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SHORT NOTE

Large-scale spatial variation in epilithic algal matrix cryptofaunal assemblages on the Great Barrier Reef

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Abstract Spatial variation in the epilithic algal matrix (EAM) cryptofauna was investigated at three locations on the Great Barrier Reef: two inner shelf—Orpheus Island and the Turtle Island group—and a mid-shelf location, Lizard Island. Although the EAM appears to be a relatively simple and consistent habitat, significant differences in cryptofaunal assemblages were found between locations. EAM assemblages from Orpheus Island were markedly different. This appears to be a function of the sediment profile characteristics (grain size >60 μm) at Orpheus Island, as many cryptofaunal taxa displayed positive relationships with sediment volume. However, sediment volumes did not differ significantly between the three locations, highlighting the possibility of cyclonic activity affecting the sediment profile at Orpheus Island in the months preceding the study, in addition to the nutrient input from major terrigenous sources. The results of this study show that EAM cryptofaunal assemblages are not uniform across the Great Barrier Reef and suggest that dissolved nutrients, sediment loads and distance from river systems may be significant drivers of cryptobenthic faunal compositions.

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Introduction

Investigations of marine assemblages across large spatial scales often reveal distinct patterns of species distributions and community structure, particularly in latitudinal or cross-shelf studies (Stevens 1989; Bellwood and Wainwright 2001; Wismer et al. 2009). Spreading nearly 2,000 km along the coastline and up to 200 km offshore, Australia's Great Barrier Reef shows clear divisions between inshore, mid- and offshore reefs. This pattern holds true for a wide variety of organisms, ranging from fishes (Bellwood and Wainwright 2001; Hoey and Bellwood 2008) and benthic macroalgae (Wismer et al. 2009), to crustose coralline algae (Fabricius and De'ath 2001) and crustaceans (Preston and Doherty 1994).

Factors that may drive the divisions in the cross-shelf distributions include wave energy (Bellwood and Wainwright 2001), benthic composition (Wismer et al. 2009), the availability of nutrients (Uthicke and Nobes 2008; Uthicke and Altenrath 2010), turbidity (Cooper et al. 2007), and sedimentation (Preston and Doherty 1994; McCook 1996; Fabricius and De'ath 2001). Relatively high rates of sedimentation on inner shelf reefs appear to be particularly influential on benthic organisms (McCook 1996; Fabricius and De'ath 2001; McCulloch et al. 2003). For example, in high sedimentation locations, crustose coralline algae cover is low (Fabricius and De'ath 2001) and crustacean communities in dead corals have distinctly different assemblages and lower abundances (Preston and Doherty 1994). Sediment, per se, does little to explain the large-scale community structure of Foraminifera, however, turbidity and nutrient profiles appear to have a much greater influence on these benthic organisms (Cooper et al. 2007; Uthicke and Nobes 2008; Uthicke and Altenrath 2010).

The epilithic algal matrix (EAM) is a significant, and often dominant, component of benthic assemblages on coral reefs, covering approximately 30–70 % of the available surface area (Klumpp and McKinnon 1992; Goatley and Bellwood 2011). Within the EAM, short filamentous and crustose algal species are common (Scott and Russ 1987; Connell et al. 2014) in addition to nutrient-rich detritus (Crossman et al. 2001; Wilson et al. 2003), inorganic sediments and a community of small organisms (Kramer et al. 2012). Once thought to be exploited solely by herbivorous fishes, the EAM has progressively gained recognition as being a valuable resource for detritivorous (Wilson et al. 2003, 2004) and small carnivorous fishes (Kramer et al. 2013). Although the EAM is structurally simple, based on a short algal turf ranging from 1 to 6 mm in height (Bonaldo and Bellwood 2011) it supports a surprisingly diverse and abundant community of motile taxa (Kramer et al. 2012) that are likely to be important contributors to ecosystem function (Kennedy and Jacoby 1999; Schratzberger et al. 2000). In the present study, the term 'cryptofauna' will be used to include both meiofauna (0.06–0.5 mm; Giere 2009) and larger taxa (up to 5 mm).

Environmental factors are capable of having both positive and negative effects on the abundance of organisms and the overall structure of a community. One such factor is the effect of sediments, which consist of both organic and inorganic settled particulate matter. The amount of sediment is particularly important to coral reefs, as high levels are known to place corals under metabolic stress (Rogers 1990), inhibit coral settlement (Birrell et al. 2005) and suppress grazing by herbivorous fishes (Bellwood and Fulton 2008). The influence of sediment and dissolved nutrients on the abundance of small organisms is relatively well known (Preston and Doherty 1994; Cooper et al. 2007; Uthicke and Altenrath 2010; Kramer et al. 2012). However, whilst the abundance of cryptofauna is reported to remain relatively temporally consistent (Klumpp et al. 1988; Logan et al. 2008) not much is known about spatial variability. The present study aims to investigate the spatial differences in cross- and along-shelf variation of EAM cryptofauna using two inner shelf locations and a typical mid-shelf location on the GBR. In addition, sediment volumes were measured and proximity to major river systems was determined to examine the relationship between sediment, nutrients and EAM cryptofauna at these locations.

Methods

Sampling locations

Samples of EAM fauna were collected from three locations across the Great Barrier Reef: Orpheus Island, the Turtle Island group and Lizard Island (Fig. 1). Orpheus Island is located on the inner Great Barrier Reef (18° 36′40″S, 146° 29′20″E), 16 km from the mainland. Samples were collected from four sites across the reef of Pioneer Bay, Orpheus Island. A detailed description of Pioneer Bay habitats is given in Fox and Bellwood (2007). The Turtle Island group is similarly located on the inner-shelf of the GBR, 12 km offshore and approximately 450 km north of Orpheus Island (14° 43′55″S, 145° 11′00″). Composed of nine small islands and reefs, two islands (2 sites each) were sampled for EAM cryptofauna. Lizard Island is located on the mid-shelf GBR (14° 40′40″S, 145° 26′ 55″E) 30 km offshore and on similar latitude to the Turtle Island group. Samples were collected from the reef in Mermaid Cove and the Lagoon Entrance (2 sites each). Sampling at all locations was conducted during the austral summer months (November–March) to reduce variation due to seasonal effects, although seasons usually have a minimal influence on cryptofaunal populations (Klumpp et al. 1988; Logan et al. 2008). For consistency, sampling at all locations was conducted from similar depths (2–3 m depth at high tide) on the fringing reef crest of the leeward shore where live coral and EAM were dominant and macroalgae sparse. All locations are marine protected areas where fishing is prohibited and removal of organisms is only granted for approved research. As such, the marine communities are considered to be relatively intact and include all major functional groups of herbivorous fishes (Bellwood et al. 2004; Green and Bellwood 2009), thereby subjecting the EAM to similar grazing pressure. The EAM at all sites was of a similar height (4–6 mm) and morphology (short, filamentous Chlorophyta and Rhodophyta). Samples were taken from open planar areas away from territorial damselfish territories that may modify EAM composition (Klumpp et al. 1988). Sampling on Orpheus Island occurred 1 month after a tropical cyclone (Cyclone Yasi, Category 5) passed over the island (Great Barrier Reef Marine Park Authority 2011) and 3 months after extensive coastal flooding due to Cyclone Tasha (Hayes and Goonetilleke 2012).

Sample collection

Samples from all locations were collected using SCUBA from the reef crest zone. A total of 60 samples was obtained, consisting of five individual samples from each of the four sites at each of the three locations. An underwater vacuum apparatus based on the design described in Kramer et al. (2012) was utilised to remove all particulate material within a defined area. The sampling area was delimited by a section of PVC pipe 51 mm in diameter, representing 20.4 cm^2 of EAM. The sampling area was vacuumed thoroughly for 30 s, during which time the resident organisms and particulate matter were drawn into the apparatus and retained by a 60 μm plankton mesh filter bag. The filter bag

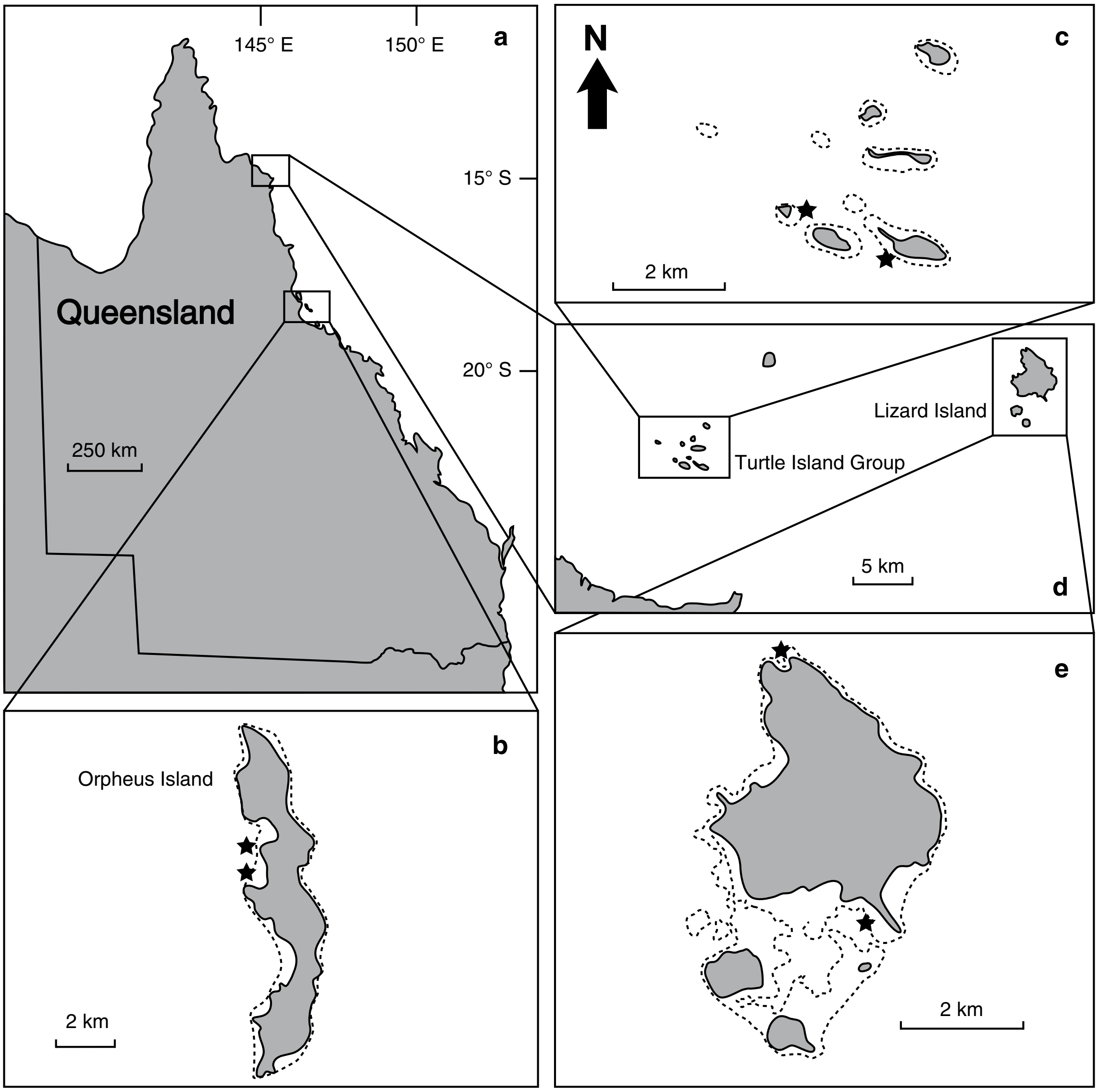

Fig. 1 Sampling locations. **a** Queensland, Australia, indicating regions where sampling was conducted. **b** Orpheus Island. **c** Turtle Island group. **d** Northern sampling locations: Turtle Island group and Lizard Island. **e** Lizard Island. *Dashed lines* indicate fringing reefs and stars are sampling sites. Two sites were sampled at *each star*

was then sealed, transported to the surface and the contents fixed in 4 % formaldehyde solution in seawater.

Sample and data analysis

Samples were stained with eosin erythrosin to aid in distinguishing organisms amongst the particulate matter. Collected material was washed onto a petri dish, which had a grid affixed to the bottom to prevent observing the same organism twice. Samples were examined using an Olympus SZ40 binocular microscope under 40× magnification to identify taxa to the lowest functional taxonomic level (usually order). This level of taxonomic resolution was deemed appropriate for the purpose of detecting spatial differences in the EAM fauna and comparing overall community composition (cf. Beattle and Oliver 1994; Krell 2004). The abundance of the respective organisms was recorded and standardised to 100 cm^2. The sediment volume of each sample was calculated following Kramer et al. (2012). Using digital vernier calipers (accuracy: ±0.02 mm), the depth of the settled particulates within the sample vial was measured and the volume estimated based on a calibrated vial.

The dataset used for the analysis incorporated abundant organisms and excluded those taxa with fewer than 10 individuals 100 cm^{-2}. Thus, taxa considered in the analysis were Amphipoda, Cumacea, Gastropoda, Harpacticoida, Isopoda, Polychaeta, Ostracoda and Tanaidacea. Organisms that were observed, but not included in the analysis due to low abundances, were Chaetognatha, Chironomida, Cumacea and Decapoda. The cryptofaunal community data were explored using a non-metric multidimensional scaling (nMDS) ordination of a Manhattan distance matrix based on standardised data, thus representing proportions rather than raw abundance and preventing the over-representation of abundant taxa. Taxa vectors (based on maximum correlation with taxon variables) were added to the ordination to aid interpretation of the data (Oksanen et al. 2013). A permutational multivariate analysis of variance (PERMANOVA) was conducted to elucidate differences in sites and locations. Spearman rank correlations were conducted to investigate the relationship between sediment and the abundance of organisms. Additionally, a one-way ANOVA was used to test the difference in sediment volume among locations. Multivariate analyses, Spearman rank correlations and ANOVA were conducted using the R packages vegan (Oksanen et al. 2013) and Hmisc (Harrell 2014). Pairwise comparisons were calculated using Primer 6 with PERMANOVA.

Results

PERMANOVA analysis found no significant difference in cryptofaunal assemblages among sites within locations, or in the interaction between sites and locations. Site data were therefore pooled within locations for the remainder of the analyses. Investigation of the nMDS revealed that each location could be separated into distinct ordination groupings. This is supported by the PERMANOVA, which indicates that locations were statistically significant (PERMANOVA, $P < 0.001$). The pairwise PERMANOVA further indicated that all locations were significantly different from each other (pairwise PERMANOVA, $P < 0.05$). From the vectors fitted to the nMDS ordination (Fig. 2), Orpheus Island showed strong gradients for Polychaeta and Gastropoda, whereas the Turtle Islands and Lizard Island are represented by a gradient towards the Harpacticoida. Vectors also indicate that Amphipoda, Cumacea and Tanaidacea exhibit strong gradients toward the Turtle Islands. Although Orpheus Island did not exhibit any shared multivariate space with the other locations, the Turtle Islands and Lizard Island did have a small degree of overlap, indicating that some sampling locations between these two regions were somewhat similar in EAM community composition.

Data were further explored by investigating the relationship between sediment and the abundance of organisms in the EAM. The only taxon not to have a significant correlation with sediment was Isopoda (Spearman rank correlation, $r_s = 0.125$, $N = 60$, $P = 0.340$). All other taxa had a significant, positive, relationship with sediment, ranging from ($r_s = 0.571$, $N = 60$, $P < 0.001$) to ($r_s = 0.280$, $N = 60$, $P = 0.03$) for Polychaeta and Amphipoda, respectively (Fig. 3). However, sediment volumes among locations revealed no significant difference in the volume of sediment at each location (ANOVA, $F_{(2,\ 57)} = 1.819$, $P = 0.171$).

Discussion

Cross-shelf studies on the GBR have consistently revealed a distinct separation between inner, mid and outer shelf reefs. This pattern applies to community assemblages (Done 1982; Preston and Doherty 1994; Bellwood and Wainwright 2001), benthic composition (McCook 1996;

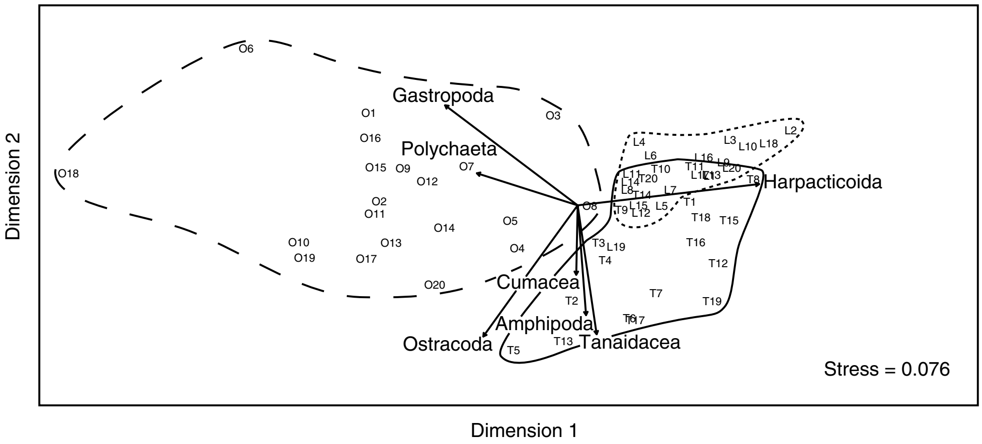

Fig. 2 Non-metric multidimensional scaling (nMDS) ordination of epilithic algal matrix fauna from Orpheus Island (*dashed line*), Lizard Island (*dotted line*) and Turtle Island group (*solid line*). *Vectors* indicate strength and direction of taxa gradients. All locations are significantly different (pairwise PERMANOVA, $P < 0.05$)

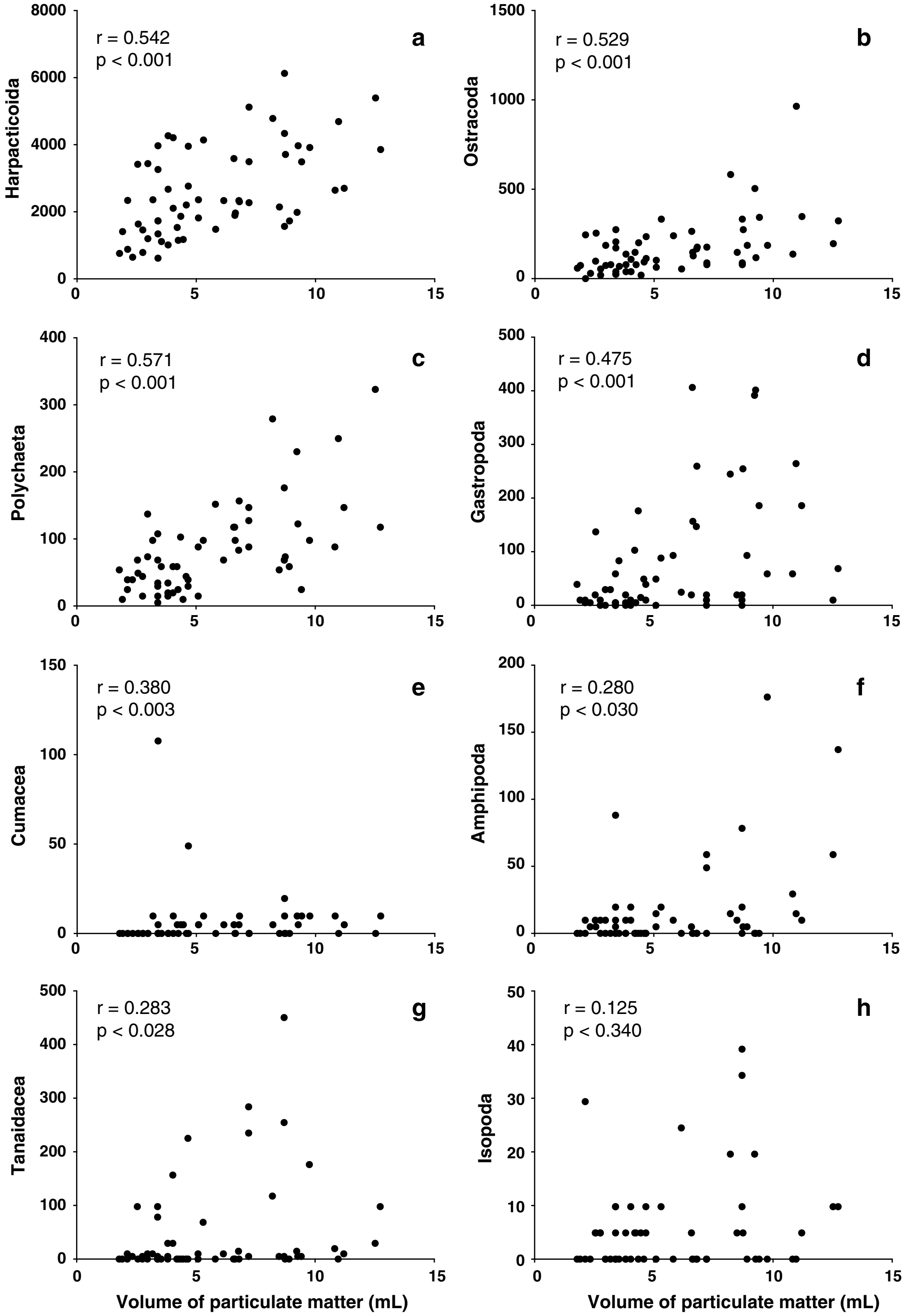

Fig. 3 Spearman rank correlations of the relationships between sediment volume and abundance of cryptofaunal organisms. Correlation coefficients and statistical significance values for each relationship are inserted onto the respective correlations

Fabricius and De'ath 2001; Wismer et al. 2009) and ecosystem processes (Russ and McCook 1999; Hoey and Bellwood 2008). The preliminary observations in the present study suggest that there is not only a cross-shelf difference in EAM cryptofauna composition, but also a distinct along-shelf separation. Somewhat surprisingly, the nMDS suggests that an inner shelf reef (Orpheus Island) differs more from another inner shelf location (Turtle Island group) than the Turtle Islands differ from a nearby mid-shelf system (Lizard Island). This result contrasts with other cross-shelf studies, which typically report that features such as hydrodynamics (Bellwood and Wainwright

2001), sediments (Preston and Doherty 1994; Fabricius and De'ath 2001), abundance of macroalgae (Wismer et al. 2009), or a combination of the above (Hoey and Bellwood 2008), drive the differences across large spatial scales. The samples of the EAM collected in the present study were taken from largely similar environments, thereby controlling for the effect of depth, reef zone, season, proximity of macroalgae and hydrodynamics. Yet, the EAM cryptofauna differed significantly among all locations.

Whilst these results were unexpected, there are indications that this variation in EAM cryptofauna may be a result of the water quality and nature of sediments at each location. The coastline adjacent to the sampling locations is subject to tropical seasonal fluctuations, namely a dry season and a wet season. During the wet season, extensive flooding is common, where large amounts of terrigenous sediments and anthropogenic contaminants are flushed into major rivers and out into coastal waters (Devlin and Brodie 2005; Brodie et al. 2010). The resulting sediment plumes typically move in a northerly direction along the Queensland coastline (McCulloch et al. 2003; Brodie et al. 2010). The catchments that are most likely to affect the locations in the present study are the Mossman–Daintree and a small section of the Northeastern Cape York catchment (Turtle Island group and Lizard Island) and the Burdekin-Haughton and Ross-Black catchments (Orpheus Island) (Neil et al. 2002; Bainbridge et al. 2012). It is important to note the difference in catchment areas that deliver floodwaters into the GBR lagoon. River catchments that affect the Turtle Island group and Lizard Island are much smaller than those that influence Orpheus Island (Neil et al. 2002). In addition, of all the rivers along the Queensland coast, the Burdekin River produces the highest volume of suspended sediments to the GBR lagoon, emitting an estimated 3×10^8 kg year^{-1} (Neil et al. 2002; McCulloch et al. 2003; Kroon et al. 2012). Although Orpheus Island is not in the direct path of the flood plume stemming from the Burdekin River, excessive nutrients and (to a lesser extent) suspended sediments from the Burdekin River have been documented at considerable distances that easily extend past, and encompass, Orpheus Island (Devlin and Brodie 2005; Devlin et al. 2008; Bainbridge et al. 2012).

In the present study, although almost all taxa displayed significant positive relationships with sediment volume, four taxa in particular appear to be influenced most strongly: Gastropoda, Harpacticoida, Ostracoda and Polychaeta. Of these, Gastropoda and Polychaeta were characteristic of Orpheus Island, whereas Harpacticoida and Ostracoda were dominant taxa at the Turtle Islands and at Lizard Island. The major trophic role of these four taxa is primary consumption (Ruppert et al. 2004), thus it would be expected that an increase in primary productivity due to nutrient input would increase populations (Montagna et al. 1995). It is likely that the sediment composition and nutrient profile created by local terrigenous inputs (i.e. flood plumes from the Burdekin-Haughton and Ross-Black catchments) produces a distinctive EAM environment at Orpheus Island. Furthermore, it appears that Harpacticoida and Ostracoda are abundant EAM taxa in all locations, therefore it is the paucity of Gastropoda and Polychaeta at the Turtle Islands and Lizard Island locations that most clearly drove the distinctly different ordination groups. Future analyses that incorporate a finer taxonomic resolution, particularly of these four Orders (Gastropoda, Harpacticoida, Ostracoda and Polychaeta), may provide greater detail in regards to how families, genera or species respond to specific environmental conditions, or how the abundance of specific trophic categories may vary.

Although the sediment volumes were not significantly different among locations, it is likely that it was the composition (i.e. particle size or nutrient profiles) rather than volume, per se, that most heavily influenced the abundance of certain taxa and thus, community composition. In this regard, the effect of cyclonic activity on the GBR may also be important. Cyclones subject the reef to substantial hydrodynamic action, causing resuspension and flushing of sediment from the reef, especially in shallow waters (Wolanski et al. 2005). As the majority of the fringing reef of Orpheus Island is less than 10 m depth, extensive resuspension and removal of sediment from the reef crest during cyclones is likely. Additionally, extensive flooding is often associated with cyclones, which increases the amount of terrigenous material being flushed out into the GBR lagoon. There is a strong possibility that the sediment profile at Orpheus Island observed in the present study was influenced by the combined effect of Cyclone Tasha's coastal flooding (December 2010) and Cyclone Yasi's wind-generated waves (February 2011). Nutrients and sediments previously flushed into the GBR lagoon may have been resuspended and re-released by the cyclonic events (Gagan et al. 1987, 1990; Russ and McCook 1999), causing an increase in the availability of primary producers and subsequently the abundance of primary consumers in the EAM cryptofauna at Orpheus Island. Furthermore, sediments that were previously established within the EAM may have been relocated due to major wave action (Wolanski et al. 2005). Physical disturbance of the cryptofauna itself is not expected to have a great impact on the populations, as these small organisms are known to recover to pre-disturbance abundances in <24 h (Sherman and Coull 1980; Johnson et al. 2007).

While the effect of sediment and dissolved nutrients on corals, algae and cryptofauna are well documented on faunal communities, knowledge of the impact of sediment and nutrients on the EAM is in its infancy. The apparent sensitivity of most cryptofauna to sediment emphasises the potential of natural and human-induced modification of sediment and water quality to impact coastal ecosystems. Although the EAM is increasingly recognised as an important contributor to reef processes in terms of productivity of detritus and algae (Klumpp and McKinnon 1992; Wilson et al. 2003; Bonaldo and Bellwood 2011), the present study provides the first, preliminary, account of the cross- and along-shelf variation in the cryptofauna of the EAM. Data presented herein provides a baseline by which to compare the condition of EAM communities in the respective locations. The present study indicates that EAM cryptofaunas are not uniform across the GBR and that particulate and dissolved nutrient input, sediment loads and position relative to catchment areas may be more important than shelf position in shaping cryptobenthic communities.

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