer-shelf sites (Figs. 4a & 5; Table 1).

To assess differences in the species composition of cryptobenthic fish assemblages — rather than the relative abundances of species within the assemblages — all multivariate analyses were repeated using chi-squared distance matrices. Overall the patterns remained similar. The nMDS (Fig. 6) and CAP (Fig. 7; $\delta^2 = 0.990$, $p = 0.0001$) still showed shifts in assemblage structure across the shelf. However, as expected, more species were important in separating the samples. The key species of gobies still play a major role in distinguishing reefs by shelf position;

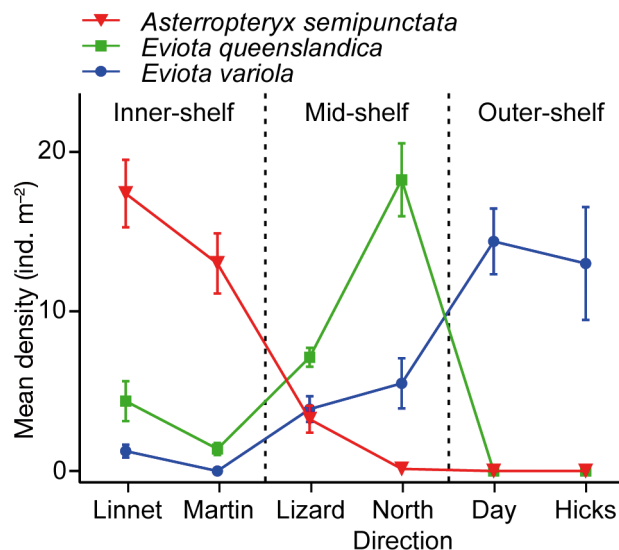


Fig. 3. Distribution of the 3 key species (see Fig. 2) across the continental shelf of the Great Barrier Reef. Data represent the mean number of individuals found at each reef ($n = 10$ sites at each reef), standardised to ind. m⁻². Error bars are \pm SE

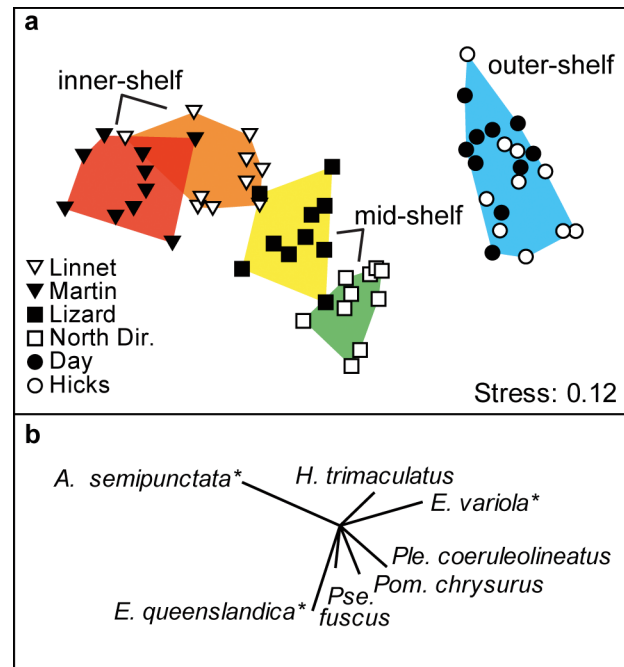


Fig. 4. (a) Non-metric multi-dimensional scaling plot (nMDS) based on a Bray-Curtis dissimilarity matrix of non-standardised, $\log(x + 1)$ -transformed abundance data of all species in the cryptobenthic reef fish assemblages at each reef. Coloured polygons represent statistically significant groupings identified by PERMANOVA. (b) Vectors associated with the nMDS were calculated following a multiple correlation model. Full species list in Appendix 1; asterisks indicate the 3 key species found in our study

however, suites of other species play similarly important roles, particularly several labrid, plesiopid and pseudochromid species. The variability in the presence of these rarer species separated the reefs further than when using a Bray-Curtis matrix, with a PERMANOVA revealing each reef as a separate community (Pseudo- $F_{5,54} = 3.094$, $p_{(perm)} = 0.0001$; Table 2). Care must be taken in the interpretation of the data, however, as the dispersion of data between reefs differed (PERMDISP: $F_{2,57} = 5.285$, $p_{(perm)} = 0.014$), although it is interesting to note that mid-shelf reefs have a less variable assemblage structure than inner- or outer-shelf reefs (Fig. 6).

DISCUSSION

While the literature has often referred to 3 shelf positions across the GBR (inner-, mid- and outer-), community composition of coral reef organisms has rarely supported this pattern. Most studies have revealed a binary community structure with discrete

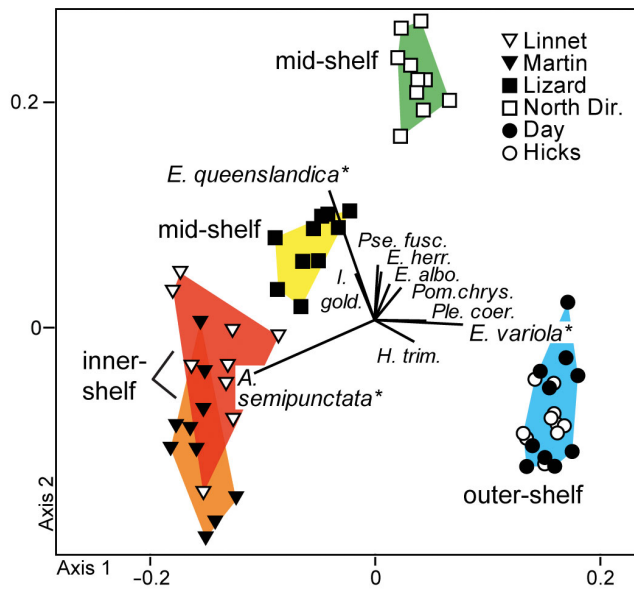


Fig. 5. Canonical analysis of principal coordinates (CAP), based on a Bray-Curtis dissimilarity matrix of non-standardised, $\log(x + 1)$ -transformed abundance data of all species in the cryptobenthic reef fish assemblages at each reef. Coloured polygons represent statistically significant groupings identified by PERMANOVA. Vectors on the plot were calculated following a multiple correlation model. Full species list in Appendix 1; asterisks indicate the 3 key species found in our study

Table 1. (a) PERMANOVA performed using a Bray-Curtis similarity coefficient matrix of non-standardised, $\log(x + 1)$ -transformed abundance data of all species, (b) pairwise analyses used to identify significant clusters. Values in **bold** are significant ($p_{(perm)} < 0.05$)

(a) Source	df	SS	MS	Pseudo- <i>F</i>	$p_{(perm)}$	Unique perms.
Reef	5	100780	20156	16.074	0.0001	9889
Residual	54	67710	1253.9			
Total	59	168490				
(b) Groups	<i>t</i>	$p_{(perm)}$	Unique perms.			
Linnet, Martin	1.9645	0.0007	9455			
Linnet, Lizard	2.6436	0.0001	9436			
Linnet, North Dir.	4.0779	0.0001	9418			
Linnet, Day	5.0075	0.0001	9401			
Linnet, Hicks	4.7137	0.0001	9341			
Martin, Lizard	3.6858	0.0001	9404			
Martin, North Dir.	4.9572	0.0001	9429			
Martin, Day	5.4221	0.0001	9379			
Martin, Hicks	5.091	0.0001	9414			
Lizard, North Dir.	2.6043	0.0001	9396			
Lizard, Day	4.0728	0.0001	9391			
Lizard, Hicks	3.9069	0.0001	9381			
North Dir., Day	4.0899	0.0001	9408			
North Dir., Hicks	3.881	0.0001	9432			
Day, Hicks	1.2725	0.1025	9435			

inner-shelf and indistinguishable mid- and outer-shelf assemblages (Russ 1984b, Newman & Williams 1996, Bellwood & Wainwright 2001, Wismer et al. 2009, Hoey et al. 2013). In contrast, cryptobenthic reef fishes support the concept of 3 separate faunas across the GBR continental shelf. Each shelf position is characterised by 1 key species of goby, which accounts for more than 30% of all individuals recorded at that location. This pattern of differentiation between locations, characterised by single species offers clearer cross-shelf distinctions than most previous studies (cf. Wilkinson & Cheshire 1989, Hoey & Bellwood 2008) and highlights the high levels of habitat selectivity displayed by cryptobenthic reef fishes.

When considering the structure and composition of cryptobenthic fish assemblages, the resolution of this selectivity becomes even more apparent. Indeed, multivariate analyses revealed fine-scale differences in cryptobenthic fish assemblages among reefs within shelf positions. Primarily seen on the inner- and mid-shelf reefs, assemblages were dominated by their respective key species; however, the composition of other species including labrids, plesiopids and pseudochromids also distinguished the reefs within the shelf positions. Essentially the main characters remained, while the supporting roles were filled by a different cast.

Where previous studies have revealed both temperate and tropical cryptobenthic reef fishes to be highly selective at a microhabitat scale (Willis & Anderson 2003, Munday 2004, Feary & Clements 2006, Ahmadi 2012a,b, Tornabene et al. 2013), we have shown that this sensitivity also applies at larger biogeographical scales, across broad environmental gradients. Our data indicate that cryptobenthic reef fish assemblages may be better indicators of changing conditions within shelf positions than larger reef taxa. However, it is crucial that we understand what drives the differences among cryptobenthic reef fish assemblages so we can fully exploit the potential of their responsiveness to environmental changes.

While all fishes for this study were collected from structurally similar rubble beds, the surrounding benthic cover (e.g. coral or macroalgae) will have differed at each shelf position (Wismer

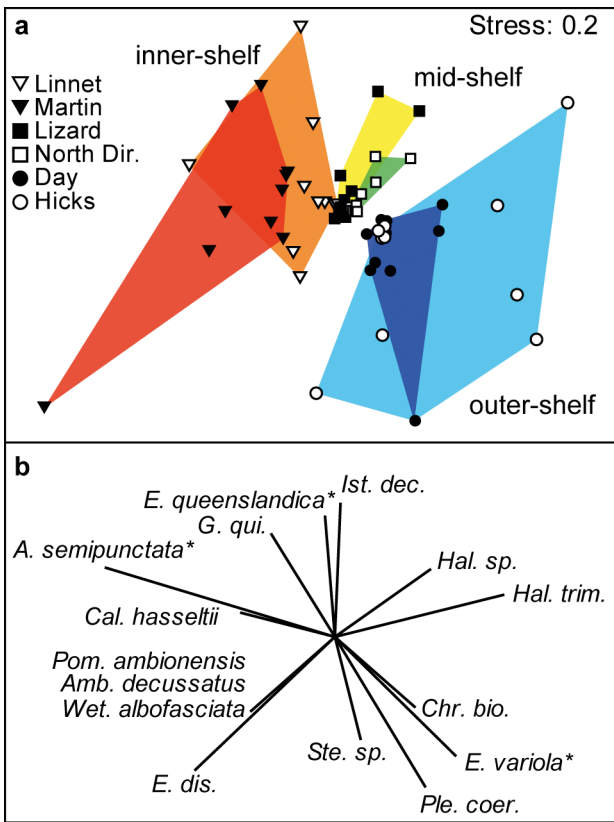


Fig. 6. (a) Non-metric multi-dimensional scaling plot (nMDS) based on a chi-squared distance matrix of non-standardised, $\log(x + 1)$ -transformed abundance data of all species in the cryptobenthic reef fish assemblages at each reef. Coloured polygons represent statistically significant groupings identified by PERMANOVA. (b) Vectors associated with the nMDS were calculated following a multiple correlation model. Full species list in Appendix 1; asterisks indicate the 3 key species found in our study

et al. 2009) and may have affected the cryptobenthic reef fish assemblage. Broad-scale changes in benthic cover, however, have repeatedly been shown to have little effect on rubble-dwelling cryptobenthic fish, with degraded reefs often housing broadly similar assemblages to healthy reefs (Willis & Anderson 2003, Feary & Clements 2006, Ahmadiya et al. 2012a), and little evidence of changes following increases in surrounding coral cover (Bellwood et al. 2012) or minor disturbances (Lefèvre & Bellwood 2015). Other factors must therefore be affecting the distribution and abundance of cryptobenthic reef fishes.

One likely factor driving assemblage structure among reefs is the benthic sediment load on the rubble. Proximity to terrestrial sediment inputs and differences in hydrodynamic activity among reefs will lead to differences in the sediment loads across the continental shelf (Fabricius 2005, Orpin & Ridd 2012). Sediments affect the availability of detritus (Purcell & Bellwood 2001) and benthic microcrustacea (Kramer et al. 2014), both significant sources of nutrition for cryptobenthic reef fishes (Depczynski & Bellwood 2003, Wilson et al. 2003, Kramer et al. 2012). Therefore, differences in sediment loads, which are known to affect herbivory and other ecological processes (Bellwood & Fulton 2008, Birrell et al. 2008, Wenger et al. 2013, Goatley & Bellwood 2013, Gordon et al. 2015), may also play important roles in shaping cryptobenthic fish assemblages. This, in turn, may modify energy flows among reefs as cryptobenthic fishes form a crucial link between detrital material and higher trophic levels (Depczynski et al. 2007).

Anthropogenic disturbances, including poor coastal land-use practices, dredging and sediment dumping, and increased storm frequency as a result of climate

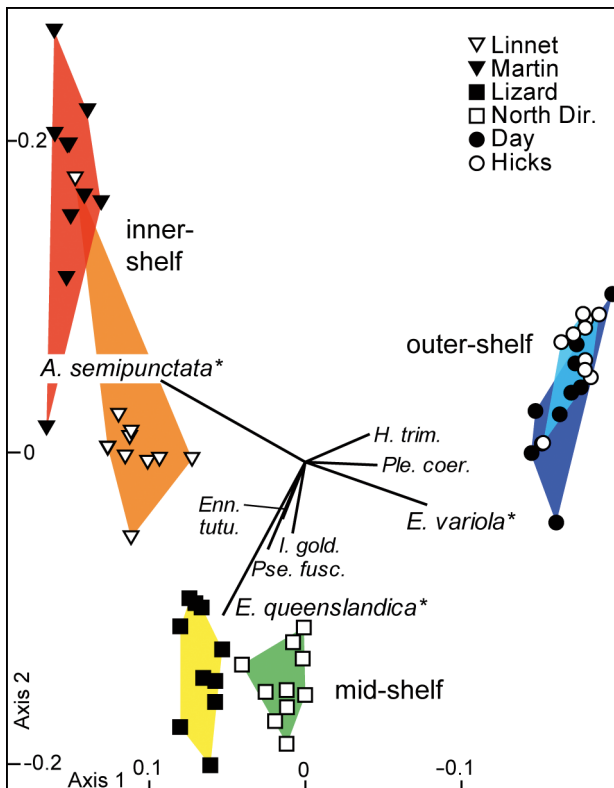


Fig. 7. Canonical analysis of principal coordinates (CAP), based on a chi-squared distance matrix of non-standardised, $\log(x + 1)$ -transformed abundance data of all species in the cryptobenthic reef fish assemblages at each reef. Coloured polygons represent statistically significant groupings identified by PERMANOVA. Vectors on the plot were calculated following a multiple correlation model. Full species list in Appendix 1; asterisks indicate the 3 key species found in our study

Table 2. (a) PERMANOVA performed using a chi-squared distance matrix of non-standardised, $\log(x + 1)$ -transformed abundance data of all species, (b) pairwise analyses used to identify significant clusters. Values in **bold** are significant ($p_{(\text{perm})} < 0.05$)

(a) Source	df	SS	MS	Pseudo- <i>F</i>	$p_{(\text{perm})}$	Unique perms.
Reef	5	1763.5	352.7	3.094	0.0001	9629
Residual	54	6155.4	114.0			
Total	59	7918.8				

(b) Groups	<i>t</i>	$p_{(\text{perm})}$	Unique perms.
Linnet, Martin	1.2360	0.0031	9296
Linnet, Lizard	1.3756	0.0001	9339
Linnet, North Dir.	1.8249	0.0001	9299
Linnet, Day	1.9723	0.0001	9296
Linnet, Hicks	1.8312	0.0001	9300
Martin, Lizard	1.6756	0.0001	9379
Martin, North Dir.	1.9866	0.0001	9361
Martin, Day	2.0686	0.0001	9345
Martin, Hicks	1.9401	0.0004	9371
Lizard, North Dir.	1.5988	0.0001	9378
Lizard, Day	1.8618	0.0001	9364
Lizard, Hicks	1.7371	0.0001	9334
North Dir., Day	1.9905	0.0001	9364
North Dir., Hicks	1.8278	0.0001	9369
Day, Hicks	1.2016	0.0181	9317

change, are causing increased degradation on coral reefs, especially those close to shore (Hughes et al. 2015). As a result, we may see changes in benthic assemblages across the continental shelf, as inner-shelf conditions and communities move progressively off-shore. Due to their exceptional site specificity, short lifespans (Depczynski & Bellwood 2005, Depczynski et al. 2007) and potentially rapid responses to change (Bellwood et al. 2006, 2012), cryptobenthic fishes are likely to be key indicators of environmental change (cf. Munday 2004), and may provide a novel and sensitive metric of reef degradation.

Our results also identify new considerations for coral reef biogeography. To date, most biogeographic studies of reef fishes reveal relatively broad-scale trends across regions or between reefs, maintained by long distance connectivity of planktonic larvae (e.g. Lessios & Robertson 2006, Floeter et al. 2008, Harrison et al. 2012, Kulbicki et al. 2013). Cryptobenthic fishes show finer-scale partitioning, with assemblages differing not only between shelf positions but also between individual reefs. These findings are supported by molecular evidence identifying localised genetic separation in multiple small reef fish taxa (Gerlach et al. 2007). Indeed, previous studies have identified genetic distinctions in populations of *Eviota queenslandica* (one of our 3 key spe-

cies) between North Direction Island, Lizard Island and nearby inner-shelf reefs (Farnsworth et al. 2010). Such fine-scale partitioning of cryptobenthic reef fish assemblages is particularly surprising as most cryptobenthic families have planktonic larval durations comparable to those of larger reef fishes (Depczynski & Bellwood 2005, Winterbottom & Southcott 2008, Winterbottom et al. 2011). They thus have the potential to disperse over large distances. Habitat needs, competition among species, or behavioural attributes of pelagic-stage cryptobenthic fishes must therefore play a key role in driving these highly specific distributions.

Our findings reveal that the exceptional sensitivity and selectivity of cryptobenthic fish assemblages, previously known at ecological scales, now applies across broader biogeographic scales. As crucial links between lower trophic levels and higher predators, cryptobenthic reef fish assemblages may play a key role in maintaining energy flows on coral reefs and, as such, may represent exceptionally sensitive and potentially responsive indicators of coral reef ecosystem processes.

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Appendix 1. Species list from the 60 samples collected from back reef rubble conglomerates across the continental shelf of the GBR. Data presented are mean densities (ind. m⁻²) at each reef (n = 10 replicates per reef). The average density of cryptobenthic reef fishes was 30.7 ± 3.9 ind. m⁻² across all reefs; numbers in parentheses below reef names represent the mean density of cryptobenthic reef fishes at each reef

Family	Species	Linnet (31.0)	Martin (21.4)	Lizard (29.9)	North Dir. (48.8)	Day (27.0)	Hicks (26.0)
Antennariidae	<i>Antennarius coccineus</i>	–	–	–	–	0.3	0.1
Apogonidae	<i>Apogon compressus</i>	–	–	0.1	–	–	–
	<i>Apogon doryssa</i>	–	–	0.1	–	–	–
	<i>Apogon fuscus</i>	–	–	–	–	–	0.1
	<i>Apogon novemfasciatus</i>	–	–	–	–	–	0.1
	<i>Cheilodipterus quinquelineatus</i>	–	0.1	–	–	–	–
	<i>Fowleria marmorata</i>	0.3	0.3	–	–	–	–
Blenniidae	<i>Escenius australianus</i>	–	–	–	–	0.1	–
	<i>Escenius stictus</i>	–	–	–	0.1	–	–
	<i>Salarias alboguttatus</i>	–	–	0.1	0.5	0.1	–
	<i>Salarias fasciatus</i>	–	–	0.5	0.4	–	–
	<i>Salarias patzneri</i>	–	–	–	1.0	0.1	–
Callionymidae	<i>Synchiropus</i> sp.	0.3	–	0.1	–	–	–
Gobiesocidae	<i>Lepadichthys</i> sp.	–	–	0.1	0.1	–	–
Gobiidae	<i>Amblygobius decussatus</i>	–	0.1	–	–	–	–
	<i>Amblygobius phalaena</i>	–	0.3	0.9	–	0.1	–
	<i>Asterropteryx semipunctata</i>	17.4	13.0	3.3	0.1	–	–
	<i>Bathygobius</i> sp.	–	–	–	0.3	–	0.3
	<i>Callogobius</i> cf. <i>clitellus</i>	1.3	0.3	0.4	0.8	0.3	–
	<i>Callogobius hasseltii</i>	0.3	0.1	–	–	–	–
	<i>Callogobius sclateri</i>	0.5	0.9	0.5	0.3	–	–
	<i>Ctenogobius feroculus</i>	–	–	0.1	–	–	–
	<i>Eviota albolineata</i>	–	–	–	1.9	0.6	0.1
	<i>Eviota</i> cf. <i>distigma</i> (sp. 2)	–	1.0	–	0.3	–	–
	<i>Eviota</i> cf. <i>herrei</i> (sp.3)	–	–	–	5.8	–	–
	<i>Eviota melasma</i>	0.3	0.3	–	–	–	–
<i>Eviota queenslandica</i>	4.4	1.4	7.1	18.3	–	–	

Appendix 1 (continued)

Family	Species	Linnet (31.0)	Martin (21.4)	Lizard (29.9)	North Dir. (48.8)	Day (27.0)	Hicks (26.0)
Gobiidae	<i>Eviota</i> sp. 1	–	0.4	0.1	2.1	–	–
	<i>Eviota</i> sp. 4	–	–	0.1	–	0.1	–
	<i>Eviota variola</i>	1.3	–	3.9	5.5	14.4	13.0
	<i>Fusigobius duospilus</i>	–	0.1	–	–	0.4	0.1
	<i>Fusigobius neophytus</i>	0.3	–	0.1	–	–	–
	<i>Gnatholepis scapulostigma</i>	–	–	–	–	1.4	1.3
	<i>Gnatholepis</i> sp.	–	–	–	–	–	0.1
	<i>Gobiodon quinquestrigatus</i>	–	0.3	–	–	–	–
	<i>Gobiodon</i> sp.	–	–	–	0.3	–	–
	<i>Istigobius decoratus</i>	0.3	–	–	–	–	–
	<i>Istigobius goldmanni</i>	1.0	0.6	4.4	2.0	–	–
	<i>Paragobiodon echinocephalus</i>	–	–	–	0.3	–	–
	Labridae	<i>Anampses geographicus</i>	–	0.1	0.4	–	0.1
<i>Coris batuensis</i>		0.1	–	0.4	0.4	–	–
<i>Halichoeres melanurus</i>		–	–	0.1	0.3	–	–
<i>Halichoeres</i> sp.		–	–	–	–	–	0.3
<i>Halichoeres trimaculatus</i>		–	–	–	–	1.3	2.1
<i>Scarus</i> sp.		–	–	0.1	0.1	0.1	0.9
<i>Wetmorella albofasciata</i>		–	0.1	–	–	–	–
Muraenidae	<i>Echidna</i> sp.	–	–	0.3	–	–	–
	<i>Gymnothorax fimbriatus</i>	–	–	0.1	–	–	0.1
	<i>Gymnothorax</i> sp.	0.1	–	–	–	–	–
Nemipteidae	<i>Parapercis cylindrica</i>	0.1	–	0.8	–	–	–
	<i>Parapercis lineopunctata</i>	–	0.3	–	–	–	–
Plesiopidae	<i>Plesiops coeruleolineatus</i>	–	–	0.3	0.8	1.5	2.1
	<i>Plesiops</i> sp.	–	–	0.3	–	–	–
Pomacentridae	<i>Chromis xanthura</i>	–	–	–	–	–	0.1
	<i>Chrysiptera biocellata</i>	–	–	–	–	–	0.3
	<i>Chrysiptera rollandi</i>	–	0.3	–	–	–	–
	<i>Dascyllus aruanus</i>	–	–	–	–	–	0.1
	<i>Dischistodus pseudochrysopoecilus</i>	0.1	–	0.5	0.5	0.4	0.1
	<i>Pomacentrus ambionensis</i>	–	0.1	–	–	–	–
	<i>Pomacentrus bankanensis</i>	–	–	–	0.1	1.4	0.6
	<i>Pomacentrus chrysurus</i>	0.4	–	0.9	2.9	1.1	1.5
	<i>Pomacentrus grammorhynchus</i>	–	–	0.5	–	–	–
	<i>Pomacentrus moluccensis</i>	0.1	–	–	–	–	–
	<i>Pomacentrus</i> sp.	–	–	–	–	1.3	–
	<i>Pomacentrus wardi</i>	–	–	–	–	0.1	–
Pseudochromidae	<i>Stegastes</i> sp.	–	–	–	–	0.1	–
	<i>Pseudochromis cyanotaenia</i>	0.1	–	–	0.6	–	–
Scorpaenidae	<i>Pseudochromis fuscus</i>	0.4	0.1	1.5	2.8	0.4	0.3
	<i>Sebastapistes bynoensis</i>	–	–	–	–	0.1	0.5
Syngnathidae	<i>Sebastapistes strongia</i>	0.1	–	0.4	0.1	1.0	0.9
	<i>Choeroichthys brachysoma</i>	0.1	0.1	0.3	–	–	–
Tripterygiidae	<i>Halicampus</i> sp.	–	0.1	–	–	–	–
	<i>Micrognathus brevirostris</i>	0.5	1.1	0.4	–	–	–
	<i>Enneapterygius atrogulare</i>	–	–	–	0.3	–	–
	<i>Enneapterygius</i> sp. A	–	–	–	–	0.1	0.5
Tripterygiidae	<i>Enneapterygius</i> sp. B	0.3	–	–	–	–	0.1
	<i>Enneapterygius tutuilae</i>	1.1	–	0.9	0.3	0.1	–