1 **High biomass and productivity of epifaunal invertebrates living**

2 **amongst dead coral**

3 K. M. Fraser*, R. D. Stuart-Smith, S. D. Ling, G. J. Edgar.

4 Institute for Marine and Antarctic Studies, University of Tasmania, Taroona, TAS 7053,

5 Australia

6 *Corresponding author email: kate.fraser@utas.edu.au

7 Corresponding author ORCID: 0000-0002-3057-5257

9

1 Abstract

2 Climate change is transforming coral reef structures, with important yet largely unknown

3 consequences for reef food webs. Crustaceans, molluscs, polychaetes, and other small motile

4 invertebrates living as epifauna on coral habitats represent an essential trophic link between

5 primary producers and a diverse and abundant invertivorous fish fauna. Here, we investigate

6 variation in assemblages of motile epifaunal invertebrates on live coral and dead coral

7 heavily overgrown by turf algae. Sampling was conducted 2–3 years following mass

8 bleaching within the study region at four locations broadly spanning the distribution of corals

9 on the eastern seaboard of Australia – along the northern and central Great Barrier Reef, and,

10 adjacent to the central east coast, the Solitary Islands and offshore Elizabeth and Middleton

11 Reefs (>2000km total distance). Epifaunal assemblages differed significantly between live

12 and dead 'turf-covered' coral habitats, with overall density, biomass, and productivity of

13 epifauna more than an order of magnitude greater on dead than on live coral. The size

14 structure and composition of assemblages also differed: turf-covered dead coral supported

15 greater abundances of small animals than live coral, notably harpacticoid copepods, while

16 live coral assemblages had proportionately greater abundances of larger decapods. A ten-fold

17 increase in secondary productivity of motile invertebrates is predicted as live corals are

18 replaced by turf-covered dead coral, however this productivity will predominantly be

19 available as small harpacticoid copepod prey (size range: 0.125–0.25 mm). Associated flow-

20 on effects through reef food webs are likely, as changes to epifauna will directly affect

21 invertivore communities, which in turn potentially influence larger carnivores and other

22 functional groups.

23

24

1 Introduction

2 Climate change is transforming coral reef ecosystems worldwide through increasing

3 frequency and severity of heat-induced coral bleaching events (Hughes et al. 2017b) and

4 increasing intensity of tropical storms (Cheal et al. 2017). Corals that do not recover from

5 bleaching become overgrown with turfing algae and break down into turf-covered rubble

6 (Nelson et al. 2016; O'Brien and Scheibling 2018), a process accelerated by storm

7 disturbance (Kobluk and Lysenko 1987; Cheal et al. 2017). Climate change predictions

8 suggest coral reef degradation will continue to increase (Hughes et al. 2017a; Bindoff et al.

9 2019), with significant implications for reef fauna, food webs, and ultimately reef ecosystem

10 structure.

11 Small motile invertebrates comprise the highest density and diversity of animals directly

12 associated with coral reef substrates (Plaisance et al. 2011), providing substantial biomass

13 and productivity to reef food webs (Kramer et al. 2017). Epifaunal invertebrates, ranging in

14 size from macroscopic (i.e. >1 cm) to microscopic (≤1 mm), are ubiquitous inhabitants of the

15 surfaces of reef structures, while another group – the cryptobenthic invertebrates – inhabit the

16 interstices within the coral reef framework (Enochs and Hockensmith 2008). Live, healthy

17 corals support abundant assemblages of epifauna including obligate symbionts and associates

18 (Glynn 2011). Structurally diverse species of live coral often host taxonomically distinct

19 epifauna (Stella et al. 2010), with greater variation observed among individual coral heads

20 than among reef sites (Counsell et al. 2018). Dead coral structures also host abundant

21 assemblages of epifauna, however the taxonomic composition of assemblages inhabiting

22 dead coral can differ considerably from those inhabiting live coral (Kramer et al. 2014;

23 Nelson et al. 2016; González-Gómez et al. 2018; Fraser et al. 2020c). The fine-scale structure

24 of the immediate habitat is a major driver of variation in epifaunal assemblages (Kramer et al.

25 2014; Fraser et al. 2020a; Fraser et al. 2020c), often due to a combination of complexity

1 (Enochs et al. 2011; Enochs 2012), surface area (Preston and Doherty 1994), and the

2 diversity of 'nano-habitats' at scales available to invertebrates across a range of body sizes

3 (Klumpp et al. 1988; Glynn and Enochs 2011).

4 Coral mortality and the transformation of coral reef-scapes from live coral dominance

5 towards turf-covered dead coral and coral rubble will likely have substantial impacts on

6 epifaunal invertebrate assemblages. Coral mortality has been shown to affect the ecological

7 interactions among obligate live coral-associated decapods large enough for in-situ or

8 aquarium-based visual census and observation (Stella et al. 2014), resulting in decreased

9 density and fecundity of some species (Stella et al. 2011) and potentially leading to

10 extinctions (Glynn 2011). Epifaunal assemblages associated with living corals are often

11 characterised by these macroscopic decapods (Abele and Patton 1976; Stella et al. 2010;

12 Kramer et al. 2014). In contrast, dead coral and coral rubble tend to host assemblages

13 characterised by a greater diversity of taxa, including amphipods, decapods, cumaceans,

14 tanaids and harpacticoid copepods (Klumpp et al. 1988; Kramer et al. 2014). Assemblage-

15 based studies have suggested dead coral can support significantly higher abundances of

16 epifauna than live coral, despite relatively few visible decapod species (Kramer et al. 2014;

17 Nelson et al. 2016).

18 Epifaunal invertebrates play a crucial secondary productivity role in shallow reef food webs

19 (Edgar 1990b), by which they link benthic primary producers and invertivores (Edgar and

20 Moore 1986; Taylor 1998; Kramer et al. 2013). Epifauna are amongst the most prolific

21 trophic groups at some coral reef sites (Kramer et al. 2015). As such, it is important to

22 quantify epifaunal assemblages using metrics that represent their availability as a food

23 source. Epifaunal density, biomass and productivity provide useful metrics for understanding

24 energy transfer via benthic pathways. These metrics alone, however, are inadequate for

25 accurate predictions of energy transfer via epifauna, as predation and consumption patterns

1   vary considerably depending on epifaunal body size, behaviour, and palatability (Edgar and

2   Aoki 1993; Kramer et al. 2015). Epifaunal crustacean taxa have been examined in relation to

3   variation in density, biomass and productivity among coral reef habitats (Kramer et al. 2014),

4   and biomass and productivity calculations are generally based on some measure of body size

5   multiplied by abundance (Edgar 1990b). Community size structure itself, however, may

6   provide a more broadly applicable indication of availability of epifaunal assemblages as prey,

7   and may differ markedly between live and dead coral. Community size structure is often

8   quantified by the slope of the size spectrum: the linear relationship between log abundance

9   (or log biomass or log productivity) and body size, regardless of taxonomic identity (White et

10 al. 2007; Edwards et al. 2017). The steepness of the slope indicates variation in abundance (or

11 biomass or productivity) within the assemblage attributed to larger versus smaller animals

12 (Trebilco et al. 2015). Understanding the contribution of different sized epifauna to density,

13 biomass and productivity of assemblages is critical for predicting variation in the availability

14 of food for benthic invertivores on coral reefs, given species-specific variation in food-size

15 preferences among invertivorous fishes (Kramer et al. 2015).

16 Here we compare epifaunal invertebrate assemblages (0.125 – 22 mm body size) associated

17 with live and dead scleractinian coral from four locations broadly spanning the distribution of

18 corals along the eastern seaboard of Australia. Given our overarching aim of understanding

19 consequences of the loss of live corals, we test the hypotheses that: 1) turf-covered dead coral

20 generally supports significantly higher density, biomass and productivity of epifaunal

21 invertebrates than live coral; and 2) the composition of the epifaunal assemblage and its size-

22 structure differs between turf-covered dead coral and live coral, with live coral hosting

23 proportionally more larger decapods and shallower size spectrum slope, and turf-covered

24 dead coral hosting proportionally more smaller taxa such as amphipods and harpacticoid

25 copepods and a steeper size spectrum slope.

1 Materials and methods

2 Study area and sample collection

3 Shallow reefs were sampled during the period February to November 2018 at four distinct

4 locations across the range of coral reefs in eastern Australia, including Lizard Island on the

5 northern Great Barrier Reef (GBR), Whitsunday Islands on the central GBR, the offshore

6 subtropical Elizabeth and Middleton atolls, and inshore subtropical Solitary Islands (Fig. 1).

7 These sampling locations spanned a distance greater than 2000km. A total of 40 epifaunal

8 samples sourced from live and dead coral were collected. Additional epifaunal samples were

9 collected in association with other habitat types (e.g., macroalgae, sponges), as analysed and

10 discussed elsewhere (Fraser et al. 2020a; Fraser et al. 2020b; Fraser et al. 2020c). Samples

11 from both live and dead coral were collected haphazardly across a depth range of $1 - 10$ m.

12 Sampling was conducted in relatively sheltered zones (e.g., lagoonal reefs, leeward reef

13 slopes, and off island shores sheltered from the prevailing swell direction). The most recent

14 mass bleaching and mortality of corals across the study locations prior to sampling was in

15 2016, hence we assume that most mortality of collected dead coral samples occurred during

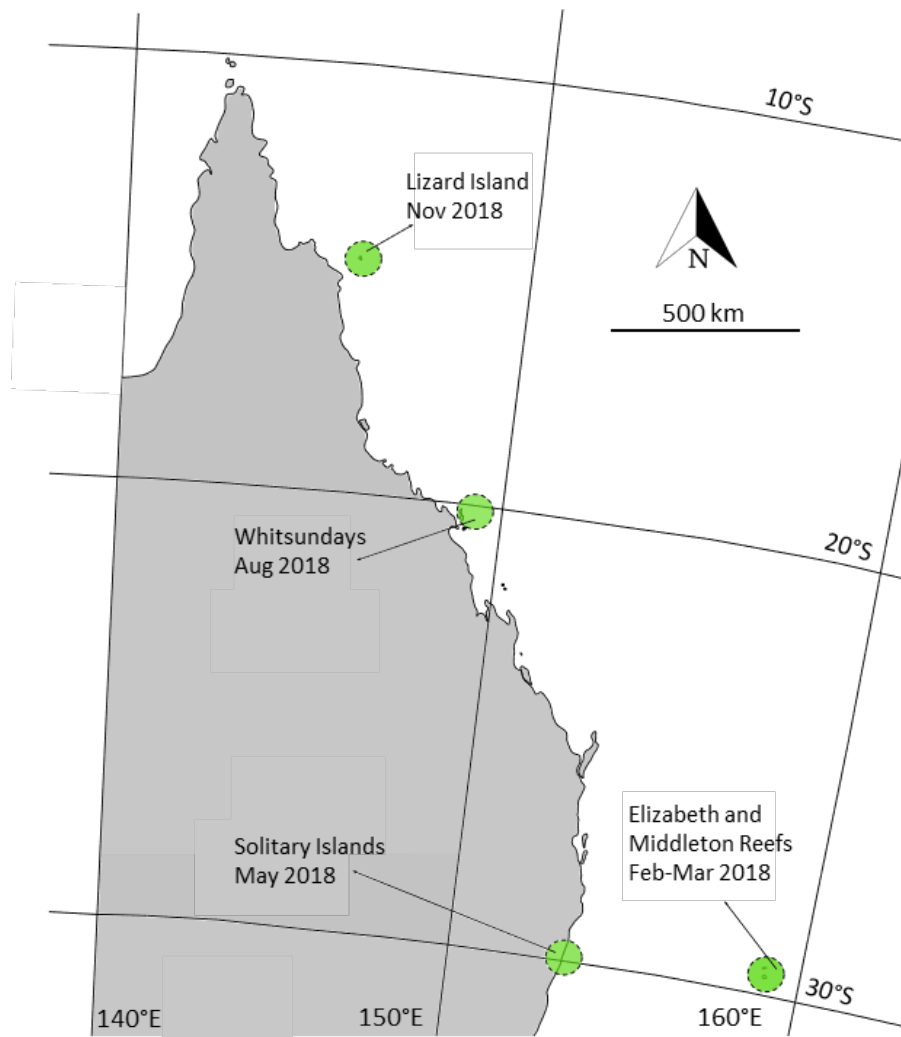16 that event (Hughes et al. 2017b; Kim et al. 2019).

Fig. 1 Map of eastern Australian sampling locations showing month sampling was performed during 2018

Sampling involved haphazard SCUBA-based collection of epifauna associated with 6 different live and dead coral microhabitats. Samples were categorised into microhabitats according to taxonomy and morphology (Table 1), following previous studies to classify reef habitat types (Cresswell et al. 2017) and by the CATAMI scheme (Althaus et al. 2015). CATAMI provides an Australian national standard for benthic habitat classification. Microhabitats were selected for sampling as they were sighted, ensuring samples were separated by >5 m on the reef. Each microhabitat was categorised dichotomously as either live or dead coral (Table 1).

1   **Table 1** Microhabitats sampled, with live or dead coral classification, sample size

2   (parentheses contain the number of total samples collected at each location; LI = Lizard

3   Island, Whit = Whitsundays, EMR = Elizabeth and Middleton Reefs, Sol = Solitary Islands),

4   description, and example genera

Microhabitat category	Live or dead coral	Number of samples	Description	Example genera
Pocillopora	Live coral	9 (LI = 3, Whit = 2, EMR = 2, Sol = 2)	Stony corals forming branching colonies, genus *Pocillopora*	*Pocillopora*
Branching *Acropora*	Live coral	6 (Whit = 1, EMR = 3, Sol = 2) *	Stony corals forming branching colonies, genus *Acropora*	*Acropora*
Tabula *Acropora*	Live coral	3 (EMR = 3) *	Stony branching corals forming tabular colonies, genus *Acropora*	*Acropora*
Other branching/erect coral	Live coral	8 (LI = 2, Whit = 1, EMR = 4)	Fine or robust branching, columnar or foliaceous stony coral colonies	*Seriatopora, Stylopora*
Erect dead coral	Dead coral	9 (LI = 3, Whit = 2, EMR = 3, Sol = 1)	Dead erect coral skeleton overgrown predominantly by fine filamentous turfing algae	*Acropora* (dead), *Pocillopora* (dead)
Coral rubble	Dead coral	5 (LI = 3, EMR = 2)	Broken dead coral rubble overgrown predominantly by fine filamentous turfing algae	*Acropora* (dead), *Pocillopora* (dead), *Porites* (dead)

5   * Permit conditions prevented collection epifauna on live *Acropora* sp. from Lizard Island

6

7   Prior to collection, a 25 cm x 25 cm grid-subdivided quadrat was placed over the selected

8   sample and photographed to quantify the planar area of sampled habitat. Erect live and dead

corals were enclosed in plastic 22 x 22 cm zip-lock bags, chiselled off the reef, and bags

immediately sealed following Stella et al. (2010). Coral rubble was collected by hand by

placing a zip-lock bag over the hand, collecting coral rubble, and immediately sealing the

bag. All samples within sealed zip-lock bags were transported to a boat, where they were

flushed three times in fresh water to remove motile invertebrates. Flushing involved placing

samples in a sorting tray, covering with fresh water and agitating for 1 minute, following

Stella et al. (2010), before the water and dislodged invertebrates were poured through a 125

μm sieve. This method excluded boring invertebrates; therefore, complete coral-associated

invertebrate assemblages are likely to differ from those discussed here. After three flushes,

invertebrates retained on the sieve were transferred to a 70 mL sample jar and fixed in 5%

buffered formalin solution. Dead coral and coral rubble samples were returned to the reef and

placed within rubble beds. Live coral samples were re-immersed in seawater after the

epifaunal wash, and re-attached to their colonies where possible (or to nearby substrate) using

marine epoxy putty following Stella et al. (2010).

Laboratory processing

Invertebrates from each sample were washed of formalin and passed through a nested series

of 12 sieves stacked in descending order of mesh size, following a $\log_{\sqrt{2}}$ series (5.6, 4.0, 2.8,

2.0, 1.4, 1.0, 0.71, 0.5, 0.355, 0.25, 0.18, 0.125 mm). Animals retained on each sieve were

washed into petri dishes for identification and counted under a dissecting microscope, with

data binned by sieve mesh size. Soft-bodied animals may disintegrate during the sieving

process, therefore data presented may under-represent some taxa, albeit with consistent biases

between sample treatments. Identification of epifauna was performed to order-level where

possible, otherwise to phylum (<2% of animals). Animals retained on the 5.6 mm sieve were

measured with calipers at their widest dimension and counts placed into additional $\log_{\sqrt{2}}$ size

bins (8, 11, 16, 22 mm).

Data analysis

Preliminary analyses contrasted order-level taxonomic composition among microhabitats nested within coarse categories 'live coral' and 'dead coral' using the PERMANOVA add-on in Primer 7 (Clarke and Gorley 2015). Results indicated relative homogeneity in epifaunal communities associated with the different coral microhabitats grouped as live or dead coral (PERMANOVA; $df = 4, 23$, Pseudo-$F = 0.85$, $P > 0.05$; Table 2), with significant variation between coarse categories 'live coral' and 'dead coral' ($P \leq 0.001$; Table 2). Larger sample sizes within live and dead coral categories provided greater statistical power than when samples were separated according to finer microhabitats, consequently microhabitats have not been considered further. Moreover, previous field research has identified similar assemblages of epifaunal crustaceans associated with erect dead coral and coral rubble (Kramer et al. 2014).

Density, biomass, and productivity

Given that strong relationships exist between epifaunal biomass and light (Edgar 1993), which is ultimately a planar metric, epifaunal abundance by taxa and size were standardised to 1 m^2 planar seabed area (density) (Fraser et al. 2020c), accounting for the area of sampled microhabitat photographed underwater prior to collection. Standardisation by planar area also allows comparison of epifaunal assemblage metrics to densities of other trophic groups (e.g., primary producers, benthic invertebrates, fishes), which are typically expressed per square metre of seabed. Moreover, standardisation of habitats in other ways generates bias towards species that respond to a particular habitat feature (Edgar 1983).

Epifaunal biomass as ash-free dry weight (AFDW) of individuals within each size bin was derived from published estimates of mean biomass across macrofaunal taxonomic groups

1 (Edgar 1990b). Productivity estimates of individuals within each size bin were calculated

2 using the general allometric equation given by Edgar (1990b):

3 $P = (10\^((-2.31 + 0.8*\log10(B*1000) + 0.89*\log10T)))/1000$

4 where P is productivity of an individual (mg AFDW d^{-1}), B is the biomass of an individual

5 (mg AFDW), and T is water temperature (°C) at the time of sampling. Biomass and

6 productivity estimates of individual animals were then summed to provide total biomass (mg

7 AFDW m^{-2}) and total productivity estimates (mg AFDW m^{-2} d^{-1}) for each sample. We note

8 that this method was originally established for estimating biomass and productivity for

9 individuals ⩾0.5 mm; here we assume the equations by Edgar (1990b) also apply to smaller

10 individuals (⩾0.125 mm) based on linear extrapolation of well-supported trends (i.e. R^2

11 ranging from 0.87 to 0.98 (Fraser et al. 2020b)).

12 The influence of habitat (live vs. dead coral) and location on total density, biomass and

13 productivity per m^2 of epifaunal assemblages was assessed using univariate permutational

14 analyses of variance in Primer 7 (PERMANOVA; (Anderson 2001; McArdle and Anderson

15 2001; Clarke and Gorley 2015; Anderson 2017)) on Euclidean distance resemblance matrices

16 of log(x+1) transformed density, biomass, and productivity data. Use of Euclidean distance

17 results in F-values similar to those calculated by traditional analysis of variance, but with

18 probability values calculated through permutation rather than Gaussian expectations.

19 *Assemblage size spectra*

20 Density, biomass, and productivity data for each sample were partitioned into sieve mesh size

21 bins. For each sample, the slopes for density, biomass, and productivity size spectra were

22 calculated using linear regression ($\log_{10}$(density, biomass, or productivity) against $\log_{10}$(mid-

23 point of each size bin)) in R (R Core Team 2019) and the *tidyverse* package (Edwards et al.

24 2017; Wickam et al. 2019). Mean size spectra were plotted for live coral and dead coral using

1   the same packages, with R^2 values indicating the consistency in size spectra among samples.

2   Variation in R^2 values for each size spectrum represents a general ecological indicator of

3   consistency among samples, rather than a statistical measure given the points related to each

4   sample are not independent. Zero counts in larger size bins affected the linear fit of data,

5   therefore data were included up to the largest size bin in which animals were present.

6   Variation in sample-level size spectra slopes between live coral and dead coral was examined

7   using univariate permutational analysis of variance ((PERMANOVA; (Anderson 2001;

8   McArdle and Anderson 2001; Anderson 2017)).

9   *Taxonomic composition*

10   Multivariate community analyses were conducted using PRIMER 7 (Clarke and Gorley

11   2015). A permutational analysis of variance (PERMANOVA; (Anderson 2001; McArdle and

12   Anderson 2001; Anderson 2017)) was conducted on a Bray-Curtis resemblance matrix of

13   $\log_{10}$ (x+1) transformed density, biomass, and productivity data by taxa to test for assemblage

14   differences between live and dead coral. In order to visualise similarity among epifaunal

15   samples according to taxonomic composition, a cluster analysis was undertaken using the

16   Bray-Curtis resemblance matrix of $\log_{10}$ (x+1) transformed density data by taxa.

17   Pairwise PERMANOVA was used to make comparisons between epifauna associated with

18   live and dead coral. Similarity percentages analysis (SIMPER; (Clarke 1993)) of density data

19   was used to identify taxa most influential to dissimilarity among epifauna associated with the

20   two habitats. Mean percent composition of these influential taxa (with additional taxa

21   grouped as 'other') inhabiting live and dead coral was visualised using stacked bar charts in

22   R (R Core Team 2019) and the *tidyverse* package (Wickam et al. 2019).

23

24

Results

Epifaunal communities associated with live versus dead coral

No significant variation was evident in epifaunal assemblages among sampling locations, with regards to overall density, biomass, productivity, or taxonomic composition (PERMANOVA; density: $df = 3, 32$, Pseudo-$F = 0.44$, $P > 0.05$; biomass: $df = 3, 32$, Pseudo-$F = 0.33$, $P > 0.05$; productivity: $df = 3, 32$, Pseudo-$F = 0.17$, $P > 0.05$; taxonomic composition: $df = 3, 23$, Pseudo-$F = 1.04$, $P > 0.05$; Tables 2, 3, Fig. 2). Thus, local scale variation associated with location characteristics (e.g., depth, currents, wave exposure, habitat structure) was apparently very low relative to live/dead coral differences. Location was consequently omitted from all subsequent analyses by testing hypotheses based on data pooled within live or dead coral across all locations. Epifaunal assemblages associated with live and dead coral were significantly different, with overall density, biomass, and productivity of epifauna more than an order of magnitude greater on dead than on live coral habitat (Fig. 2; Table 3).
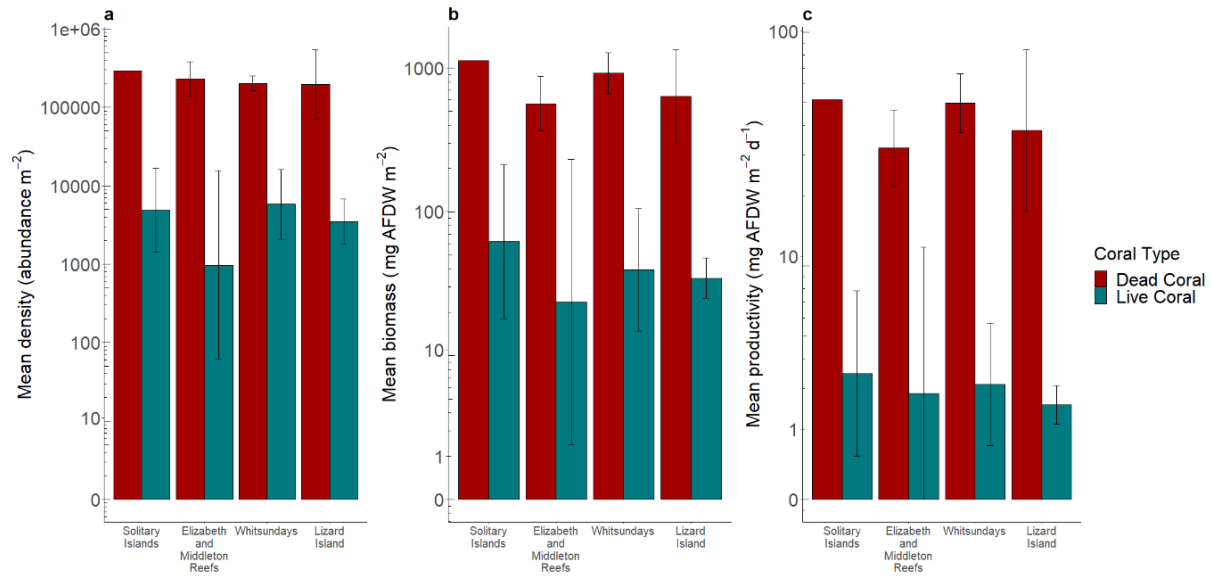
1

2   **Fig. 2** Mean (a) density (abundance m^{-2}), (b) estimated biomass (mg AFDW m^{-2}), and (c)

3   estimated daily productivity (mg AFDW m^{-2} d^{-1}) of epifauna within 1 m^2 planar area

4   associated with live coral and dead coral at the four sampling locations: Solitary Islands,

5   Elizabeth and Middleton Reefs, Whitsundays, and Lizard Island. Error indicates standard

6   deviation

7

8   **Table 2** Multivariate PERMANOVA assessing effects of live vs. dead coral, location,

9   microhabitat (nested within live vs. dead coral), and interactions between live vs. dead coral

10 and location, and microhabitat (nested with live vs. dead coral) and location on the order-

11 level composition of epifaunal assemblages. Effects highlighted in bold were significant at α

12 <0.05

Source of variation	Degrees of freedom	Mean square	Pseudo-*F* ratio	*P*-value (by permutation)
Live/Dead	**1**	**9248**	**7.51**	**<0.001**
Microhabitat (Live/Dead)	4	923	0.85	0.632
Location	3	1072	1.04	0.459
Live/Dead x Location	3	818	0.79	0.618
Microhabitat x Location	5	1054	1.70	0.056
Residual	23	619		
Total	39			

13

14

1 **Table 3** PERMANOVA table assessing differences in overall assemblage density, biomass,

2 and daily productivity on live and dead coral habitats, among sampling locations, and under

3 the interacting effects of live vs. dead coral and location. Live vs. dead coral habitat is a fixed

4 factor, location is random. Effects highlighted in bold were significant at α <0.05

Source of variation	Degrees of freedom	Mean square	Pseudo F-value	P-value
		Density		
Live/Dead	**1**	**110.87**	**52.70**	**<0.05**
Location	3	1.48	0.44	0.707
Live/Dead x Location	3	1.76	0.52	0.621
Residuals	32	3.36		
		Biomass		
Live/Dead	**1**	**55.73**	**105.17**	**<0.05**
Location	3	0.77	0.33	0.784
Live/Dead x Location	3	0.05	0.02	0.995
Residuals	32	2.31		
		Productivity		
Live/Dead	**1**	**42.49**	**161.22**	**<0.01**
Location	3	0.17	0.17	0.920
Live/Dead x Location	3	0.06	0.06	0.977
Residuals	32	1.00		

5

6

7 **Assemblage size spectra**

8 The epifaunal size spectra slopes were also significantly different between live and dead

9 corals (PERMANOVA; density: $df = 1, 38$, Pseudo-$F = 21.4$, P <0.001; biomass: $df = 1, 38$,

10 Pseudo-$F = 14.7$, P <0.001; productivity: $df = 1, 38$, Pseudo-$F = 29.8$, P <0.001). The two

11 density size spectra both had negative slopes, indicating higher densities of smaller animals

12 within assemblages (Fig. 3). However, densities on dead corals showed a much steeper slope

13 than on live coral (Fig. 3), indicating the dominance of small animals and increasingly similar

14 densities of larger individuals. R^2 values suggest dead coral density and productivity size

15 spectra were more consistent than the live coral equivalents, while the live coral biomass size

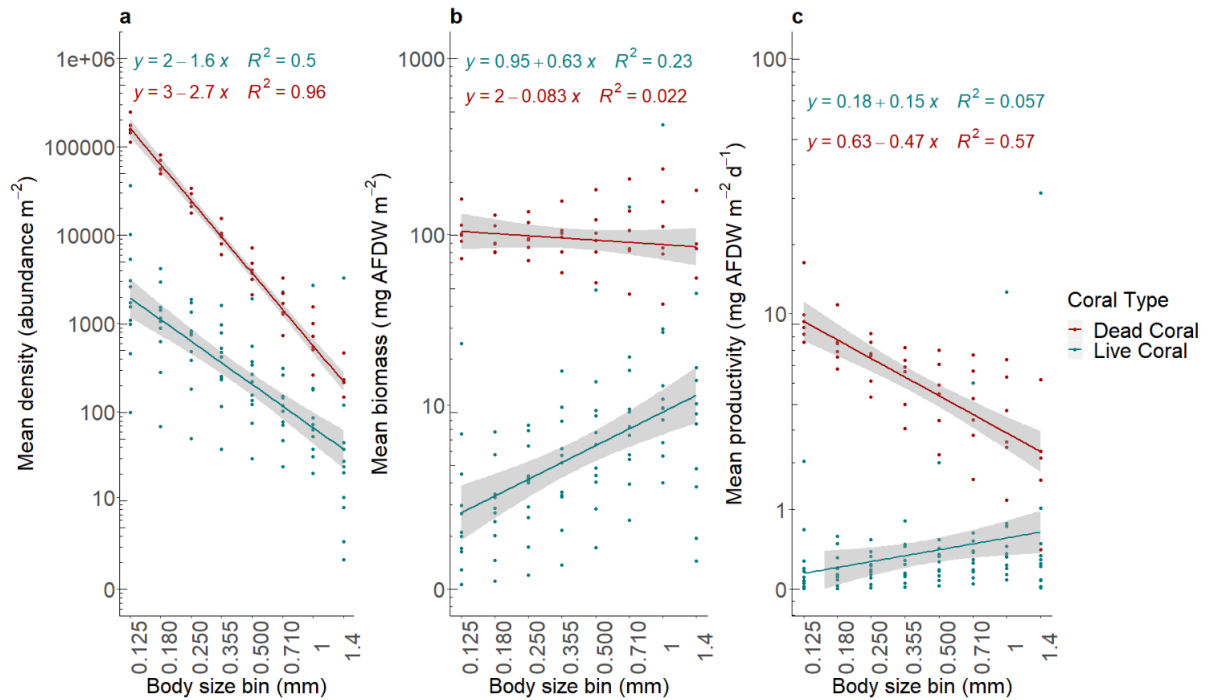16 spectrum was more consistent among samples than the dead coral equivalent (Fig. 3).

Fig. 3 Contribution of epifaunal invertebrates across size spectra: (a) overall assemblage density (abundance m^{-2}), (b) estimated biomass (mg AFDW m^{-2}), and (c) estimated daily productivity (mg AFDW m^{-2} d^{-1}) in association with live coral and dead coral. Grey shading represents 95% confidence intervals; dots represent sample data within each size bin

Epifaunal biomass and productivity were also consistently higher on dead coral than on live coral. However, in contrast to densities, trends in biomass and productivity across size spectra were either not as pronounced (dead coral) or reversed, i.e., positive (live coral). The invertebrate body size distribution on dead coral was relatively flat for biomass and negative for productivity. Both biomass and productivity showed a positive trend across size spectra on live coral. Again, these results indicated that the higher productivity of dead coral-associated epifauna was largely driven by the smallest size classes.

Taxonomic composition

Epifaunal assemblages associated with live and dead coral were further analysed for the relative contribution of major invertebrate taxa to overall density, estimated biomass, and

1   estimated productivity. Pairwise PERMANOVA indicated that live and dead coral supported

2   distinct epifaunal assemblages (PERMANOVA; density: $df = 1/38$, $t = 2.7$, $P < 0.001$;

3   biomass: $df = 1/38$, $t = 2.4$, $P < 0.01$; productivity: $df = 1/38$, $t = 2.6$, $P < 0.001$). The

4   dendrogram grouping samples by faunal similarity identified three clear clusters of samples

5   with <60% similarity: one cluster comprising all the dead coral samples, and two clusters

6   grouping live coral samples (Fig. 4).

7

8
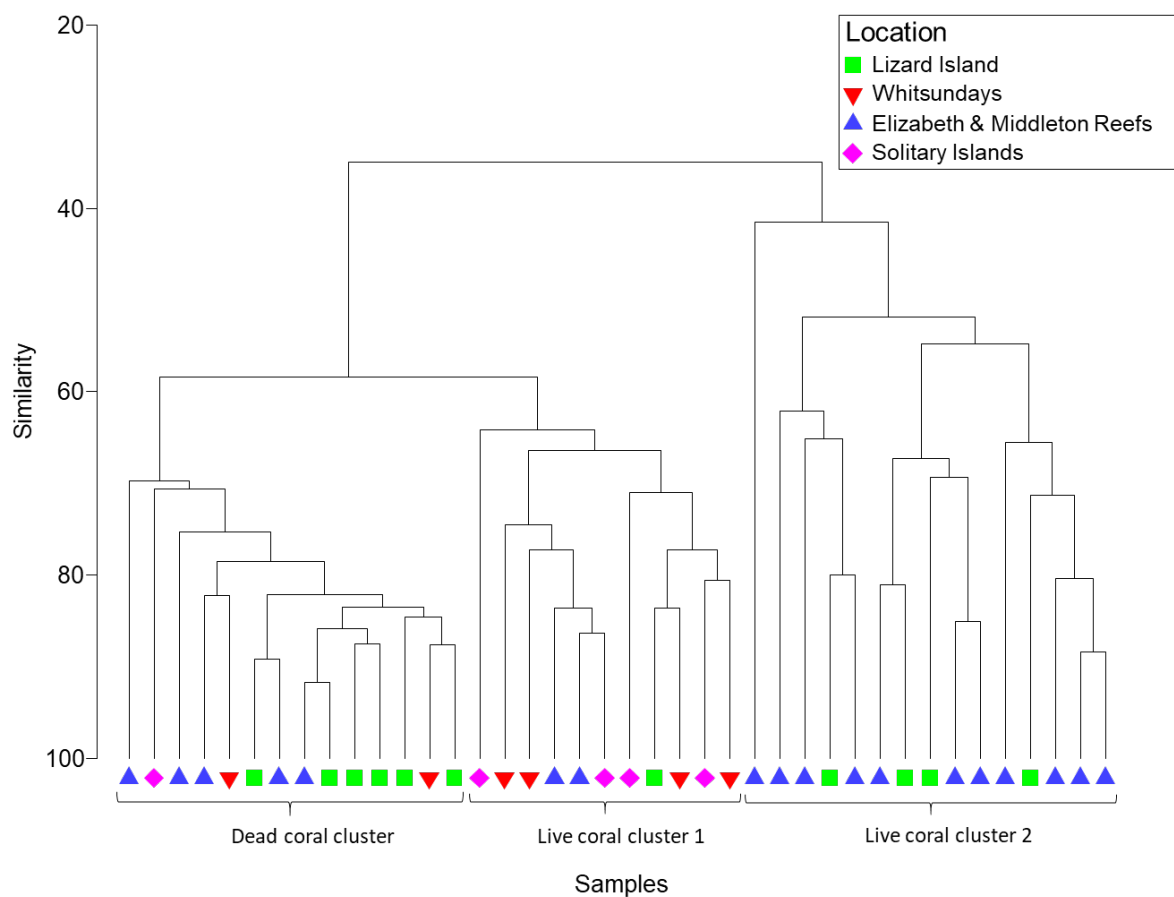
9   **Fig. 4** Cluster dendrogram showing live and dead coral samples, clustered according to

10   similarity in the contribution of different taxa to the overall density of animals in each

11   sample. The Dead coral cluster comprised all the dead coral samples, while live coral samples

12   were distributed between Live coral clusters 1 and 2

On both live and dead coral, harpacticoid copepods comprised most invertebrate individuals

(Fig. 5). By contrast, decapods occurred at low densities, but dominated biomass estimates in

both live and dead coral (Fig. 5). Decapods also contributed most productivity to live coral-

associated assemblages, but harpacticoid copepods were most important for productivity in
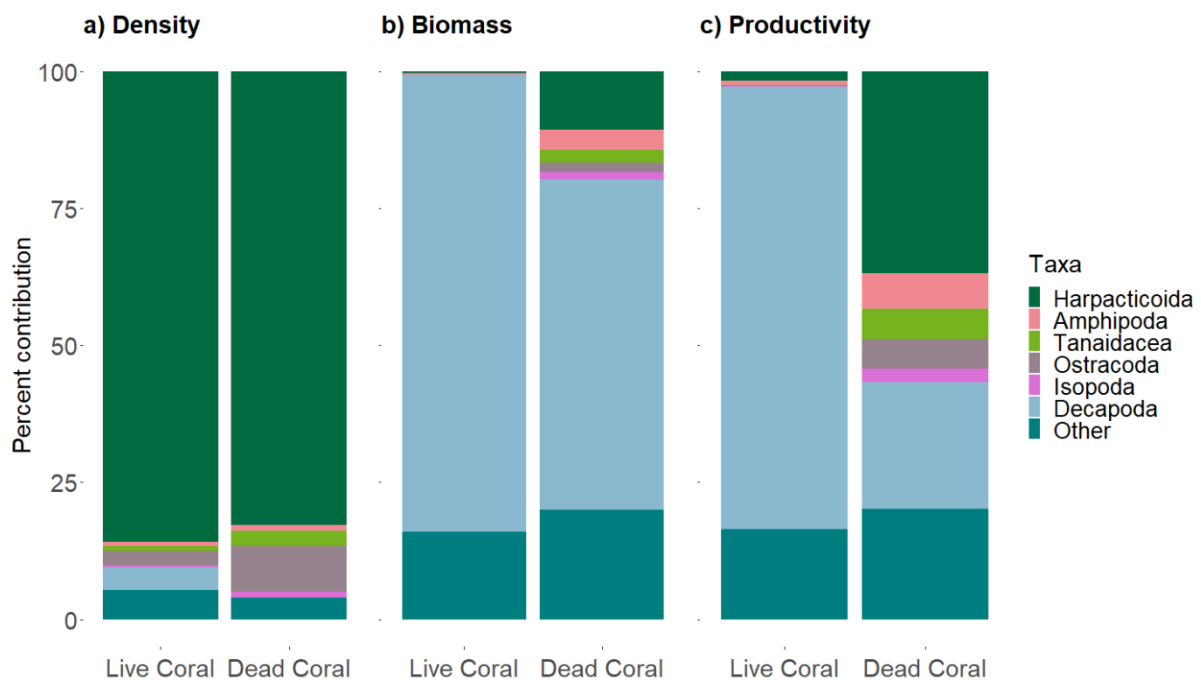
dead coral assemblages (Fig. 5).

Fig. 5 Percent contribution to (a) overall epifaunal density (abundance m^{-2}), (b) estimated

biomass (mg AFDW m^{-2}), and (c) estimated daily productivity (mg AFDW m^{-2} d^{-1}) of the

taxa identified by SIMPER analysis as most influential to dissimilarity between live- and

dead coral-associated assemblages. Data showing the contribution of decapods are included

given their importance to biomass and productivity. Additional taxa grouped as 'other'

comprise: Anthozoa, Bivalvia, Chitonida, Gastropoda, Holothuroidea, Mysida, Nematoda,

Nemertea, Ophiuroidea, Platyhelmithes, Polychaeta, Pycnogonida, Sabellida, Terebellida

1

2 Harpacticoid copepods were more abundant on dead than on live coral and accounted for

3 80% of the dissimilarity in epifaunal density between live and dead coral (Table 4).

4 Differences in epifaunal biomass between live and dead coral were primarily driven by

5 harpacticoid copepods, amphipods, tanaidaceans, ostracods, and isopods, which together

6 accounted for 74% of dissimilarity (Table 4). In terms of daily productivity, harpacticoid

7 copepods, amphipods, tanaidaceans, and ostracods together accounted for 77% of

8 dissimilarity between live and dead coral (Table 4).

9

10 **Table 4** Results of SIMPER analysis showing epifaunal taxa (by order-level identification)

11 contributing to 70% of dissimilarity between samples of live and dead coral. Density values

12 are expressed as abundance m^{-2}, biomass as mg AFDW m^{-2}, productivity as mg AFDW m^{-2}

13 d^{-1}

	Live coral	Dead coral				
Taxa	Average values	Average values	Average dissimilarity	Dissimilarity/ SD	Contribution (%)	Cumulative (%)
Density						
Harpacticoida	11692	231906	73.55	4.41	80.41	80.41
Biomass						
Harpacticoida	19.46	387.65	36.76	2.08	40.60	40.60
Amphipoda	10.02	123.78	11.31	1.40	12.49	53.09
Tanaidacea	1.39	132.51	8.74	1.05	9.65	62.74
Ostracoda	0.52	66.42	6.25	1.60	6.90	69.65
Isopoda	0.59	44.05	4.31	1.11	4.76	74.41
Productivity						
Harpacticoida	1.32	27.79	47.88	2.58	52.59	52.59
Amphipoda	0.28	4.66	7.88	1.24	8.65	61.24
Tanaidacea	0.06	6.25	7.40	0.95	8.13	69.37
Ostracoda	0.04	4.35	7.09	1.94	7.78	77.15

14

15

16

Discussion

Epifaunal assemblages differed markedly between samples of live and dead coral, with dead coral hosting 1–2 orders of magnitude more epifauna when quantified in terms of overall density, biomass, or productivity. This outcome was consistent at four locations spanning over 2000 km distance. For dead coral-associated assemblages, biomass and productivity size spectra were distinctly flatter than the corresponding density size spectrum. This result is consistent with metabolic theory, whereby much of the energy available to small animals is lost due to metabolic and ecological inefficiencies with each step up the food chain into larger size classes, while turnover rate is slower for larger animals (Sheldon et al. 1972; Sprules and Barth 2016). Epifaunal assemblages, however, cannot necessarily be represented by a simple food chain in which larger epifauna consume their smaller counterparts. While a large proportion of epifaunal taxa are herbivores, depending on microphytobenthos as a food resource (Edgar 1993), small invertebrates on coral reefs represent a wide range of trophic groups, including predatory or opportunistic carnivores, detritivores, filter-feeders (Glynn and Enochs 2011; Poore et al. 2012; Kolasinski et al. 2016) and obligate coral-associates that consume live coral mucus or particles trapped by coral polyps (Galil 1987; Stella et al. 2011). Hence, the relatively shallow slopes of biomass and productivity size spectra may be driven by turnover rate relative to body size, under an assumption that absolute consumption per size class is relatively stable, with more small animals consuming comparable amounts of a food resource to fewer large animals.

In contrast, biomass and productivity in live coral assemblages were higher among larger size classes, and a considerably smaller contribution was made by smaller epifauna to overall density, biomass, and productivity than in assemblages associated with dead coral. This may be explained by the reduced availability of microphytobenthic and detrital food sources on live corals, resulting in less food available for small herbivorous and detritivorous epifauna

(Edgar 1993; Poore et al. 2012). Some larger decapod crustaceans rely on basal food sources directly associated with live coral, such as coral mucus or particles trapped by coral polyps (Galil 1987; Stella et al. 2011; Stella et al. 2014). Predation may also influence size structure, for example, the relative paucity of smaller epifauna, predominantly harpacticoid copepods, on live coral may be related to consumption of very small invertebrates by coral polyps (Goreau et al. 1971; Gochfeld 2004; Houlbréque and Ferrier-Pagés 2009).

Moreover, structure and shelter are key physical components of coral reef ecosystems, with the size of available shelter or refugia correlating with the size structure of associated fauna (Klumpp et al. 1988; Moran and Reaka 1988; Rogers et al. 2014). While we did not quantify the availability and size of refugia among coral habitats, the hard structure of live branching coral may be decrease the ability of invertivorous fishes – a prolific trophic group on coral reefs (Williams and Hatcher 1983) – to penetrate in order to extract prey, particularly compared with coral rubble (Hixon and Jones 2005). Hence, live branching coral may serve as prey refugia for larger decapods, making live coral habitats favourable to these particular taxa and size classes of invertebrates (Rogers et al. 2014).

The abundance of epifaunal invertebrates on coral reefs has been shown to relate more to the density of turfing algae than to the structural complexity of the coral substratum (Klumpp et al. 1988). This may be explained in part by the increased availability of detrital and algal food sources in turfing algae habitat, but turfing algae may also provide substantial shelter for small invertebrates from visual predators and environmental stress (Klumpp et al. 1988).

The consistency in patterns evident among the four reef locations, despite variability in local-scale factors (e.g., season, nutrient availability, wave exposure, depth, and fish/predator biomass), indicates that environmental effects had far less influence on epifaunal assemblages than the differences between live coral and dead coral. This aligns with results of previous

research investigating small invertebrates associated with one species of live coral across

spatial scales and environmental gradients (Counsell et al. 2018). Variation in assemblage

abundance and species richness was greatest at the scale of the individual coral colony and

lowest among sites (Counsell et al. 2018). An associated study comparing the taxonomic

composition of epifaunal assemblages among diverse benthic microhabitats (e.g.,

taxonomically and morphologically distinct algal, sponge, and coral microhabitats) on

temperate to tropical reefs also found strong correlations with habitat structure that were

largely independent of sampling location (Fraser et al. 2020c). Similarly, when the influence

of environmental variables on the productivity of epifaunal assemblages was explicitly tested

using a continental-scale dataset (Fraser et al. 2020a), productivity was largely invariant to

environmental influences, instead relating primarily to the immediate habitat (e.g., live coral,

macroalgae, and turfing algae (including dead coral and coral rubble)).

Secondary productivity on changing reefs

Despite the limited breadth of this study, the pronounced and consistent difference in

secondary productivity of small motile invertebrates between live and dead coral samples has

notable implications in the context of climate change and changing reefs. Our results suggest

that secondary productivity of motile epifauna in coral reef ecosystems may increase with

further loss of live coral, with a shift from larger decapods to small harpacticoid copepods.

Such a shift will affect the flow of energy in reef food webs and the structure of other faunal

communities directly and indirectly. Biomass of benthic invertivores and richness of small

cryptobenthic fish have been shown to increase following heatwaves and coral bleaching

(Stuart-Smith et al. 2018), at least in the short term, with these changes potentially influenced

by an increase in secondary productivity and availability of smaller prey. Thus, an increase in

dead coral habitat within reef systems has the potential to substantially shift the amount of

energy transferred through basal levels of reef food webs.

Thus, the effects of coral mortality on reef food webs are likely to involve complex interactions involving changing food resources, habitat structure and temperature. While live coral loss may lead to higher availability of food for small fishes, degradation of reef structural complexity, most notably the loss of small refugia in the reef matrix, can potentially expose small fishes to increased predation risk (Nash et al. 2013). Habitat structural complexity has been positively correlated with density, biomass, and productivity of epifauna (Edgar 1990a; Edgar et al. 1994; Taylor 1998; Kramer et al. 2014; Kramer et al. 2017). Following coral death, coral skeletons become overgrown with turfing algae, then break down into turf-covered rubble, and eventually degrade further into gravel and sand (Moran and Reaka 1988).

The structural complexity of turf-covered erect coral skeletons and coral rubble sampled here is probably even higher than that of branching live coral habitats at the tiny scales to which small epifaunal invertebrates respond (Kramer et al. 2014). Sand, however, has much less structural complexity for small epifauna, and supports invertebrate communities with generally lower density, biomass and productivity (Kramer et al. 2014; Nelson et al. 2016). Over time, and without recovery of live corals, the secondary productivity supporting critical functions on healthy reefs may therefore be lost resulting in declines in species dependant on this food source and associated effects throughout reef food webs (Enochs and Manzello 2012; Kramer et al. 2015).

Thus, invertebrate productivity appears to be affected by trade-offs involving benefits from increased resources associated with turfs and costs of declines in refugia within the reef matrix, with net outcomes affecting invertivorous fish biomass (Rogers et al. 2018a). If reefs continue to erode, structural complexity will be lost at scales providing refugia for both small epifaunal prey and larger invertivores, likely leading to declines in ecosystem biomass and productivity (Rogers et al. 2018b).

In summary, the differences observed in epifaunal assemblages associated with live coral and turf-covered dead coral suggest increased secondary productivity is possible in the short-term with widespread loss of live coral. Such a shift would likely enhance resource availability for benthic invertivores, particularly those specialising on small harpacticoid copepod prey. The consequences of live coral loss, however, can be expected to accentuate over time, as dead corals progressively degrade towards structurally simple sand habitats (Enochs and Manzello 2012). Similarly, effects of live coral loss on fish productivity will reflect trade-offs between potential increases in epifaunal prey availability and progressive decline in structural complexity (Rogers et al. 2014). Critically, the spatial scale over which coral loss occurs will play a key role in framing the cascading impact of live coral loss on trophic dynamics of reef ecosystems.

Acknowledgements

Declarations

Conflict of Interest

On behalf of all authors, the corresponding author states that there is no conflict of interest.

Funding

3   *Data Availability*

4   Data will be made available upon reasonable request.

5   *Animal Welfare*

6   Animal ethics approval was not required for the research presented here, as the taxa studied

7   were exempt from Australian animal ethics standards at the time of publication.

8   *Authors' Contribution*

9   KMF conducted fieldwork, processed samples, analysed data and wrote the manuscript. GJE

10   conceived the project and assisted sample identification. GJE and SDL received funding

11   support and assisted with fieldwork and sample processing. All authors contributed to

12   methodology and edited the manuscript.

Literature cited

Abele LG, Patton WK (1976) The size of coral heads and the community biology of associated decapod crustaceans. J Biogeogr: 35-47

Althaus F, Hill N, Ferrari R, Edwards L, Przeslawski R, Schonberg CHL, Stuart-Smith R, Barrett N, Edgar G, Colquhoun J, Tran M, Jordan A, Rees T, Gowett-Holmes K (2015) A standardised vocabulary for identifying benthic biota and substrata from underwater imagery: the CATAMI classification scheme. PLoS One 10: 1-18 doi 10.1371/journal.pone.0141039

Anderson MJ (2001) A new method for non-parametric multivariate analysis of variance. Austral Ecol 26: 32-46

Anderson MJ (2017) Permutational Multivariate Analysis of Variance (PERMANOVA). In: N. Balakrishnan TC, B. Everitt, W. Piegorsch, F. Ruggeri and J. L. Teugels (ed) Wiley StatsRef: Statistics Reference Online

Bindoff NL, Cheung WWL, Aristegui J, Guinder VA, Hallberg R, Hilmi N, Jiao N, Karim MS, Levin L, O'Donoghue S, Purca Cuicapusa SR, Rinkevich B, Suga T, Tagliabue A, Williamson P (2019) IPCC special report on the oceans and cryosphere in a changing climate, In press

Cheal AJ, Macneil MA, Emslie MJ, Sweatman H (2017) The threat to coral reefs from more intense cyclones under climate change. Global Change Biol 23: 1511-1524 doi 10.1111/gcb.13593

Clarke K, Gorley R (2015) PRIMER version 7: user manual/tutorial. PRIMER-E 192

Clarke KR (1993) Non-parametric multivariate analyses of changes in community structure. Aust J Ecol 18: 117-143

Counsell CWW, Donahue MJ, Edwards KF, Franklin EC, Hixon MA (2018) Variation in coral-associated cryptofaunal communities across spatial scales and environmental gradients. Coral Reefs 37: 827-840 doi 10.1007/s00338-018-1709-7

Cresswell AK, Edgar GJ, Stuart-Smith RD, Thomson RJ, Barrett NS, Johnson CR (2017) Translating local benthic community structure to national biogenic reef habitat types. Global Ecol Biogeogr 26: 1112-1125 doi 10.1111/geb.12620

Edgar GJ (1983) The ecology of south-east Tasmanian phytal animal communities. I. Spatial organization on a local scale. J Exp Mar Biol Ecol 70: 129-157

Edgar GJ (1990a) The influence of plant structure on the species richness, biomass and secondary production of macrofaunal assemblages associated with Western Australian seagrass beds. J Exp Mar Biol Ecol 137: 215-240

Edgar GJ (1990b) The use of the size structure of benthic macrofaunal communities to estimate faunal biomass and secondary production. J Exp Mar Biol Ecol 137: 195-214 doi 10.1016/0022-0981(90)90185-F

Edgar GJ (1993) Measurement of the carrying capacity of benthic habitats using a metabolic-rate based index. Oecologia 95: 115-121

Edgar GJ, Aoki M (1993) Resource limitation and fish predation: their importance to mobile epifauna associated with Japanese Sargassum. Oecologia 95: 122-133

Edgar GJ, Moore PG (1986) Macro-algae as habitats for motile macrofauna. Monografias Biologicas 4: 255-277

Edgar GJ, Shaw C, Watson GF, Hammond LS (1994) Comparisons of species richness, size-structure and production of benthos in vegetated and unvegetated habitats in Western Port, Victoria. J Exp Mar Biol Ecol 176: 201-226

Edwards AM, Robinson JPW, Plank MJ, Baum JK, Blanchard JL (2017) Testing and recommending methods for fitting size spectra to data. Methods in Ecology and Evolution 8: 57-67 doi 10.1111/2041-210x.12641

Enochs I, Hockensmith G (2008) Effects of coral mortality on the community composition of cryptic metazoans associated with Pocillopora damicornis Proc 11th Int Coral Reef Symp, pp 1368-1372

Enochs I, Toth L, Brandtneris V, Afflerbach J, Manzello D (2011) Environmental determinants of motile cryptofauna on an eastern Pacific coral reef. Mar Ecol Prog Ser 438: 105-118 doi 10.3354/meps09259

Enochs IC (2012) Motile cryptofauna associated with live and dead coral substrates: implications for coral mortality and framework erosion. Mar Biol 159: 709-722 doi 10.1007/s00227-011-1848-7

Enochs IC, Manzello DP (2012) Responses of cryptofaunal species richness and trophic potential to coral reef habitat degradation. Diversity 4: 94-104 doi 10.3390/d4010094

Fraser KM, Lefcheck JS, Ling SD, Mellin C, Stuart-Smith RD, Edgar GJ (2020a) Production of mobile invertebrate communities on shallow reefs from temperate to tropical seas. Proceedings of the Royal Society B 287: 20201798 doi 10.1098/rspb.2020.1798

Fraser KM, Stuart-Smith RD, Ling SD, Edgar GJ (2020b) Small invertebrate consumers produce consistent size spectra across reef habitats and climatic zones. Oikos doi 10.1111/oik.07652

Fraser KM, Stuart-Smith RD, Ling SD, Heather FJ, Edgar GJ (2020c) Taxonomic composition of mobile epifaunal invertebrate assemblages on diverse benthic microhabitats from temperate to tropical reefs. Mar Ecol Prog Ser 640: 31-43 doi 10.3354/meps13295

Galil BS (1987) The adaptive functional structure of mucus-gathering setae in trapezid crabs symbiotic with corals. Symbiosis 4: 75-86

Glynn PW (2011) In tandem reef coral and cryptic metazoan declines and extinctions. Bull Mar Sci 87: 767-794

Glynn PW, Enochs IC (2011) Invertebrates and their roles in coral reef ecosystems Coral reefs: an ecosystem in transition. Springer, pp 273-325

Gochfeld D (2004) Predation-induced morphological and behavioral defenses in a hard coral: implications for foraging behavior of coral-feeding butterflyfishes. Mar Ecol Prog Ser 267: 145-158 doi 10.3354/meps267145

González-Gómez R, Briones-Fourzán P, Álvarez-Filip L, Lozano-Álvarez E (2018) Diversity and abundance of conspicuous macrocrustaceans on coral reefs differing in level of degradation. PeerJ 6: e4922

Goreau TF, Yonge CM, Goreau NI (1971) Reef corals - autotrophs or heterotrophs? Biological Bulletin 141: 247-260 doi 10.2307/1540115

Hixon MA, Jones GP (2005) Competition, predation, and density‒dependent mortality in demersal marine fishes. Ecology 86: 2847-2859

Houlbréque F, Ferrier-Pagés C (2009) Heterotrophy in tropical scleractinian corals. Biological Reviews 84: 1-17 doi 10.1111/j.1469-185x.2008.00058.x

Hughes TP, Barnes ML, Bellwood DR, Cinner JE, Cumming GS, Jackson JB, Kleypas J, Van De Leemput IA, Lough JM, Morrison TH (2017a) Coral reefs in the Anthropocene. Nature 546: 82

Hughes TP, Kerry JT, Álvarez-Noriega M, Álvarez-Romero JG, Anderson KD, Baird AH, Babcock RC, Beger M, Bellwood DR, Berkelmans R, Bridge TC, Butler IR, Byrne M, Cantin NE, Comeau S, Connolly SR, Cumming GS, Dalton SJ, Diaz-Pulido G, Eakin CM, Figueira WF, Gilmour JP, Harrison HB, Heron SF, Hoey AS, Hobbs J-PA, Hoogenboom MO, Kennedy EV, Kuo C-y, Lough JM, Lowe RJ, Liu G, McCulloch MT, Malcolm HA, McWilliam MJ, Pandolfi JM, Pears RJ, Pratchett MS, Schoepf V, Simpson T, Skirving WJ, Sommer B, Torda G, Wachenfeld DR, Willis BL, Wilson SK (2017b) Global warming and recurrent mass bleaching of corals. Nature 543: 373 doi 10.1038/nature21707

Kim SW, Sampayo EM, Sommer B, Sims CA, Gomez-Cabrera MdC, Dalton SJ, Beger M, Malcolm HA, Ferrari R, Fraser N, Figueira WF, Smith SDA, Heron SF, Baird AH, Byrne M, Eakin CM, Edgar R, Hughes TP, Kyriacou N, Liu G, Matis P, A., Skirving WJ, Pandolfi JM (2019) Refugia under threat: mass bleaching of coral assemblages in high-latitude eastern Australia. Global Change Biol 25: 3918-3931

Klumpp D, McKinnon A, Mundy C (1988) Motile cryptofauna of a coral reef: abundance, distribution and trophic potential. Mar Ecol Prog Ser 45: 95-108

Kobluk DR, Lysenko MA (1987) Impact of two sequential Pacific hurricanes on sub-rubble cryptic corals: the possible role of cryptic organisms in maintenance of coral reef communities. J Paleontol: 663-675

Kolasinski J, Nahon S, Rogers K, Chauvin A, Bigot L, Frouin P (2016) Stable isotopes reveal spatial variability in the trophic structure of a macro-benthic invertebrate community in a tropical coral reef. Rapid Communications in Mass Spectrometry 30: 433-446

Kramer MJ, Bellwood DR, Bellwood O (2014) Benthic Crustacea on coral reefs: a quantitative survey. Mar Ecol Prog Ser 511: 105-116

Kramer MJ, Bellwood DR, Taylor RB, Bellwood O (2017) Benthic Crustacea from tropical and temperate reef locations: differences in assemblages and their relationship with habitat structure. Coral Reefs 36: 971-980 doi 10.1007/s00338-017-1588-3

Kramer MJ, Bellwood O, Bellwood DR (2013) The trophic importance of algal turfs for coral reef fishes: the crustacean link. Coral Reefs 32: 575-583 doi 10.1007/s00338-013-1009-1

Kramer MJ, Bellwood O, Fulton CJ, Bellwood DR (2015) Refining the invertivore: diversity and specialisation in fish predation on coral reef crustaceans. Mar Biol 162: 1779-1786 doi 10.1007/s00227-015-2710-0

McArdle BH, Anderson MJ (2001) Fitting multivariate models to community data: a comment on distance-based redundancy analysis. Ecology 82: 290-297

Moran DP, Reaka ML (1988) Bioerosion and availability of shelter for benthic reef organisms. Mar Ecol Prog Ser 44: 249-263

Nash KL, Graham NAJ, Wilson SK, Bellwood DR (2013) Cross-scale habitat structure drives fish body size distributions on coral reefs. Ecosystems 16: 478-490 doi 10.1007/s10021-012-9625-0

Nelson HR, Kuempel CD, Altieri AH (2016) The resilience of reef invertebrate biodiversity to coral mortality. Ecosphere 7: e01399

O'Brien J, Scheibling R (2018) Turf wars: competition between foundation and turf-forming species on temperate and tropical reefs and its role in regime shifts. Mar Ecol Prog Ser 590: 1-17 doi 10.3354/meps12530

Plaisance L, Caley MJ, Brainard RE, Knowlton N (2011) The diversity of coral reefs: what are we missing? PLoS One 6: 7 doi 10.1371/journal.pone.0025026

Poore AG, Campbell AH, Coleman RA, Edgar GJ, Jormalainen V, Reynolds PL, Sotka EE, Stachowicz JJ, Taylor RB, Vanderklift MA (2012) Global patterns in the impact of marine herbivores on benthic primary producers. Ecol Lett 15: 912-922

Preston NP, Doherty PJ (1994) Cross-shelf patterns in the community structure of coral-dwelling Crustacea in the central region of the Great Barrier Reef. II. Cryptofauna. Mar Ecol Prog Ser 104: 27-27

R Core Team (2019) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria

Rogers A, Blanchard Julia L, Mumby Peter J (2014) Vulnerability of coral reef risheries to a loss of structural complexity. Curr Biol 24: 1000-1005 doi 10.1016/j.cub.2014.03.026

Rogers A, Blanchard JL, Mumby PJ (2018a) Fisheries productivity under progressive coral reef degradation. J Appl Ecol 50: 1041-1049 doi 10.1111/1365-2664.13051

Rogers A, Blanchard JL, Newman SP, Dryden CS, Mumby PJ (2018b) High refuge availability on coral reefs increases the vulnerability of reef-associated predators to overexploitation. Ecology 99: 450-463

Sheldon R, Prakash A, Sutcliffe Jr W (1972) The size distribution of particles in the ocean. Limnol Oceanogr 17: 327-340

Sprules WG, Barth LE (2016) Surfing the biomass size spectrum: some remarks on history, theory, and application. Can J Fish Aquat Sci 73: 477-495 doi 10.1139/cjfas-2015-0115

Stella J, Munday P, Walker S, Pratchett M, Jones G (2014) From cooperation to combat: adverse effect of thermal stress in a symbiotic coral-crustacean community. Oecologia 174: 1187-1195

Stella JS, Jones GP, Pratchett MS (2010) Variation in the structure of epifaunal invertebrate assemblages among coral hosts. Coral Reefs 29: 957-973 doi 10.1007/s00338-010-0648-8

Stella JS, Munday PL, Jones GP (2011) Effects of coral bleaching on the obligate coral-dwelling crab Trapezia cymodoce. Coral Reefs 30: 719-727 doi 10.1007/s00338-011-0748-0

Stuart-Smith RD, Brown CJ, Ceccarelli DM, Edgar GJ (2018) Ecosystem restructuring along the Great Barrier Reef following mass coral bleaching. Nature 560: 92-96 doi 10.1038/s41586-018-0359-9

Taylor RB (1998) Density, biomass and productivity of animals in four subtidal rocky reef habitats: the importance of small mobile invertebrates. Mar Ecol Prog Ser 172: 37-51

Trebilco R, Dulvy NK, Stewart H, Salomon AK (2015) The role of habitat complexity in shaping the size structure of a temperate reef fish community. Mar Ecol Prog Ser 532: 197-211 doi 10.3354/meps11330

White EP, Ernest SM, Kerkhoff AJ, Enquist BJ (2007) Relationships between body size and abundance in ecology. Trends Ecol Evol 22: 323-330

Wickam H, Averick M, Bryan J, Chang W, D'Agostino McGowan L, Francois R, Grolemund G, Hayes A, Henry L, Hester J, Kuhn M, Lin Pedersen T, Miller E, Milton Bache S, Muller K, Ooms J, Robinson D, Seidel P, Spinu V, Takahashi K, Vaughan D, Wilke C, Woo K, Yutani H (2019) Welcome to the tidyverse. Journal of Open Source Software 4: 1986 doi 10.21105/joss.01686

Williams DM, Hatcher AI (1983) Structure of fish communities on the outer slopes of inshore, midshelf and outershelf reefs of the Great Barrier Reef. Mar Ecol Prog Ser 10: 239-250