



REPORT

A stratified transect approach captures reef complexity with canopy-forming organisms

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Abstract On the Great Barrier Reef (GBR), persistent changes to reef communities have begun to be documented, and on inshore reefs these shifts may favour the proliferation of macroalgae. Critical to understanding changes to reef community structure in response to anthropogenic impacts is developing effective methods to accurately document the abundance of different reef organisms. Effective monitoring must be time and cost efficient, replicable, and able to sufficiently and accurately detect disturbances to allow development of strategies to mitigate their impacts. Traditional techniques to document coral reef communities (i.e. photo-quadrats, benthic intercept transects) rely on planar views, which tend to either over- or under-represent canopy-forming organisms. As canopy-forming organisms are likely to be affected by anthropogenic influences (corals negatively, algae positively), it is essential for monitoring programs to

implement methods sufficient to document changes to the vertical dimension of coral reefs. Here we build on previous work to document the canopy effect in coral-dominated ecosystems and propose a new survey approach suitable for implementation in algal-dominated systems. A vertically stratified transect, modified from a traditional point intercept transect, captures benthic and canopy-forming members of reef communities and provides information on three-dimensional complexity. To test the capability of the new method to detect changes in vertical reef structure, seaweed was removed from experimental quadrats and monitoring techniques were applied before and after four months of regrowth. A stratified method more accurately captured the three-dimensional change resulting from algal canopy growth, while resolving the over- and under-representation of algal biomass in two traditional techniques. We propose that a stratified transect method improves abundance estimates of canopy-forming organisms whilst maintaining data compatibility with traditional methods.

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Introduction

Coral reefs are inherently complex structures, playing host to a diverse array of organisms. Physical complexity is principally constructed by scleractinian corals, whose three-dimensional structure is directly linked to biodiversity through the creation of multiple overlapping spatial and ecological niches (Kiessling et al. 2010; Graham and Nash 2013). However, habitat complexity is one of many attributes of tropical coral reefs that are negatively impacted

by anthropogenic disturbances (Alvarez-Filip et al. 2009; Graham 2014). High seawater temperatures and decreased pH threaten the calcification processes and survival of reef-building corals (Harvey et al. 2013; Cornwall et al. 2021). Combined with increased storm intensity (Knutson et al. 2010), disease, and predators such as crown-of-thorns starfish (De'ath et al. 2012), these processes have the potential to reduce complexity of reef structures, with a subsequent loss of biodiversity (Newman et al. 2015). The loss of live corals through storms and bleaching is often followed by reduced larval supply (Edmunds et al. 2018; Hughes et al. 2019) and hence with shorter periods between disturbances, the potential for natural recovery is diminished.

On near-shore reefs, local influences can also have detrimental effects on reef structure, where changes in water quality due to coastal development and land use practices can result in increased sedimentation and eutrophication, further impacting coral health and driving changes in ecosystem function (Lam et al. 2018; Otaño-Cruz et al. 2019). Many inshore reefs of Australia's Great Barrier Reef (GBR) are exposed to the challenges posed by coastal development (i.e. high sediment and nutrient runoff; De'ath and Fabricius 2010), conditions which can lead to an increase in macroalgae, particularly *Sargassum*, at the expense of corals (De'ath and Fabricius 2010; Ceccarelli et al. 2020). Increased abundance of macroalgae on the GBR follows a seasonal growth curve, with large "blooms" of *Sargassum* through the Austral summer leading into a late summer reproductive period (Vuki and Price 1994). Stands of macroalgae can form dense thickets, with the canopy growing to over a meter above the sea floor. Summer growth and reproduction is followed by tissue degeneration and senescence in winter, leaving perennial, persistent, bare thalli through the colder months (Vuki and Price 1994). While seasonal changes in algal abundance are natural in many reef systems, persistent dominance of macroalgae is one attribute that is characteristic of degraded reefs, where community shifts favour the establishment of fast-growing, highly tolerant species (Hughes 1994). Furthermore, where *Sargassum* has established and persists outside of seasonal growth cycles, it is difficult to reverse, with biological, chemical, and physical feedback mechanisms reinforcing the continued recruitment and growth of the alga (River and Edmunds 2001; Box and Mumby 2007; Mumby 2009; Rasher et al. 2011; Löffler and Hoey 2018).

The structural complexity of reefs naturally inhibits exhaustive documentation of all organisms present within a given area, especially within ecosystems with pronounced canopies. However, survey methods should aim to understand changes in community composition and three-dimensional structure. Throughout the 1900s, development and testing of survey methods was widespread, with broad interchange of ideas between terrestrial and marine systems (Canfield 1941; McIntyre 1953; Heady et al. 1959; Loya

1978; Weinberg 1981). In the mid 1900s, these traditional assessment techniques began to be applied within marine systems, and by the late 1900s certain methodologies predominated in reef ecology studies (e.g. the line or point intercept transect and quadrat methods) and these remain in widespread use today (Supplementary Table 1). Over recent decades there has been a transition in benthic monitoring programs from visual in situ surveys towards digital photo or video capture, or even satellite imagery, with subsequent analysis by the human user or artificial intelligence algorithms (Beijbom et al. 2015; Hedley et al. 2016; Williams et al. 2019; Nunes et al. 2020). However, similar to traditional methods, these techniques largely rely on a planar view. Recent technological advances have been applied by contemporary researchers in attempts to rectify this known issue, with three-dimensional photogrammetry becoming more common in reef monitoring programs (Burns et al. 2015; Casella et al. 2017; Rossi et al. 2020; Kornder et al. 2021). Like other digital techniques, photogrammetry can be expensive, relies on specialist equipment, and has limited backwards-compatibility with traditional survey techniques. Furthermore, because of their fleshy, canopy-forming morphology, complex and varied macroalgal growth forms present a particular challenge to both traditional in situ and newer 3D digital reef monitoring methods. As such, development of standard procedures to capture algal biomass in reef monitoring has been highlighted as essential to gain a more nuanced understanding of global reef health (Obura et al. 2019).

A common feature among almost all frequently used methods to assess reef benthic community assemblages is the use of a planar view. This two-dimensional view is problematic as it over-represents canopy-forming organisms and can skew documentation of the true benthic cover. For example, just as an aerial survey of a rainforest would not allow for identification of small shrubs, measuring benthic cover in canopy-forming reefs using a planar view obscures the true diversity of the system. To address this, Goatley and Bellwood (2011) proposed a chain transect method to more fully capture the rigid canopy formed by scleractinian corals as well as the organisms underneath, which would be capable of documenting the structural loss of coral canopies. However, where coral-based structural complexity is already jeopardised and soft-bodied organisms form canopies, the chain method is not feasible. For example, on algal dominated reefs, such as those common in the Caribbean and reported at some inshore reefs of the GBR, a planar view would over-represent algae, while a chain transect method would flatten the non-rigid algal biomass. Since a change in the vertical structure of an ecosystem is expected in response to ecological and environmental change (Bozec et al. 2015), it is critical to capture this portion of the reef community in benthic reef assessments.

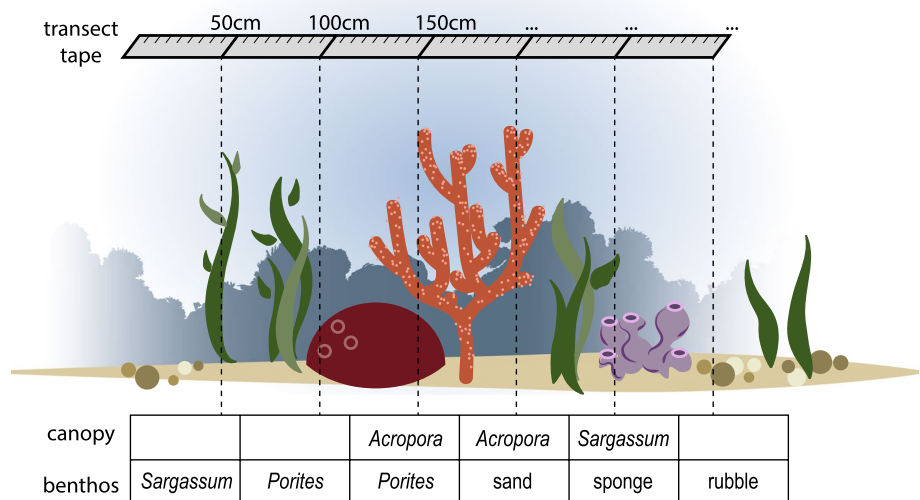
Canopy-forming macroalgae have been identified as a key indicator of low reef resilience (McClanahan et al. 2012; Donovan et al. 2021), hence it is necessary to accurately capture their biomass to understand reef dynamics. However, scientific assessments often do not provide sufficient detail to incorporate their vertical dimension, and this is also true for the underlying manuals. In a web search of 20 reef monitoring manuals published between 1994 and 2020 (Supplementary Table 1), 18 (90%) did not clarify how canopy-forming species (both rigid and soft-bodied) were handled in the data collection. Of the two monitoring manuals that did specify how to handle canopy-forming species, one instructed the observer to ignore the canopy (Almada-Villela et al. 2003), while the other allowed for up to 300% cover to be calculated (Reef Watch Community Monitoring Program 2004). Depending on the season of data collection, this precludes meaningful comparisons between datasets, and may potentially skew benthic patterns. Here we propose a vertically stratified transect method, which improves on capturing three-dimensionality of layered ecosystems, whilst not significantly increasing data collection time in situ and therefore cost. We contrast this with previously proposed techniques for capturing canopy effects on coral-dominated reefs (i.e. chain transect; Goatley and Bellwood (2011)). Whilst in using the chain technique it is assumed that a coral canopy is overrepresented (Goatley and Bellwood 2011), here we propose that an algal canopy is under-represented when using traditional techniques (i.e. benthic surveys in historical data push algae aside and record organisms underneath). The stratified method is suitable for detecting increased macroalgal biomass in a state of reef decline, but is equally applicable to detect reef recovery, measured by an increase in rigid canopy-forming scleractinians.

Materials and Methods

This study was conducted in Florence Bay at Magnetic Island (− 19° 7′ 15″, 146° 52′ 52″), a reef that has low coral cover and high macroalgal abundance (Ceccarelli et al. 2020). Six 25 m² quadrats were established (Supplementary Fig. S1), and all macroalgae within the quadrats were removed by hand to simulate a low algal biomass (i.e. zero canopy) baseline. Transect tapes were laid across both diagonals of each 25 m² quadrat to record reef communities, resulting in a 14 m transect per quadrat (7 m per diagonal). Data were collected in October 2019 immediately after removing macroalgae, and again in March 2020 at the end of the high algal growth season.

A diver swam along the transect tape laid across the reef-scape and recorded the organism(s) directly below every 50 cm (excluding the starting point of the tape), identified to genus level. A single observer recorded all data to minimise bias in individual variation. Observations were made at two points in space and recorded as the “Canopy” and “Benthic” point intercept transects. A Canopy transect point was recorded only if there was an obstructing organism, and the Benthic point was recorded as the benthos occurring below the algal canopy. Where an obstructing Canopy was not present, the Benthic substrate equivalent was recorded in the Canopy dataset. For the Benthic transect, macroalgae were only recorded if the transect directly intersected the holdfast, otherwise the thallus was swept aside to reveal the benthic cover below (Fig. 1). Data were collated as counts per organism category in each of the Canopy, Benthic, and “Combined” transects, whereby the Canopy transect represents a planar view (i.e. equivalent to photo-quadrat data), the Benthic transect represents a typical point intercept transect

Fig. 1 Schematic of the stratified transect method. In this example, the canopy transect (equivalent to a photo-quadrat or photo-transect) percent cover would be calculated as 33% *Sargassum*, 50% coral, and 17% rubble ($n=6$ data points; use “benthos” points where a canopy does not exist). The benthic transect would be calculated as 17% *Sargassum*, 33% coral, 17% sponge, and 33% other; $n=6$ data points. The combined transect would be calculated as 22% *Sargassum*, 44% coral, 11% sponge, and 22% other; $n=9$ data points



(PIT) recording only the benthic cover, and the Combined transect uses all organisms recorded on both levels. For example, a 14 m transect consists of a minimum of 28 and a maximum of 56 possible points (28 Benthic points and 0–28 Canopy points) depending on the abundance of canopy-forming or obstructing organisms. Percent cover of each benthic category was calculated for each transect type in order to test the method. Percent cover calculations for the Combined transect were made by pooling all points across the two strata. Substrate categories included hard corals, *Sargassum*, other algae (including turfs), sponges, crustose coralline algae, and “other” substrata including sand, rock, loose rubble, and dead coral (i.e. where the intact skeleton had not broken down into small pieces of loose rubble).

The change in *Sargassum* cover per transect type was evaluated using a generalised linear mixed effects model with a beta distribution and logit link function, with the interaction between time point (i.e. October and March) and transect type as the fixed effects, and quadrat as a random effect. Planned contrasts were used to determine significant differences between transect types. Community diversity was evaluated using the Shannon diversity index. A generalised linear mixed effects model with a Gamma distribution and log link function were used to explore differences in Shannon diversity between transect types at the two time points. Model fit and assumptions were evaluated using simulated residual plots and tests of dispersion, which were satisfactory in all cases. Planned contrasts were used to determine significant pairwise differences in diversity. The difference in overall community structure per transect type in March was visualised using a constrained redundancy analysis performed on a Bray Curtis distance matrix calculated from Wisconsin-transformed count data. The benthic groups with the highest eigenscores contributing to the discrimination were superimposed on the biplot to visualise the contribution of each group towards separation of the data clouds. To determine if community composition varied between transect types in March, the same distance matrix was used for permutational multivariate analysis of variance (PERMANOVA) based on transect type, blocked by quadrat, run with 9999 permutations. Post-hoc pairwise comparisons were significance-adjusted using the Bonferroni correction for multiple comparisons. Community stratification was evaluated using the percentage of transect points with more than one layer to provide a simple index of three-dimensional complexity. All analyses were performed in R version 4.0.2 (R Core Team 2021) using the packages pairwiseAdonis (Martinez Arbizu 2020), vegan (Oksanen et al. 2020), MuMIn (Bartoń 2020), DHARMA (Hartig 2021), glmTMB (Brooks et al. 2017), and emmeans (Lenth 2021), and visualised with ggplot2 (Wickham 2016).

Results

Removal of algae from the six experimental quadrats yielded 15.4 ± 2.4 kg (mean \pm SE) of wet weight algal biomass per quadrat. Surveys immediately following removal of algal biomass recorded no canopy-forming organisms, so the baseline transects (i.e. Benthic, Canopy, and Combined) were identical within each quadrat. In October, five algal genera, four hard coral genera, sponges, and two “other” benthic substrata (i.e. rubble, sand) were detected across all quadrats regardless of transect type. In March, eight algal genera, five hard coral genera, sponges, and three “other” benthic substrata (i.e. rubble, sand, dead coral) were detected across all quadrats regardless of transect type (Supplementary Fig. S2 and Supplementary Table 2).

Trends in broad benthic categories showed distinct differences between transect types (Fig. 2). For example, between October and March, *Sargassum* displayed a 94-fold increase in percent cover in Canopy transects (56.3% cover; $z = 6.19$, $p < 0.001$) and a 58-fold increase in Combined transects (35.4% cover; $z = 5.15$, $p < 0.001$). The Benthic transect recorded a threefold increase in *Sargassum* cover, though remained below 2% cover ($z = 0.94$, $p = 0.35$). Planned contrasts of estimated marginal means further revealed that the Canopy and Combined transect types detected significantly different levels of *Sargassum* cover in March ($df = 34$, $t = 3.68$, $p < 0.001$). Hard coral cover declined in all transect types, with the Benthic transect recording 15% loss, the Canopy transect recording 70% loss, and the Combined transect showing 44% loss (Fig. 2). Despite variations in the percent cover of each benthic group between the Benthic and Combined transect types, both of these transects recorded similar endpoint community diversity (Shannon Diversity Index; $t = -0.24$, $df = 34$, $p = 0.8$; Fig. 3A). In contrast, the Combined transect type recorded significantly higher diversity compared to the Canopy type ($t = 4.37$, $df = 34$, $p < 0.001$; Fig. 3A). The Canopy transect type showed declines in hard coral, other substrata, and other algae, however these declines in percent cover and community diversity are likely artificial due to the considerable rise in *Sargassum* obstructing the benthos below, rather than reflecting actual coral mortality or benthic changes.

Community composition in March varied significantly between transect types (PERMANOVA; $df = 2$, $F = 1.75$, $p < 0.001$; Fig. 3C), which was driven by a significant pairwise difference between Canopy and Benthic transect communities ($df = 1$, $F = 2.56$, adjusted $p = 0.048$). Pairwise comparisons showed no significant differences in community structure between Canopy and Combined transects ($df = 1$, $F = 1.36$, adjusted $p = 0.71$) or between Benthic and Combined transects ($df = 1$, $F = 1.28$, adjusted $p = 0.91$). Loading vectors for *Sargassum*, *Montipora*, *Goniopora*, *Acropora*, and *Cyphastrea* had the five highest eigenvalues

Fig. 2 Trends in broad benthic categories from October to March for each transect type. Ribbons represent 95% confidence intervals based on the generalised linear mixed effects model

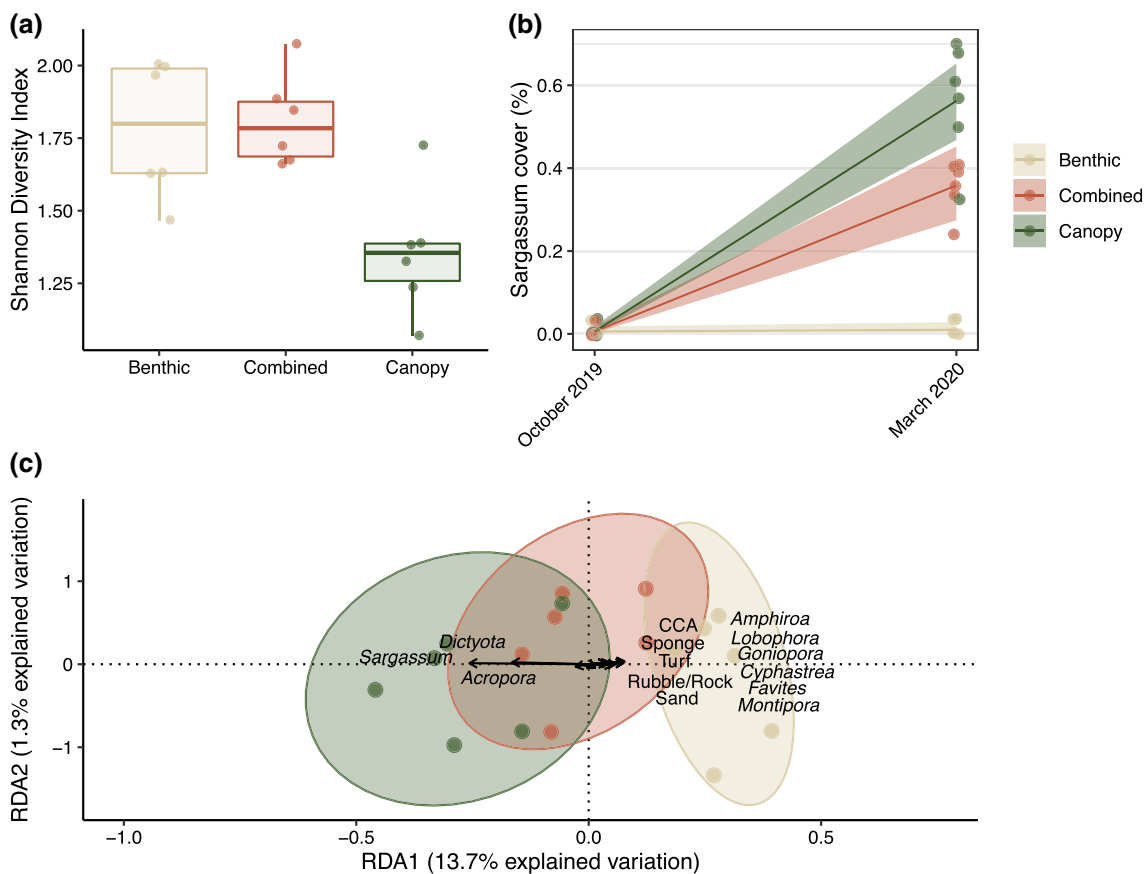
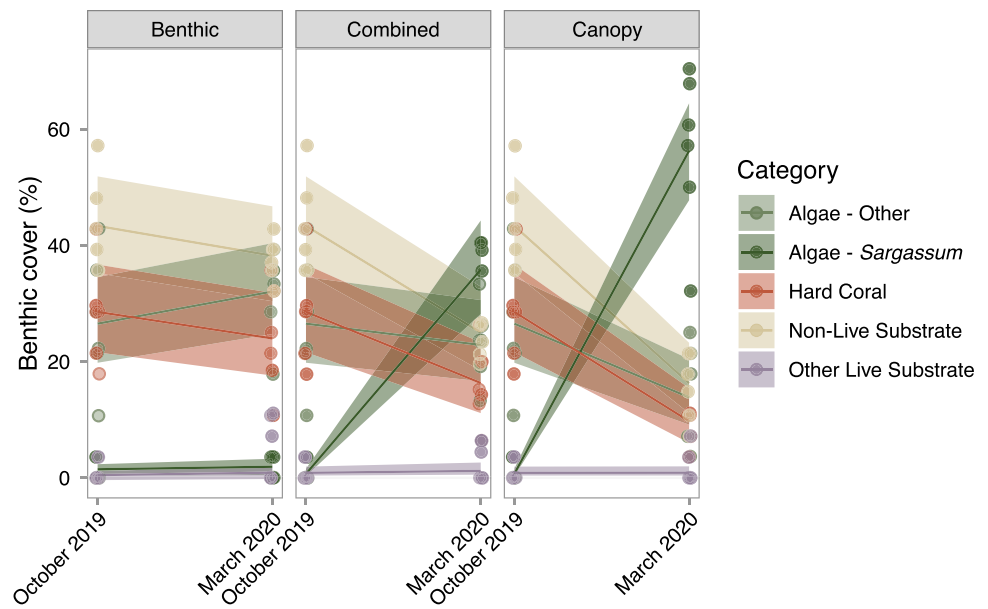


Fig. 3 **a** Shannon Diversity Index of Canopy, Benthic and Combined transect types. **b** Generalised linear mixed effect model predictions for *Sargassum* percent cover over time for three different transect types. Points are raw data, ribbons represent a 95% confidence

interval. **c** Redundancy analysis of community composition based on Bray–Curtis distance matrix, with ellipses representing 90% confidence intervals for each of three transect types

associated with the two axes, with high *Sargassum* cover associated with the negative side of the first principal component, and consistent with the Canopy transect data cloud position (Fig. 3C). The stratification index (i.e. percent of point intercepts with multiple strata) using the Combined transect type, increased from no stratification in October to 59% stratification in March. Less than 1% of the stratification was from hard coral strata, with the remainder representing algal canopy growth.

Discussion

As environmental disturbances continue to cause structural changes to reefs globally, effective ecological monitoring techniques are vital to document and understand resulting changes in community composition. The influence of canopy-forming organisms on monitoring data can fundamentally skew our perception of reef ecology. As changes in canopy components of reefs are expected with climate change (i.e. decreased coral and increased macroalgae), and these community members respond differently to disturbances (Wilson et al. 2012; Roff et al. 2015; Loffler and Hoey 2018; Mellin et al. 2019), methods must be developed to minimise bias when monitoring coral reef communities. Simultaneously, there has been a considerable increase in reef rehabilitation research worldwide (Boström-Einarsson et al. 2020). Canopy-forming organisms are important in the decline phase of coral reefs, but also critical elements in understanding community succession during reef recovery, whether natural or assisted through restoration activities (Smith et al. 2022). If reinstating coral-based three-dimensional complexity is a goal of restoration, methods are needed to document such changes. This work clearly demonstrates how choice of monitoring method can influence data, and hence influence ecological understanding.

The three transect types in the current study produced strongly varying snapshots of reef communities at Magnetic Island. The Benthic transect type, which is equivalent to a traditional point intercept transect (PIT), showed a fairly consistent community throughout the experiment, with no considerable change in percent cover across any of the broad taxonomic groups. The two other transect types detected large increases in *Sargassum* (Canopy type: 94-fold increase; Combined type: 58-fold increase), accurately reflecting the high summer growth of this macroalgal genus. However, the Canopy transect type (equivalent to traditional photoquadrats) also reflected decreases in all other living benthic members and overall diversity, being swamped by the algal biomass. The reported decreases in hard coral, other algae, and other living benthos are an artefact of the sampling method based on a two-dimensional view and reflect the pronounced effect of canopy-forming *Sargassum*.

The implications of these two traditional methods on our understanding of reef dynamics are important. Firstly, it is clear that data collected by the two methods are not comparable, and hence caution should be applied when interpreting data of the two types across studies (see Vallès et al. 2019). In addition, the apparent loss of coral cover documented by the Canopy technique may artificially inflate our interpretation of the effects of disturbance (i.e. conclude coral loss where corals have simply been concealed by canopy). Alternately, the benthic technique may artificially lead to a conclusion that a reef is stable where a significant change has in fact occurred. On algal-dominated reefs, it should be noted that the seasonal nature of *Sargassum* growth can also bias our understanding of reef dynamics. If an initial survey is conducted in winter, when *Sargassum* cover is at its lowest, followed up by a survey in summer, misleading conclusions around a change in reef state, such as a phase shift, could be made, particularly when using a planar survey type.

Many of the issues with the two traditional transect types were resolved using the proposed Combined transect. This transect held the benefits of the Canopy type, being able to detect the summer increase in algal biomass, and additionally incorporated the benefits of the Benthic type to capture benthic cover below the canopy. The Combined transect type was the only method which accurately captured reef changes in terms of percent cover and community diversity. While the survey location in this study contained very low frequency of rigid canopy-forming members, the combined transect type should perform equally well on a coral-dominated reef, being capable of detecting both small corals and the epilithic algal matrix residing below canopy-forming corals (Goatley and Bellwood 2011), though further testing of the method is needed in such areas. Using the proportion of transect points with canopy as an index for complexity (stratification), the Combined transect allows for rough estimates of three-dimensional complexity or rugosity. In reef systems with more than two distinct spatial communities, additional strata could be measured, providing a more nuanced understanding of the reef community. In contrast to the chain method detailed in Goatley and Bellwood (2011), the layered transect proposed here does not become more challenging in bad conditions. A potential disadvantage requiring consideration during field preparation is an increase in survey time, particularly for benthic communities with high three-dimensional complexity. However, this investment is well justified given the vastly improved representation of community composition. Finally, it allows for a stratification of sampling with minimal extra effort or expertise required, and produces backwards-compatible data that can easily be modified to correspond and compare with other studies based on traditional PIT or planar methods. However, some difficulties that face most reef monitoring techniques could not be overcome with this method. Observer variation

and parallax (the phenomenon whereby a viewer's position can alter the object being viewed beneath the transect line) can be a source of bias in many survey methods including photogrammetry (Vallès et al. 2019; Lesser and Slattery 2021; Porter and Meier 1992), and the method proposed here is not immune to these challenges. Particularly where soft-bodied organisms are subject to movement with water flow, further variation in observer bias may be introduced. As with any existing in situ monitoring techniques, minimising this bias can be achieved through in-water training, sample and observer replication, using orientation aids such as plumb lines, as well as by capturing observer variation in model outcomes.

This study, as with that of Goatley and Bellwood (2011), begs the question, which method is best? Coral reefs are complex three-dimensional structures, and hence any data collection method is required to reduce dimensionality and complexity. But at what point do we concede that we have captured “enough” of the complexity to understand the system? Of course, the answer to this will depend on the question being asked. The data collected here showed that there was no difference between the transect types when algal biomass was removed, demonstrating that a planar view is sufficient for systems with minimal stratification. With high canopy cover, the data here supports the conclusions of Goatley and Bellwood (2011), with a planar view being sufficient for research questions targeting canopy forming organisms (either corals or algae); however, this technique is severely limited for other benthic members. Our data also support their conclusion that benthic transects more accurately capture reef composition in terms of substratum occupied, whereby the majority of algal biomass is held in the water column and the holdfast represents only a minor benthic component of even algal-dominated reefs. However, the combined method provides an integrated view, allowing for detailed understanding of the benthic composition as well as major contributors to reef biomass and function.

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Data availability The datasets generated during the current study are available from the corresponding author on reasonable request.

Declarations

Conflict of interest The authors declare no conflict of interest.

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References

- Almada-Villela PC, Sale PF, Gold-Bouchot G, Kjerfve B (2003) Manual of methods for the MBRS Synoptic monitoring program: selected methods for monitoring physical and biological parameters for use in the Mesoamerican region
- Alvarez-Filip L, Dulvy NK, Gill JA, Côté IM, Watkinson AR (2009) Flattening of Caribbean coral reefs: region-wide declines in architectural complexity. *Proc Royal Soc B Biol Sci* 276:3019–3025
- Bartoń K (2020) MuMin: multi-model inference
- Beijbom O, Edmunds PJ, Roelfsema C, Smith J, Kline DI, Neal BP, Dunlap MJ, Moriarty V, Fan T-Y, Tan C-J, Chan S, Treibitz T, Gamst A, Mitchell BG, Kriegman D (2015) Towards automated annotation of benthic survey images: variability of human experts and operational modes of automation. *PLoS ONE* 10:e0130312
- Boström-Einarsson L, Babcock RC, Bayraktarov E, Ceccarelli D, Cook N, Ferse SCA, Hancock B, Harrison P, Hein M, Shaver E, Smith A, Suggett D, Stewart-Sinclair PJ, Vardi T, McLeod IM (2020) Coral restoration – a systematic review of current methods, successes, failures and future directions. *PLoS ONE* 15:e0226631
- Box S, Mumby P (2007) Effect of macroalgal competition on growth and survival of juvenile Caribbean corals. *Mar Ecol Prog Ser* 342:139–149
- Bozec Y-M, Alvarez-Filip L, Mumby PJ (2015) The dynamics of architectural complexity on coral reefs under climate change. *Glob Change Biol* 21:223–235
- Brooks ME, Kristensen K, van Benthem KJ, Magnusson A, Berg CW, Nielsen A, Skaug HJ, Maechler M, Bolker BM (2017) glmmTMB balances speed and flexibility among packages for zero-inflated generalised linear mixed modeling. *R J* 9:378–400
- Burns J, Delparte D, Gates R, Takabayashi M (2015) Integrating structure-from-motion photogrammetry with geospatial software as a novel technique for quantifying 3D ecological characteristics of coral reefs. *PeerJ* 3:e1077
- Canfield RH (1941) Application of the line interception method in sampling range vegetation. *J Forest* 39:388–394
- Casella E, Collin A, Harris D, Ferse S, Bejarano S, Parravicini V, Hench JL, Rovere A (2017) Mapping coral reefs using consumer-grade drones and structure from motion photogrammetry techniques. *Coral Reefs* 36:269–275
- Ceccarelli DM, Evans RD, Logan M, Mantel P, Puotinen M, Petus C, Russ GR, Williamson DH (2020) Long-term dynamics and drivers of coral and macroalgal cover on inshore reefs of the Great Barrier Reef Marine Park. *Ecol Appl* 30:e02008
- Cornwall CE, Comeau S, Kornder NA, Perry CT, van Hooijdonk R, DeCarlo TM, Pratchett MS, Anderson KD, Browne N, Carpenter

- R, Diaz-Pulido G, D'Olivo JP, Doo SS, Figueiredo J, Fortunato SAV, Kennedy E, Lantz CA, McCulloch MT, González-Rivero M, Schoepf V, Smithers SG, Lowe RJ (2021) Global declines in coral reef calcium carbonate production under ocean acidification and warming. *Proc Natl Acad Sci USA* 118:e2015265118
- De'ath G, Fabricius K (2010) Water quality as a regional driver of coral biodiversity and macroalgae on the Great Barrier Reef. *Ecol Appl* 20:840–850
- De'ath G, Fabricius KE, Sweatman H, Puotinen M (2012) The 27-year decline of coral cover on the Great Barrier Reef and its causes. *Proc Natl Acad Sci* 109:17995–17999
- Donovan MK, Burkepile DE, Kratochwill C, Shlesinger T, Sully S, Oliver TA, Hodgson G, Freiwald J, van Woesik R (2021) Local conditions magnify coral loss after marine heatwaves. *Science* 372:977–980
- Edmunds PJ, McIlroy SE, Adjeroud M, Ang P, Bergman JL, Carpenter RC, Coffroth MA, Fujimura AG, Hench JL, Holbrook SJ, Leichter JJ, Muko S, Nakajima Y, Nakamura M, Paris CB, Schmitt RJ, Suthacheep M, Toonen RJ, Sakai K, Suzuki G, Washburn L, Wyatt ASJ, Mitarai S (2018) Critical information gaps impeding understanding of the role of larval connectivity among coral reef islands in an era of global change. *Front Mar Sci* 5:290
- Goatley CHR, Bellwood DR (2011) The roles of dimensionality, canopies and complexity in ecosystem monitoring. *PLoS ONE* 6:e27307
- Graham NAJ (2014) Habitat complexity: coral structural loss leads to fisheries declines. *Curr Biol* 24:R359–R361
- Graham NAJ, Nash KL (2013) The importance of structural complexity in coral reef ecosystems. *Coral Reefs* 32:315–326
- Hartig F (2021) DHARMA: Residual Diagnostics for Hierarchical (Multi-Level / Mixed) Regression Models
- Harvey BP, Gwynn-Jones D, Moore PJ (2013) Meta-analysis reveals complex marine biological responses to the interactive effects of ocean acidification and warming. *Ecol Evol* 3:1016–1030
- Heady HF, Gibbens RP, Powell RW (1959) A comparison of the charting, line intercept, and line point methods of sampling shrub types of vegetation. *Rangel Ecolo Manag J Range Manag Archives* 12:180–188
- Hedley J, Roelfsema C, Chollett I, Harborne A, Heron S, Weeks S, Skirving W, Strong A, Eakin C, Christensen T, Ticzon V, Bejarano S, Mumby P (2016) Remote sensing of coral reefs for monitoring and management: a review. *Remote Sens* 8:118
- Hughes TP (1994) Catastrophes, phase shifts, and large-scale degradation of a caribbean coral reef. *Science* 265:1547–1551
- Hughes TP, Kerry JT, Baird AH, Connolly SR, Chase TJ, Dietzel A, Hill T, Hoey AS, Hoogenboom MO, Jacobson M, Kerswell A, Madin JS, Mieog A, Paley AS, Pratchett MS, Torda G, Woods RM (2019) Global warming impairs stock–recruitment dynamics of corals. *Nature* 1
- Kiessling W, Simpson C, Foote M (2010) Reefs as cradles of evolution and sources of biodiversity in the phanerozoic. *Science* 327:196–198
- Knutson TR, McBride JL, Chan J, Emanuel K, Holland G, Landsea C, Held I, Kossin JP, Srivastava AK, Sugi M (2010) Tropical cyclones and climate change. *Nat Geosci* 3:157–163
- Kornder NA, Cappelleto J, Mueller B, Zalm MJL, Martinez SJ, Vermeij MJA, Huisman J, de Goeij JM (2021) Implications of 2D versus 3D surveys to measure the abundance and composition of benthic coral reef communities. *Coral Reefs* 40:1137–1153
- Lam VYY, Chaloupka M, Thompson A, Doropoulos C, Mumby PJ (2018) Acute drivers influence recent inshore Great Barrier Reef dynamics. *Proc R Soc B* 285:20182063
- Lenth RV (2021) emmeans: Estimated marginal means, aka least-squares means
- Lesser MP, Slattery M (2021) Mesophotic coral reef community structure: the constraints of imagery collected by unmanned vehicles. *Mar Ecol Prog Ser* 663:229–236
- Loffler Z, Hoey AS (2018) Canopy-forming macroalgal beds (*Sargassum*) on coral reefs are resilient to physical disturbance. *J Ecol* 106:1156–1164
- Loya Y (1978) Plotless and transect methods. In: Stoddart DR, Johannes RE (eds) *Monographs on oceanic methodology: research methods*. UNESCO Press, Coral Reefs, pp 197–218
- Martinez Arbizu P (2020) pairwiseAdonis: Pairwise multilevel comparison using adonis
- McClanahan TR, Donner SD, Maynard JA, MacNeil MA, Graham NAJ, Maina J, Baker AC, Alemu IJB, Beger M, Campbell SJ, Darling ES, Eakin CM, Heron SF, Jupiter SD, Lundquist CJ, McLeod E, Mumby PJ, Paddock MJ, Selig ER, van Woesik R (2012) Prioritizing key resilience indicators to support coral reef management in a changing climate. *PLoS ONE* 7:e42884
- McIntyre GA (1953) Estimation of plant density using line transects. *J Ecol* 41:319
- Mellin C, Thompson A, Jonker MJ, Emslie MJ (2019) Cross-shelf variation in coral community response to disturbance on the Great Barrier Reef. *Diversity* 11:38
- Mumby PJ (2009) Phase shifts and the stability of macroalgal communities on Caribbean coral reefs. *Coral Reefs* 28:761–773
- Newman SP, Meesters EH, Dryden CS, Williams SM, Sanchez C, Mumby PJ, Polunin NVC (2015) Reef flattening effects on total richness and species responses in the Caribbean. *J Anim Ecol* 84:1678–1689
- Nunes JACC, Cruz ICS, Nunes A, Pinheiro HT (2020) Speeding up coral reef conservation with AI-aided automated image analysis. *Nat Mach Intell* 2:292–292
- Obura DO, Aey G, Amornthammarong N, Appeltans W, Bax N, Bishop J, Brainard RE, Chan S, Fletcher P, Gordon TAC, Gramer L, Gudka M, Halas J, Hendee J, Hodgson G, Huang D, Jankulak M, Jones A, Kimura T, Levy J, Miloslavich P, Chou LM, Muller-Karger F, Osuka K, Samoilys M, Simpson SD, Tun K, Wongbusarakum S (2019) Coral reef monitoring, reef assessment technologies, and ecosystem-based management. *Front Mar Sci* 6:580
- Oksanen J, Blanchet FG, Friendly M, Kindt R, Legendre P, McGinn D, Minchin PR, O'Hara RB, Simpson GL, Solymos P, Stevens MHH, Szoecs E, Wagner H (2020) *vegan: Community Ecology Package*
- Otaño-Cruz A, Montañez-Acuña AA, García-Rodríguez NM, Díaz-Morales DM, Benson E, Cuevas E, Ortiz-Zayas J, Hernández-Delgado EA (2019) Caribbean near-shore coral reef benthic community response to changes on sedimentation dynamics and environmental conditions. *Front Mar Sci* 6:551
- Porter JW, Meier OW (1992) Quantification of loss and change in Floridian reef coral populations. *Am Zool* 32:625–640
- R Core Team (2021) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria
- Rasher DB, Stout EP, Engel S, Kubanek J, Hay ME (2011) Macroalgal terpenes function as allelopathic agents against reef corals. *Proc Natl Acad Sci* 108:17726–17731
- Reef Watch Community Monitoring Program (2004) Reef watch Benthic Quadrat survey manual
- River GF, Edmunds PJ (2001) Mechanisms of interaction between macroalgae and scleractinians on a coral reef in Jamaica. *J Exp Mar Biol Ecol* 261:159–172
- Roff G, Chollett I, Doropoulos C, Golbuu Y, Steneck RS, Isechal AL, van Woesik R, Mumby PJ (2015) Exposure-driven macroalgal phase shift following catastrophic disturbance on coral reefs. *Coral Reefs* 34:715–725
- Rossi P, Castagnetti C, Capra A, Brooks AJ, Mancini F (2020) Detecting change in coral reef 3D structure using underwater photogrammetry: critical issues and performance metrics. *Appl Geomat* 12:3–17

- Smith HA, Brown DA, Arjunwadkar CV, Fulton SE, Whitman T, Hermanto B, Mastroianni E, Mattocks N, Smith AK, Harrison PL, Boström-Einarsson L, McLeod IM, Bourne DG (2022) Removal of macroalgae from degraded reefs enhances coral recruitment. *Restor Ecol*. <https://doi.org/10.1111/rec.13624>
- Vallès H, Oxenford HA, Henderson A (2019) Switching between standard coral reef benthic monitoring protocols is complicated: proof of concept. *PeerJ* 7:e8167
- Vuki VC, Price IR (1994) Seasonal changes in the Sargassum populations on a fringing coral reef, Magnetic Island, Great Barrier Reef region, Australia. *Aquat Bot* 48:153–166
- Weinberg S (1981) A comparison of coral reef survey methods. *Bijdragen Tot De Dierkunde* 51:199–218
- Wickham H (2016) *ggplot2: Elegant Graphics for Data Analysis*. Springer International Publishing : Imprint: Springer, Cham
- Williams ID, Couch CS, Beijbom O, Oliver TA, Vargas-Angel B, Schumacher BD, Brainard RE (2019) Leveraging automated image analysis tools to transform our capacity to assess status and trends of coral reefs. *Front Mar Sci* 6:222
- Wilson SK, Graham NAJ, Fisher R, Robinson J, Nash K, Chong-Seng K, Polunin NVC, Aumeeruddy R, Quatre R (2012) Effect of macroalgal expansion and marine protected areas on coral recovery following a climatic disturbance: Macroalgae, MPAs, and Coral Recovery. *Conserv Biol* 26:995–1004

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