



## Comparability and complementarity of reef fish measures from underwater visual census (UVC) and baited remote underwater video stations (BRUVS)

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### ABSTRACT

The much-publicized threats to coral reef systems necessitate a considered management response based on comprehensive ecological data. However, data from large reef systems commonly originate from multiple monitoring programs that use different methods, each with distinct biases that limit unified assessments of ecological status. The effective integration of data from different monitoring methods would allow better assessment of system status and hence, more informed management. Here we examine the scope for comparability and complementarity of fish data from two different methods used on Australia's Great Barrier Reef (GBR): underwater visual census (UVC) and baited remote underwater video stations (BRUVS). We compared commonly reported reef fish measures from UVC and BRUVS on similar reef slope habitats of three central GBR reefs. Both methods recorded similar estimates of total species richness, although ~30% of recorded species were not common to both methods. There were marked differences between methods in sub-group species richness, frequency of species occurrences, relative abundances of taxa and assemblage structure. The magnitude and orientation of inter-method differences were often inconsistent among taxa. However, each method better categorized certain components of fish communities: BRUVS sampled more predatory species in higher numbers while UVC was similarly better at sampling damselfishes (Pomacentridae). Our results suggest limited scope for direct or adjusted comparisons of data from UVC and BRUVS. Conversely, complementary aspects of the two methods confirm that their integration in monitoring programs will provide a more complete and extensive assessment of reef fish status for managers than from either method alone.

### 1. Introduction

The Anthropocene poses many threats to coral reefs (Pandolfi et al., 2003; Bellwood et al., 2004; Frieler et al., 2013; Cheal et al., 2017; Hughes et al., 2017) that cannot be effectively managed unless comprehensive ecological data are available to inform responses. Monitoring programs are the most common source of these data. Ideally, monitoring of key biota (i.e. corals, fishes, invertebrates, algae etc.) within a reef system is conducted regularly over as wide a range of locations and habitats as possible. Furthermore, use of the same monitoring methodology throughout allows the most accurate assessments of system-wide patterns because different methods introduce different biases (Leujak and Ormond, 2007; MacNeil et al., 2008; Zvuloni et al., 2008; Murphy and Jenkins, 2010) that cannot always be mitigated. This has prompted calls for global standards of coral reef monitoring (English et al., 1997; Caldwell et al., 2016; Goetze et al., 2019; Obura et al., 2019)

to enable the most valid comparisons of the status of the world's reefs. Currently though, multiple monitoring programs often operate within large coral reef systems and may employ different methods despite some of the measured variables being common to each (i.e. percent coral cover, fish density etc.). Inherent methodological biases within each monitoring program limit the capacity for coalescence of common data among programs. Yet, spatial management of reef systems could be improved if these biases were better understood and alleviated to allow meaningful comparisons of important ecological data.

Fishes are one of the most important, and hence most widely monitored, coral reef inhabitants around the world. They are principal sources of food through commercial, recreational and artisanal fisheries (Teh et al., 2013; Darling and D'agata, 2017) and also provide great aesthetic pleasure through tourism operations and personal excursions, contributing to the estimated US\$36 billion value of coral reef tourism globally (Spalding et al., 2017). Additionally, the actions of reef fishes

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support the ecological functioning of coral reefs (Moberg and Folke, 1999), most commonly exemplified by the prevention of algal dominance over corals by the grazing of herbivorous fishes (Hughes, 1994; Bellwood et al., 2004; Cheal et al., 2010). However, coral reef fish communities in certain locations have already been impacted by overfishing (Jackson et al., 2001; Shantz et al., 2020), many more continue to be unsustainably harvested (Newton et al., 2007; MacNeil et al., 2015) and all are vulnerable in multiple ways to escalating climate change (Munday et al., 2008; Pratchett et al., 2017). In the face of these threats, human activities that directly or indirectly reduce reef fish diversity need to be properly managed. Long-term monitoring programs provide the fundamental information from which managers can assess and justify the need for more stringent or relaxed controls on human actions that influence reef fishes. However, methodological differences and associated biases in data among reef fish monitoring programs limit the capacity of managers to get the most comprehensive and united picture of reef fish status.

While most reef fish monitoring programs record some measure of the diversity, number and size of fishes, a wide variety of methods have been employed to do this. Underwater visual census (UVC) surveys by scuba divers have a long history (since Brock, 1954) and include belt transects (Sanderson and Solonsky, 1986; De Girolamo and Mazzoldi, 2001; Emslie and Cheal, 2018), stationary point counts (Bohnsack and Bannerot, 1986; Polunin and Roberts, 1993) and timed swims (Jones and Thompson, 1978; Williams, 1987), with various adaptations of each. While UVC is a widespread method, it does have limitations including: inherent observer bias (Mallet and Pelletier, 2014), which can be largely overcome with regular calibration and training of observers (Lowry et al., 2012; Emslie et al., 2018), passive diver presence influencing the behaviour of some fishes (Emslie et al., 2018) and restrictions to the depths at which SCUBA diving can be safely conducted (Harvey et al., 2001; Cappo et al., 2003). It does, however, have the advantages of being relatively inexpensive, requiring short post survey processing times, generally facilitating accurate species identification and allowing observers to undertake detailed searches of the reef.

Videography is a more recent tool for fish monitoring and has been utilised either on SCUBA as diver operated video (DOV; Watson et al., 2005; Pelletier et al., 2011; Wilson et al., 2018; Goetze et al., 2019), or using video cameras deployed to the sea floor, of which baited remote underwater video stations (BRUVS) have become most popular (Ellis and DeMartini, 1995; Willis and Babcock, 2000; Harvey et al., 2001; Cappo et al., 2004, 2007; Whitmarsh et al., 2016; Wellington et al., 2018; Bacheler et al., 2019), or using remotely operated video (ROV, Sward et al., 2019). Video systems are increasingly being used to survey reef fish and can be deployed as single or stereo camera units, with stereo units having the added advantage of yielding quite precise estimates of fish length, hence allowing accurate calculations of biomass (Watson et al., 2010; Schramm et al., 2020). Additionally, remote systems (i.e. BRUVS, ROVs) are not restricted by depth compared to diver survey methods, enabling deeper locations and a greater variety of habitats to be surveyed. All video methods are advantageous in that they provide a permanent survey record that can be reviewed as necessary, but they also have disadvantages including long processing times required to analyse videos, and when single camera units are used, difficulties in estimating the area in the field of view. In addition, artificial light and sound typically generated by ROVs, use of bait in BRUVS (Harvey et al., 2007) and the passive diver issues for DOVs are examples of traits specific to each video method that can alter fish behaviour; effects which may vary across families, species and trophic groups (Andradi-Brown et al., 2016).

Different fish survey methods can result in conflicting estimates of fish measures (e.g. Willis et al., 2000; Andradi-Brown et al., 2016) and inevitably introduce different biases that make it difficult to compare data among programs with dissimilar methods. Differences in the size of area surveyed (Cheal and Thompson, 1997), in the detectability of fish species (MacNeil et al., 2008), whether bait is used as an attractant

(Harvey et al., 2007) and the level of site disturbance by diver activity prior to surveys (Emslie et al., 2018) are just some sources of bias in reef fish surveys that will vary among methods. Perhaps one of the biggest issues in comparing the same measure from surveys conducted using different methods is that measurement units can differ. For example, estimates of fish species abundance may originate from: direct counts of fish within a set area (i.e. in the point counts of Bohnsack and Bannerot, 1986, and in the UVC belt transects of Emslie and Cheal, 2018), counts of fish in log<sub>5</sub> scales (i.e. in the timed swims of Williams, 1987) or from the maximum number seen in a single video frame during a set period of footage (i.e. the MaxN of BRUVS as in Priede et al., 1994; Willis and Babcock, 2000; Cappo et al., 2004). All provide an estimate of the abundance of each species and have valid reasons for their use, but the use of different measurement units makes it difficult to reliably compare these data.

Monitoring of reef fish communities could be enhanced if means were found to validly compare data derived from different methods and/or to apply those different data in a complementary fashion. The ability to integrate datasets from UVC transects and BRUVS deployments would be particularly useful as both are widely used and have unique advantages. UVC transects enable assessment of large swathes of shallow habitat, not limited to a particular field of view as in BRUVS. The use of scuba divers in UVC also enables identification of species in situ, detection of cryptic species, and finer-scale habitat characterisation compared with BRUVS videos. BRUVS are a remote, non-obtrusive method that can survey fishes on a range of habitats including those too deep or too dangerous (i.e. due to presence of crocodiles) for safe scuba diving in UVC surveys and provide an archival record that can be referred to for future analyses (Cappo et al., 2004). BRUVS can also be easily replicated, and deployed around an entire reef, providing information on multiple habitats. Clearly, use of both UVC and BRUVS would enhance spatial coverage of monitoring and provide more information on reef fish communities (Schramm et al., 2020). However, the integration of data from the two methods appears difficult as studies consistently show that UVC and BRUVS sample the same fish communities differently, resulting in assemblage structures that differ due to method-specific biases, related to the behaviour and ecological niche of individual species (Willis et al., 2000; Stobart et al., 2007; Colton and Sweare, 2010; Lowry et al., 2012; Gilmour et al., 2014). None of these studies though, addressed in detail the challenge of how to meaningfully integrate data from the two methods to increase the spatial scale of system monitoring, best categorize fish communities and better inform management.

In response to the escalating challenges facing Australia's Great Barrier Reef (GBR, Cheal et al., 2017; Wolff et al., 2018; Hughes et al., 2019), the federally driven Reef 2050 Long-Term Sustainability Plan (Australian Government, 2018) included a fundamental requirement for an integrated GBR monitoring program (Great Barrier Reef Marine Park Authority and Queensland Government, 2018) to better inform reef managers. Accordingly, there is interest in assessing the practical comparability and complementarity of UVC and BRUVS data within a new integrated program to best inform the status of reef fishes. Here we investigated how reef fish data from UVC transects and BRUVS deployments could be integrated to expand the spatial extent of monitoring and better categorize fish communities on the GBR.

### 1.1. Specifically, we assessed

- 1) The comparability of reef fish measures (i.e. species richness and abundance) from UVC and BRUVS in the same locations; can those measures be directly compared among more locations and depths by utilising data from both methods interchangeably?
- 2) The complementarity of UVC and BRUVS; does using both methods provide a more complete assessment of reef fish status than by using either method alone?

- 3) The ways in which both methods could be most meaningfully applied in an integrated monitoring program given the findings from 1) and 2) above, to better inform reef managers.

## 2. Material and methods

### 2.1. General methods

The two reef fish survey methods compared here have been employed extensively on the GBR by the Australian Institute of Marine Science (AIMS). UVC has been used for surveys in shallow water (<15 m) while BRUVS have been deployed in a range of depths to >50 m. Both methods provide fish data that informs management and ecological understanding. The AIMS UVC fish monitoring program has surveyed fixed sites at 46–56 reefs per year since 1992 and data collection is ongoing. Standard UVC surveys at each reef utilise three sites established on or near the north-east flank. Sites consist of five permanently marked 50m transects at depths between 6 m and 9 m. The abundances of fishes from a target list of 218 non-cryptic, diurnal species from 9 families (Emslie and Cheal, 2018) have been recorded since the program's inception. Fish species are recorded along each transect by divers using scuba; large mobile fishes from eight families on 5 m wide transects and damselfishes (Pomacentridae) on 1 m wide transects (Emslie and Cheal, 2018). AIMS GBR BRUVS surveys have been consistently deployed from 2001 to 2014 on 73 reefs, typically in deeper waters (>15m); BRUVS surveys are ongoing in various locations. BRUVS used in this study consisted of a metal frame fitted with a GoPro Hero4 video camera (30 frames per second, 1920x1080 pixel resolution, medium field of view) and baited with approximately 1 kg of crushed pilchards (*Sardinops sagax*). BRUVS were deployed for 60 min, separated by at least 350 m at any time to reduce the likelihood of individuals occurring on multiple cameras (Cappo et al., 2004), with a float line attached for retrieval. BRUVS videos were subsequently analysed to determine species diversity and the abundance of fish species as MaxN, the maximum number of individuals of each species seen together in one frame (hereafter referred to as 'abundance', Cappo et al., 2003).

### 2.2. Field design

To assess comparability of data from UVC and BRUVS on the GBR we evaluated data from both methods at the same location and depths, at a similar time. Annual AIMS UVC surveys of sites at three reefs (Rib, Knife, and Chicken) in the Townsville sector of the GBR (between 18 and 19° S) were completed in May 2016 and followed in July 2016 with a number of targeted BRUVS deployments (as part of the Global FinPrint Project, <https://globalfinprint.org/>) using methods described in section 2.1, in the vicinity of UVC sites at similar depths (Fig. 1). The exact locations of all BRUVS deployments were recorded and the distances from the closest UVC sites were later estimated using Google Earth to allow assessment of whether fish assemblages recorded on BRUVS further from UVC sites might have been dissimilar. At each reef the standard three UVC sites were surveyed (15 transects in total) while there were eleven BRUVS deployments at Rib Reef, nine at Knife Reef and three at Chicken Reef.

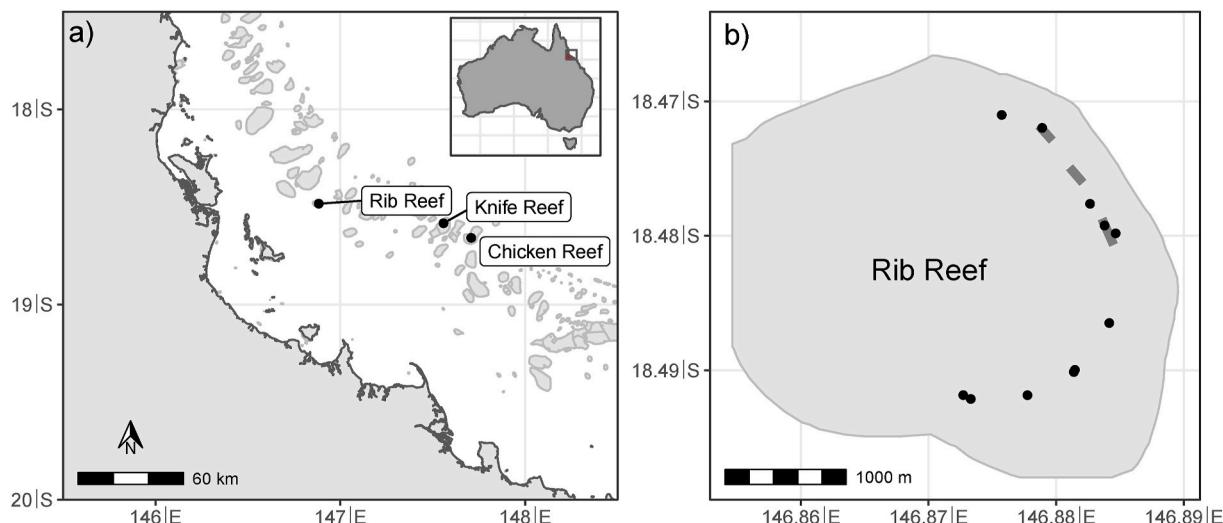
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### 2.3. Target taxa

While BRUVS recorded all species observed in video frames, to facilitate valid comparisons of UVC and BRUVS we constrained the analyses to the list of 218 species recorded during UVC surveys (Emslie and Cheal, 2018). This list of species is divided into small site attached damselfishes (all species of Pomacentridae) and select large mobile fishes from the families Acanthuridae, Chaetodontidae, Labridae, Lethrinidae, Lutjanidae, Serranidae, Siganidae and Zanclidae, noting that relatively few non-scarine labrids and serranids are in the list (Emslie and Cheal, 2018). Four focal groups of fish species were examined separately. These groups were: large herbivores (Acanthuridae, Labridae-subfamily Scarinae and Siganidae), large predators (Serranidae, Lutjanidae and Lethrinidae that consume large prey, and certain Labridae species that generally consume smaller prey), butterflyfishes (Chaetodontidae) and damselfishes (Pomacentridae). The herbivores and predators are particularly recognized as important: large herbivores for their role in limiting excessive algal growth that can outcompete corals and large predators for their value for fisheries and their ecological role as higher order consumers in the reef food chain.

### 2.4. Measures of interest

Three fish community measures provided the basis for comparisons between UVC and BRUVS: species richness, abundance (absolute counts, symbolized as N, from UVC and MaxN from BRUVS) and assemblage structure. These are commonly used as indicators of reef fish status and for assessment of change, and all are relevant to management. Because species richness and abundance estimates are influenced by the area sampled and the sample area from BRUVS is unknown (due partly to the



**Fig. 1.** a) Map of the survey reefs on the central Great Barrier Reef. b) A zoomed-in example from Rib Reef, showing the layout of UVC sites (dark grey rectangles – five 50m transects per site) and BRUVS deployments (black circles). Note the reef layer (light grey) extends to the 30m contour and is not indicative of the reef slope habitat surveyed.

indeterminate extent of bait plume effects), we had no a priori expectations that estimates of these measures from the base sampling units of UVC (transect) and BRUVS (deployment) should be similar. Furthermore, counts from UVC transects are not directly comparable with those from BRUVS due to the use of fundamentally different measurement units (N versus MaxN respectively). But, if abundance *patterns* among constituent taxa were relatively consistent between methods (i.e. reflecting similar assemblage structure), there could be scope for adjusted comparisons of data from either method. Hence, we allowed for the possibility that UVC and BRUVS species richness and abundance data could, if necessary, be directly compared after application of some correction factor or combination of sampling units; for example: average species richness from single BRUVS deployments could be comparable to that from two or more transects combined, or vice versa. As a starting point, we used the base units of transect ( $250 \text{ m}^2$  for large mobile fishes and  $50 \text{ m}^2$  for damselfishes with instantaneous counts) and deployment (sampling area unknown, but standardised sampling time of 1 h). Overall, we hoped to generate comparable estimates of important fish measures irrespective of the method.

## 2.5. Analyses

All analyses were conducted in R 3.5.0 (R Core Team 2019) unless otherwise stated. Base sampling units for analyses were transect (UVC) and deployment (BRUVS).

### 2.5.1. Ensuring BRUVS distances from UVC sites were acceptable

Although all BRUVS were deployed along the same reef slope habitat at similar depths and orientation as UVC sites, not all deployments fell within the boundaries of the UVC sites: defined as the section of reef slope running clockwise from the start of site 1 to the end of the fifth transect on site 3. As such, we first needed to determine whether the location of the BRUVS deployments relative to survey sites produced any obvious differences in fish community characteristics (i.e. possibly due to unexpected differences in habitat) that would preclude comparison. To assess this, we plotted total species richness and total abundance of fishes from BRUVS against the distance from the UVC survey sites; any major differences of estimates with increasing distance from UVC sites would signal that more distant BRUVS were likely deployed in non-comparable habitats. We then tested the effect of distance from UVC site on both total abundance and species richness using Generalized Additive Models (GAMs) using the 'gam' function in the mgcv package (Wood, 2011). Models included the distance (metres) from UVC sites as a smooth term and used a gaussian distribution. We also conducted a non-metric Multidimensional Scaling (MDS) analysis of the fish communities using BRUVS MaxN data which were fourth root transformed, similarly looking for any evidence that BRUVS at greater distances from the UVC sites had more dissimilar communities than those on UVC sites. Only Rib Reef and Knife Reef were included in these analyses as all three deployments at Chicken Reef were on UVC sites. The MDS was conducted using 'isoMDS' in the vegan package (Oksanen et al., 2018).

### 2.5.2. Comparisons of species richness, accumulation, occurrence and abundance

We compared estimates of total species richness and the richness of the four focal fish groups defined earlier. Estimates of species richness were compared between UVC and BRUVS using generalized linear mixed models with a negative binomial error distribution using the glmer.nb function in the package lme4. Spatial autocorrelation was tested using the testSpatialAutocorrelation function in the package DHARMA (Hartig, 2020), revealing no significant spatial autocorrelation in the model residuals. Issues of overdispersion and zero-inflation were assessed using 'simulateResiduals' and 'testZeroInflation' functions in the package DHARMA (Hartig, 2020). Model selection occurred using the Akaike Information Criterion (AIC) and the resultant most parsimonious models had a fixed factor of method and random term of reef.

We also calculated species accumulation curves to visually compare the expected number of species given an increasing number of samples for each method, and to show the relative sampling effort (number of sample replicates required) to obtain comparable estimates of species richness. Individual curves from UVC, BRUVS, and both methods combined were generated using the rarefaction method with 'specaccum' (in the vegan package) at the reef level and pooled for all reefs (Oksanen et al., 2018). The rarefaction method finds the expected (mean) species richness (and standard deviation) by accumulating individuals instead of replicates (allowing for differing sample sizes), by applying the 'rarefy' function with the number of individuals corresponding to the mean number of individuals per replicate (Gotelli and Colwell, 2011; Oksanen et al., 2018). The curves combining both UVC and BRUVS (a total of 68 sample units) allowed us to assess the merit of using both methods together to better categorize fish communities. We assumed that individual BRUVS deployments sampled an equal area but acknowledge that this may not hold in all cases as hydrodynamic conditions may have resulted in differential spread of the bait plume resulting in a different sampled area.

The frequency of occurrence of each species in both UVC transects and BRUVS deployments was calculated to assess the relative commonness of species between methods.

Similarly, we compared estimates of UVC transect abundance with those of BRUVS deployment MaxN values for each species common to both methods, to investigate consistency in patterns of species abundance between methods. For species abundance comparisons we assessed large mobile fishes and damselfishes separately as damselfishes were counted on different transect dimensions in UVC surveys.

Patterns of abundance of fish focal groups were investigated more formally, but as estimates of abundance from UVC (N) and BRUVS (MaxN) are not directly comparable we analysed the patterns for each method separately. Model selection occurred using the Akaike Information Criterion (AIC) and the resultant models had the fixed factor of focal taxa with four levels (e.g. herbivores, predators, damselfishes and butterflyfishes) and random term of reef. Spatial autocorrelation was tested using the testSpatialAutocorrelation function in the package DHARMA (Hartig, 2020) and after spatial autocorrelation was identified as being an issue, the models were adjusted using an exponential covariance structure. Models were run using function 'glmmTMB' in the package glmmTMB (Brooks et al., 2017). Issues of overdispersion and zero inflation were assessed using 'simulateResiduals' and 'testZeroInflation' functions in the package DHARMA (Hartig, 2020).

## 2.6. Comparisons of assemblage structure

To compare the assemblage structure of reef fishes sampled using UVC and BRUVS, we conducted an MDS analysis using 'isoMDS'. Since damselfishes were counted on transects of smaller dimensions ( $50 \times 1\text{m}$ ) compared to large mobile fishes ( $50 \times 5\text{m}$ ), we first converted damselfish abundances to densities per  $250 \text{ m}^2$ . Densities were then converted to the Hellinger metric (row-centred and fourth-root transformed, Legendre and Gallagher, 2001) to downplay the influence of highly abundant species and then converted to a Bray-Curtis dissimilarity matrix.

## 3. Results

Note that all results from both UVC and BRUVS are derived from the same subset of 218 species surveyed in the UVC program.

### 3.1. Similarity in fish measures among BRUVS with distance from UVC sites

Half of the BRUVS deployments at Rib Reef and Knife Reef were estimated to lie within UVC survey sites (nominally including two deployments at Knife Reef that were only 10's m from the start of site 1). The farthest deployment from the UVC sites was estimated to be almost

2 km distant (Fig. S1). Species richness values from BRUVS deployments outside the UVC sites had a comparable spread to values from deployments inside the UVC sites with no obvious trend with increasing distance (Fig. S1). Mean species richness from deployments within the UVC sites ( $25.4 \pm 2.1$  SE, N = 10) was similar to that outside ( $26.8 \pm 1.5$  SE, N = 10), and distance from UVC sites was not a significant predictor of species richness (GAM F = 0.003, p = 0.955). Patterns for total abundance were similar (Fig. S1) and mean total abundance from deployments within the UVC sites ( $85.6 \pm 12.9$  SE, N = 10) was almost identical to that from deployments outside the sites ( $86.2 \pm 12.1$  SE, N = 10). Furthermore, distance from UVC sites was not a significant predictor of fish abundance (GAM F = 0.464, p = 0.615).

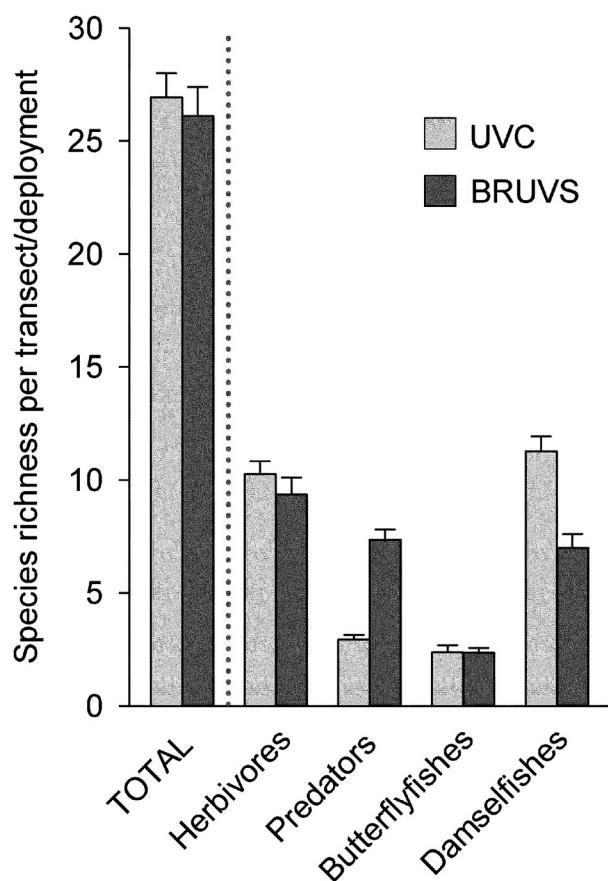
An MDS of fish community structure suggested that BRUVS communities sampled outside the UVC sites were generally comparable to those inside (Fig. S2). There was considerable variation in fish community structure both inside and outside UVC sites and there was no clear separation of inside versus outside values; in fact, there was considerable overlap. There was no spatial pattern with increasing distance from the UVC swathe for BRUVS deployed outside (data not shown). Overall, both univariate and multivariate analyses indicated that all BRUVS data should be acceptable for use in comparisons with UVC data and hence were included in subsequent analyses.

### 3.2. Species richness and accumulation curves

The average species richness per BRUVS deployment was almost identical to that per UVC transect from the three survey reefs combined ( $26.5 \pm 1.0$  SE versus  $26.6 \pm 0.8$  SE respectively, glmer: z value = 0.166, p = 0.868). Given these highly similar results using the base units of deployment and transect there was no need to examine whether various combinations of BRUVS deployments and transect numbers could improve comparability of total species richness estimates. Likewise, the total number of the subset of species recorded by both methods at the three study reefs was similar; BRUVS recorded 113 species and UVC, 110 species. However, relative sampling effort was considerably less for BRUVS at Chicken Reef meaning the BRUVS total was likely an underestimate. So, in the following we consider only Knife Reef and Rib Reef where the number of BRUVS deployments were comparable. At these two reefs BRUVS recorded a total of 111 species and UVC recorded 102. Of the total species pool recorded from the two methods (n = 125) at Knife Reef and Rib Reef, 70.4% were common to both methods, 18.4% were unique to BRUVS and 11.2% unique to UVC. The average species richness per BRUVS deployment from Knife Reef and Rib Reef ( $26.1 \pm 1.3$  SE) was almost identical to that per UVC transect ( $26.9 \pm 1.1$  SE) with no statistical difference (Fig. 2, glmer: z value = 0.171, p = 0.864). However, these results, belied differences in the species richness of fish focal groups between methods (Fig. 2).

The species richness of predators in BRUVS deployments was more than double the estimates from UVC transects (glmer: z value = -7.002, p < 0.001), and the percentage of predatory species common to both methods was 56.6%. In contrast, damselfish species richness was almost 40% lower in BRUVS (glmer: z value = 4.966, p < 0.001), yet the proportion of these species that were common to both methods was higher at 76.3%. While there was no difference in the mean species richness of herbivores (glmer: z value = 1.007, p = 0.314) and butterflyfishes (glmer: z value = 0.159, p = 0.873) between methods, the percentage of species common to both methods was higher for herbivores (77.5% vs 62.5%).

Species accumulation curves indicated that combining UVC and BRUVS datasets provided greater overall species richness estimates than from UVC alone. Reef-specific variation in species accumulation was observed between and within methods (Fig. S3), however, BRUVS curves were generally steeper than those from UVC with less tendency to asymptote, suggesting that BRUVS capture more species than UVC with increased replication. Species accumulation curves combining data from all reefs showed overall that UVC and BRUVS were both fast to record a



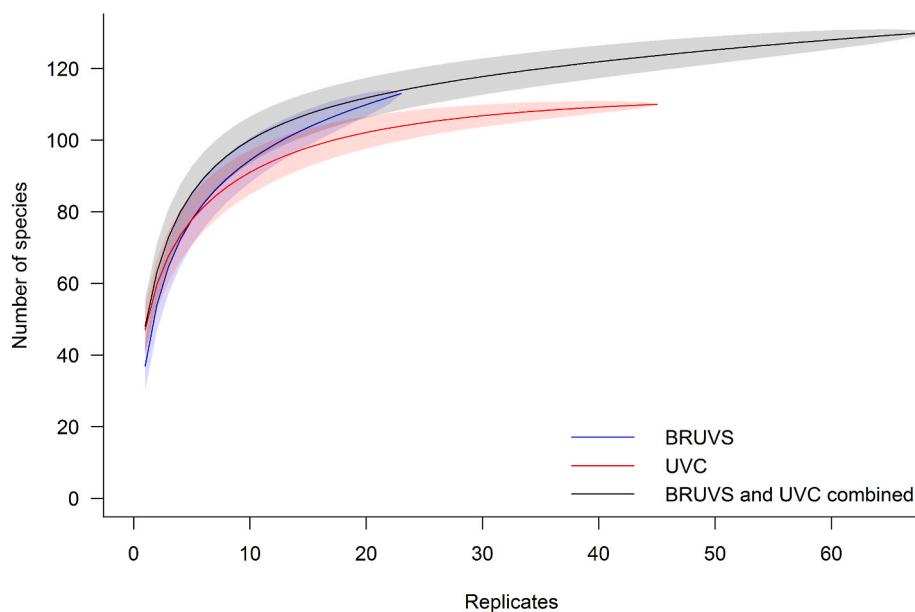
**Fig. 2.** Mean species richness of the total fish assemblage and of focal groups in UVC transects and BRUVS deployments at Knife Reef and Rib Reef combined. Error bars represent one standard error.

similar number of species for up to 6 replicates (transect and deployment respectively, Fig. 3). With increased replication, BRUVS gradually accumulated more species, with the 23 BRUVS resulting in more species than from the same number of UVC transects: 95% confidence intervals no longer overlapped. When both methods were combined, species accumulation was more rapid again, and the addition of 23 BRUVS to the UVC sampling produced a more complete estimate of species richness than by UVC alone (Fig. 3).

### 3.3. Occurrence and abundance of species

The occurrence and abundance of species among BRUVS deployments and UVC transects were calculated using data from Knife Reef (n = 9) and Rib Reef (n = 11); Chicken Reef data were excluded from these analyses due to the low sample size from BRUVS (n = 3). The average number of BRUVS deployments from Knife Reef and Rib Reef was 10 per reef: a value that resulted in accumulated species richness that was similar to that from the standard UVC reef surveys of 15 transects (Fig. 3). As such, any differences in species occurrence or abundance between the two methods using Knife Reef and Rib Reef data should represent a fair comparison.

The species that were most frequently recorded in BRUVS deployments and UVC transects varied considerably between the two methods (Fig. 4). In general, occurrences of damselfish species in BRUVS deployments were much lower than on UVC transects, with 12 species markedly less common in BRUVS deployments and only three being more common (Fig. 4). However, one of the latter three species, *Pomacentrus amboinensis*, was amongst the most encountered species overall in BRUVS deployments. Large predatory species, including both non-labrids and labrids, occurred far more frequently in BRUVS



**Fig. 3.** Species accumulation curves from BRUVS deployments and UVC transects individually and combined, using data from all three survey reefs.

deployments: 10 species that were recorded using both methods were markedly more common in BRUVS deployments than on UVC transects, and only one predatory species showed the opposite pattern.

Of the five most commonly encountered predatory species in BRUVS, three are very important fisheries species (two *Plectropomus* spp. and *Lethrinus miniatus*) and the other two were wrasse (*Choerodon fasciatus* and *Hemigymnus melapterus*); all were far less frequently encountered in UVC surveys (Fig. 4). Furthermore, an additional 11 predatory species were unique to BRUVS deployments, albeit mostly at very low frequencies of occurrence, compared to only two unique predators (*Epi-bulus insidator* and *Lutjanus lutjanus*) on UVC transects (Fig. 5). Occurrences of almost half of the 32 large herbivore species varied considerably among methods: 9 species were markedly less common in BRUVS surveys while five were markedly more common (Fig. 4). Percent occurrences of butterflyfish species ( $n = 10$ ) were mostly similar among methods. Overall, a considerable number of species from the 218 species subset were only recorded by BRUVS ( $n = 23$ ) or by UVC ( $n = 14$ , Fig. 5).

The abundances of large fish species differed considerably between methods (Fig. 6). This was unsurprising given that different units of abundance were used, N for UVC and MaxN for BRUVS. However, there was little consistency in these differences: species that were relatively abundant in UVC were not necessarily abundant in BRUVS and vice versa. For example, the top 10 most abundant species on UVC transects made up 64.5% of the total UVC large mobile fish abundance and were all herbivorous surgeonfishes (Acanthuridae) or parrotfishes (Scarinae in the Labridae); five of these had markedly higher abundances (95% confidence intervals did not overlap) than in BRUVS deployments (Fig. 6). In contrast the same 10 species made up only 31.3% of the total BRUVS large mobile fish abundance. Instead the top 10 BRUVS species by abundance included six herbivores (one of which was not in the UVC top 10) and four predators with markedly higher abundances than in UVC transects. Those predators included two commercially important species, the coral trout *Plectropomus leopardus* and the red-throat emperor *Lethrinus miniatus*, that together comprised 9.2% of BRUVS total abundance compared to only 1.6% in UVC surveys. There were no marked differences in the abundance of butterflyfish species (all from the genus *Chaetodon*) between methods, but relative patterns of abundance were inconsistent among species. Due to the general lack of consistency in relative patterns of abundance between UVC and BRUVS among large fish species when analysed at the level of transect versus

deployment, we did not assess whether various combinations of transects and deployment numbers would generally result in more comparable estimates; the inconsistencies among taxa meant that multiple different correction factors would need to be applied to improve comparability of UVC and BRUVS abundance data.

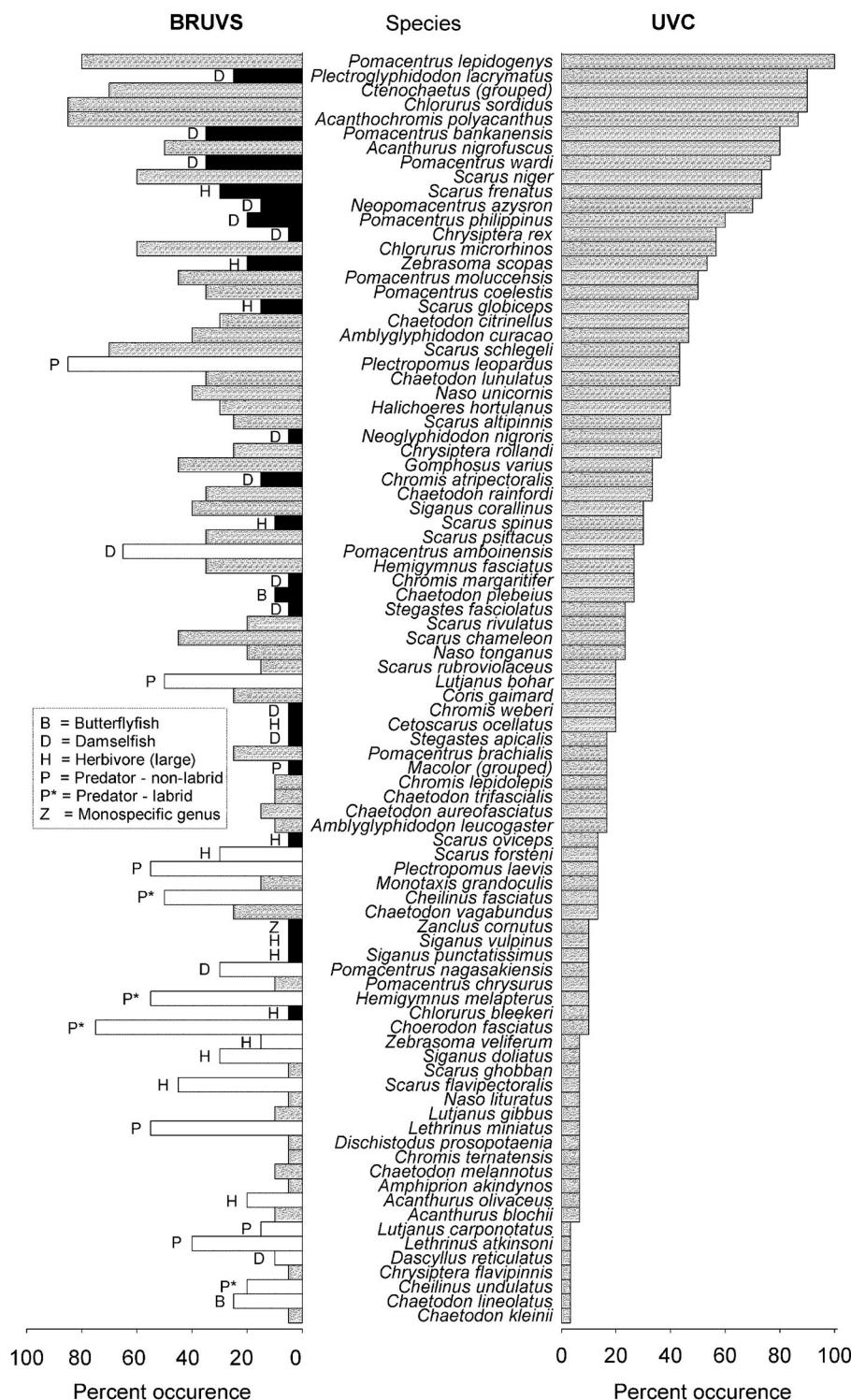
Patterns of abundance of damselfish species were also inconsistent between methods (Fig. 7). The abundances of eight of the top 10 most abundant damselfish species in UVC were markedly lower in BRUVS deployments to varying degrees (Fig. 7) with all eight species being typically associated with rugose coral habitats. In particular, the second most abundant damselfish species in UVC transects, *Neopomacentrus azyron*, that made up 27.5% of damselfish numbers was very lowly ranked at <2% in BRUVS and *Plectroglyphidodon lacrymatus* that was relatively abundant on transects was poorly represented in BRUVS deployments (Fig. 7).

In contrast, abundances of the remaining two species in the UVC top 10 were comparable in BRUVS deployments. Only one species, *Pomacentrus amboinensis*, had markedly higher abundances in BRUVS deployments (Fig. 7). Abundances of *P. amboinensis* on UVC transects made up <1% of the damselfish assemblage, but this species was the second most abundant damselfish in BRUVS making up 22.1% of the assemblage (Fig. 7).

Patterns of abundance between methods were highly inconsistent among fish focal groups (Fig. 8). Mean herbivore and damselfish abundances were underrepresented by BRUVS compared to UVC. However, the differences varied between the two groups: there were double the number of herbivores and quadruple the number of damselfishes in UVC compared to BRUVS surveys (Fig. 8). Conversely, the abundance of predatory fishes was markedly underrepresented by UVC transects compared to estimates from BRUVS deployments (Fig. 8), while the abundances of butterflyfishes were very similar between methods (Fig. 8).

### 3.4. Assemblage structure

There were marked differences in assemblage structure from UVC and BRUVS surveys using the same restricted species pool of 218 species (Fig. 9). There was minimal overlap in assemblage types between methods: assemblages at Rib Reef and Chicken Reef from BRUVS were clearly distinct from UVC assemblages and only a few BRUVS deployments at Knife Reef had assemblages that resembled some from UVC



**Fig. 4.** Frequency of occurrence of fish species (horizontal bars) from the UVC pool of 218 species at Rib Reef and Knife Reef that were common to both BRUVS deployments ( $n = 20$ ) and UVC transects ( $n = 30$ ). All bars from UVC species are coloured light grey while those from BRUVS species are light grey if the percent occurrence was similar to the corresponding UVC value (values were <double each other), white if the percent occurrence was markedly higher (double or more) and black if the percent occurrence was markedly lower (half or less). All species whose % occurrences markedly differed from those in UVC surveys were marked with a letter denoting their focal group of origin (see inset box).

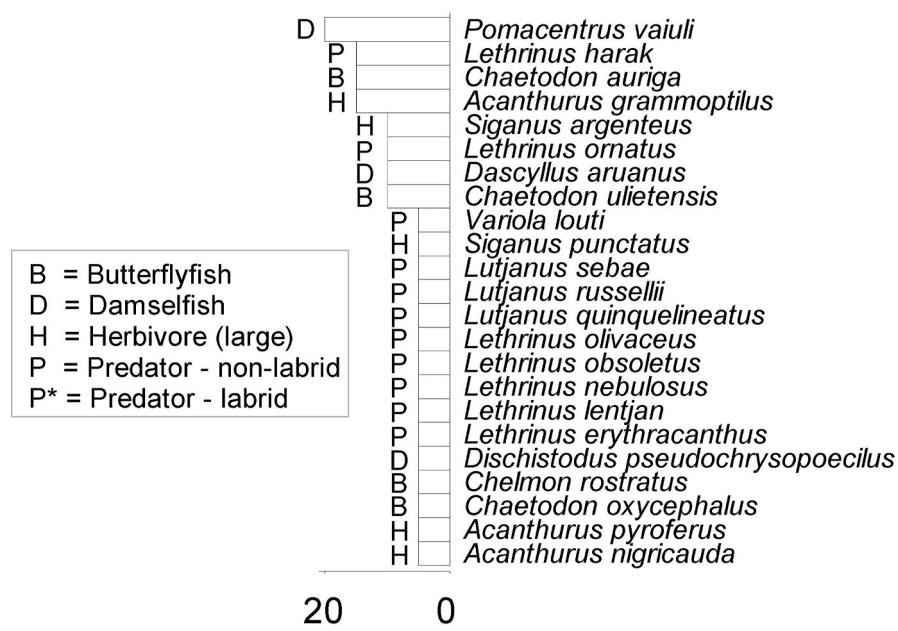
(Fig. 9). These data suggest that the different methods consistently resulted in different fish assemblages. As documented in detail in the univariate results, assemblage differences between methods were driven most by dissimilarities in species pools (despite similar estimates of species richness) and in the relative abundances of large predators, herbivores and certain damselfishes.

#### 4. Discussion

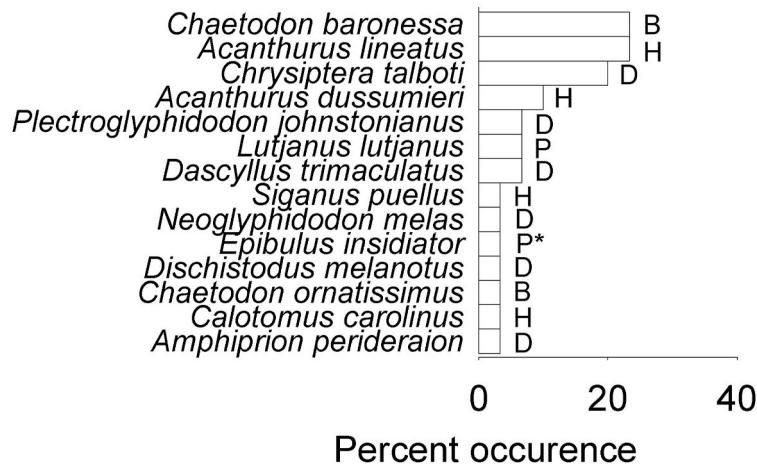
We have shown that UVC and BRUVS sampled fish communities in

different ways. While estimates of average species richness from both methods were similar and they both sample a large proportion of the same species (~70%), considerably more predatory species were sampled by BRUVS and more damselfish species by UVC per unit sample. There were also major inter-method differences in the frequency of occurrence of species, in the relative abundances of species and focal groups, and in assemblage structure. These differences were often variable in magnitude and direction among constituent taxa. While there appears to be limited scope to compare data interchangeably from UVC and BRUVS, the two methods are complementary, together providing a

## Unique BRUVS species



## Unique UVC species



Percent occurrence

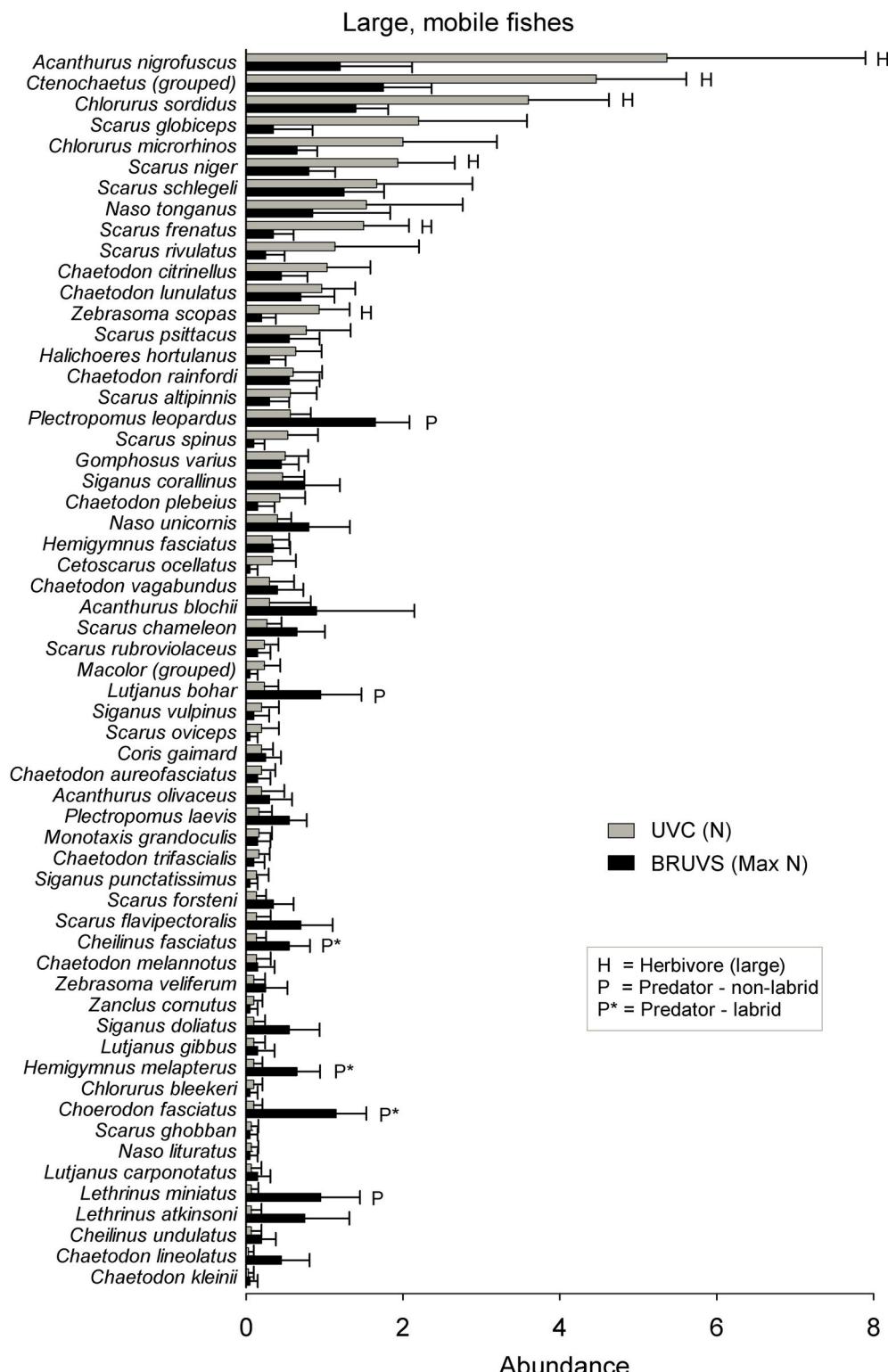
**Fig. 5.** Frequency of occurrence of fish species (horizontal bars) from the UVC pool of 218 species at Rib Reef and Knife Reef that were unique to either BRUVS deployments ( $n = 20$ ) or UVC surveys ( $n = 30$ ). Focal group origins are indicated by a letter (see inset box).

more complete picture of reef fish communities. We believe this complementarity can be applied strategically in combined UVC/BRUVS monitoring programs to better inform managers about the status of reef fish communities and the distributions of species over a wider range of habitats and depths, despite difficulties with direct inter-method comparisons.

The almost identical estimates of mean total species richness from the base units of UVC transect and BRUVS deployment provided the greatest support for direct comparisons of data irrespective of method. The similarity in species richness estimates was surprising given the unknown, and likely variable, sampling area of BRUVS, and that estimates from BRUVS have often differed with those from diver-based methods (UVC or diver-operated videos) when surveying the entire fish community (Watson et al., 2005; Stobart et al., 2007; Colton and Sweare, 2010; Langlois et al., 2010; Lowry et al., 2012). However, we restricted our study to a pool of 218 species (due to their historical precedence in UVC surveys on the GBR) that comprise non-cryptic, visually obvious and relatively common species. In practise those

species seemed amenable to capture by both UVC and BRUVS, with a 1-h BRUVS video being sufficient to record a similar number of species on average as observed on a UVC transect. Despite this result, similar estimates of total species richness did not reflect similar species complements: BRUVS sampled more predatory species, fewer damselfish species and more unique species. This means that the extremely similar estimates of total species richness from UVC and BRUVS arose partly by chance and suggests that total species richness estimates cannot be reliably compared when derived from the different methods.

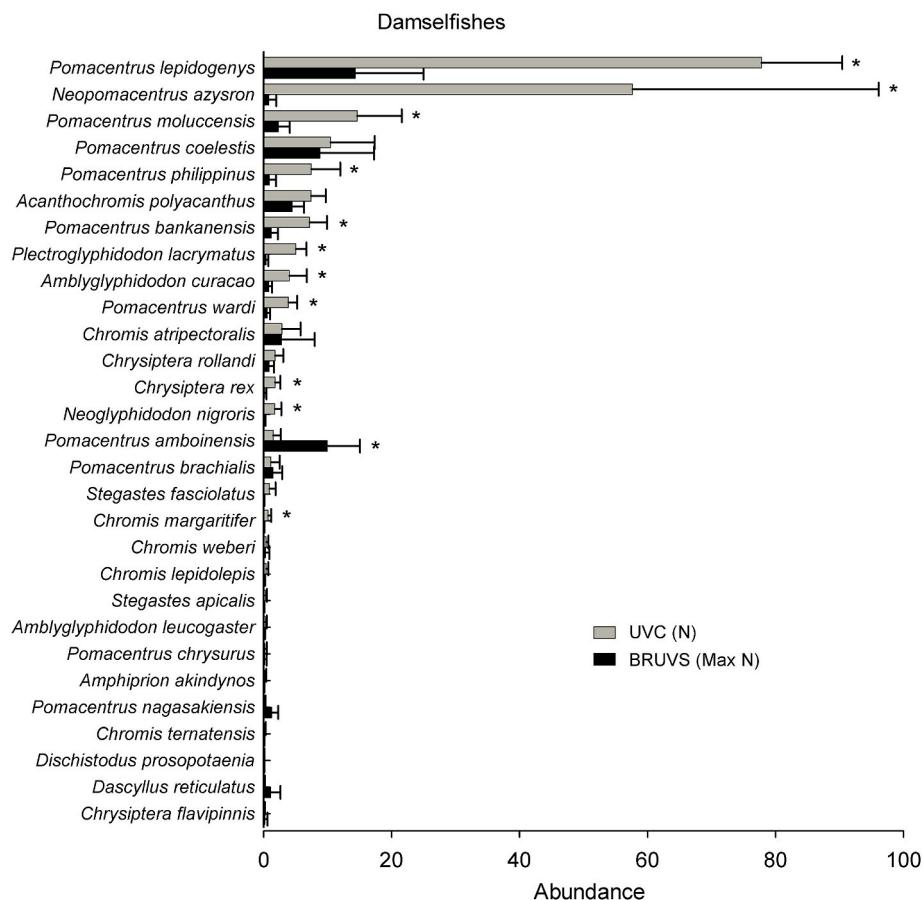
Comparisons of the species richness of two focal fish groups, large herbivores and butterflyfishes, appeared more amenable to direct comparison irrespective of method as their mean species richness estimates from UVC and BRUVS differed little. Large herbivores were the better candidate for such comparison as more species were common to both methods (77.5%) compared to butterflyfishes (62.5%). Bait is not recognized as an attractant for either group, so it is tempting to assume that use of bait did not influence their species richness estimates in BRUVS surveys. However, tropical herbivores were found to be more



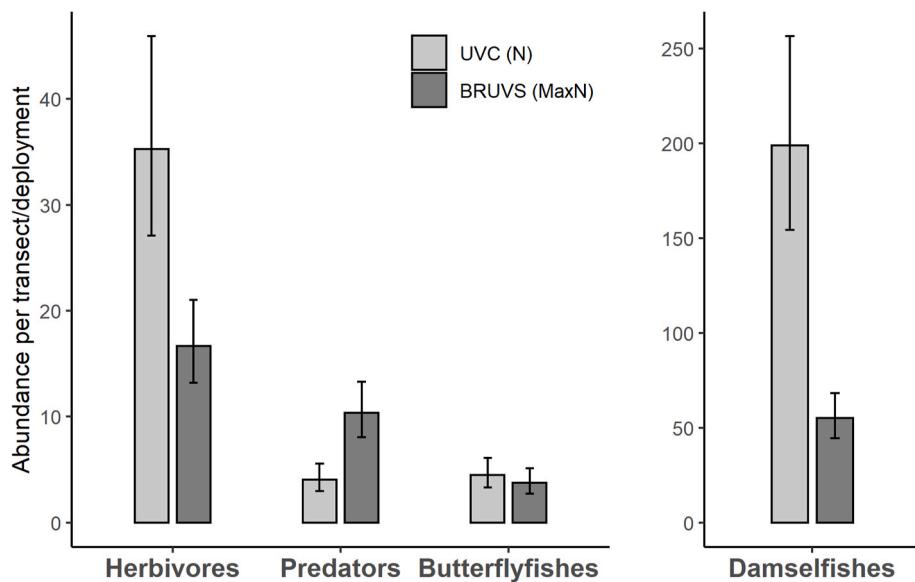
**Fig. 6.** Mean abundance of large, mobile fish species from the UVC pool of 218 species at Rib Reef and Knife Reef that were common to both UVC transects ( $n = 30$ ) and BRUVS deployments ( $n = 20$ ). Error bars represent 95% confidence intervals (CIs). All species that had markedly higher or lower abundances in either UVC or BRUVS surveys (95% CIs did not overlap) were marked with a letter denoting their focal group of origin (see inset box).

speciose and numerous on baited BRUVS compared to those without bait; possibly an indirect association where bait-neutral species are inquisitively drawn into the vicinity of BRUVS by the commotion of feeding activity or by the BRUVS unit itself (Harvey et al., 2007; Colton and Sweare, 2010; Watson et al., 2010; Wraith et al., 2013). Such associations would only cast doubt on our similar herbivore species

richness estimates between the two methods if the species richness of herbivores from BRUVS were to change under different levels of feeding activity to those we recorded. However, the behaviour of large herbivores and butterflyfishes in our BRUVS videos revealed individuals to be foraging normally or passing by under various levels of BRUVS feeding activity (AJC pers obs). Further testing of UVC versus BRUVS appears



**Fig. 7.** Mean abundance of damselfish species at Rib Reef and Knife Reef that were common to both UVC transects ( $n = 30$ ) and BRUVS deployments ( $n = 20$ ). Error bars represent 95% confidence intervals (CIs). All species that had markedly higher or lower abundances in either UVC or BRUVS surveys (95% CIs did not overlap) are marked with an asterisk.

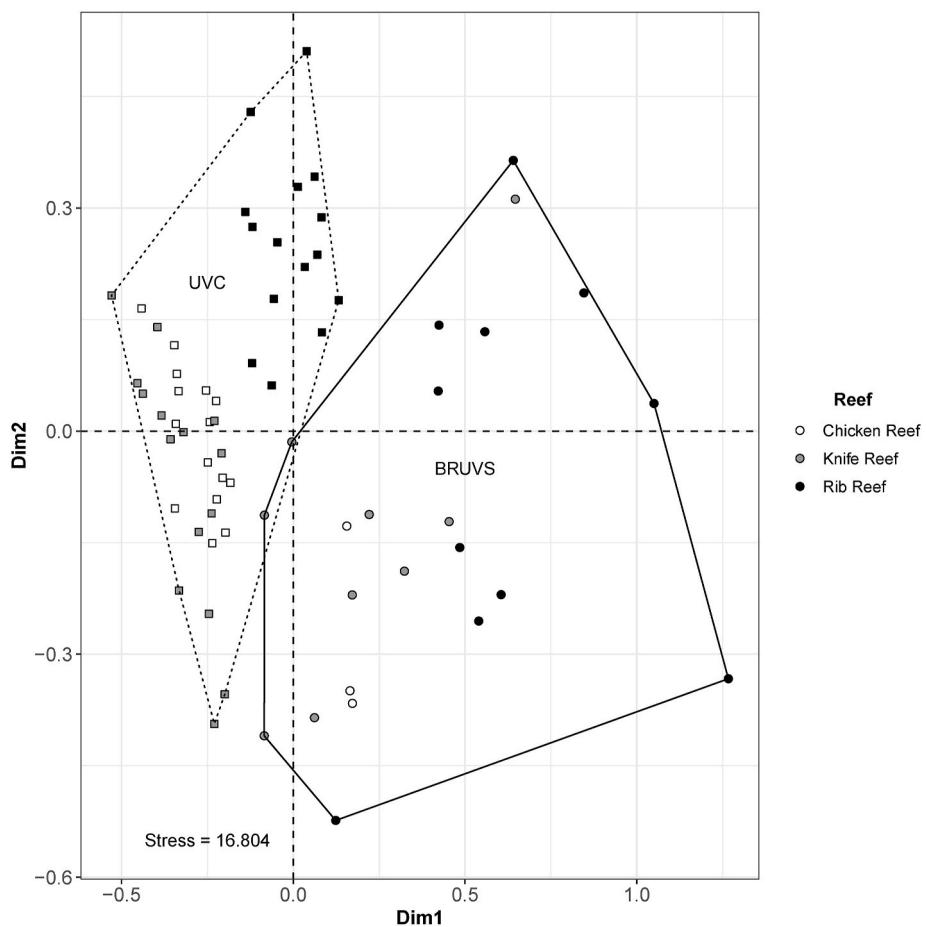


**Fig. 8.** Modelled mean abundance of focal fish groups from the UVC pool of 218 species at Rib Reef and Knife Reef from UVC transects ( $n = 30$ ) and BRUVS deployment ( $n = 20$ ). Error bars represent 95% Confidence Limits. Models were run separately for each method (UVC, BRUVS).

necessary to verify the generality of our species richness results for large herbivores and butterflyfishes. Given that large herbivores in particular are deemed to be functionally important because they can limit algal suppression of coral growth (Bellwood et al., 2004; Cheal et al., 2010;

Hoey and Bellwood, 2011) the ability to directly compare their species richness among more reef locations and depths by using both UVC and BRUVS data would be an asset for any reef monitoring program.

Comparisons of fish abundances derived from UVC and BRUVS



**Fig. 9.** MDS of fish assemblages from the three survey reefs. Each individual symbol represents a transect (UVC) or deployment (BRUVS).

appear more difficult, not just due to the fundamentally different sampling units ( $N$  vs  $\text{Max}N$  respectively), but because of inconsistencies in patterns of abundance among species and focal groups between methods and the existence of a non-linear relationship between  $\text{Max}N$  and  $N$ , especially at very high abundances (Schrobernd et al., 2014). Species that were common and abundant in UVC were often poorly represented in BRUVS and vice versa. Among fish focal groups, patterns of abundance were eclectic: compared to BRUVS, UVC sampled a higher proportion of damselfishes and herbivores, similar proportions of butterflyfishes and fewer predators. No general correction factors would be applicable for valid comparisons between methods because relative patterns were so variable among taxa. To confidently apply a range of species- or group-specific correction factors, further datasets with additional replication from a greater variety of reefs are needed to identify whether the patterns of abundance between methods we identified hold true more generally.

There are a number of explanations for differences in the frequency of occurrence and relative abundance of species between UVC and BRUVS related to the individualities of each method. The use of bait in BRUVS is well recognized to attract predatory fishes (Willis et al., 2000; Harvey et al., 2007; Stobart et al., 2007; Colton and Sweare, 2010; Lowry et al., 2012) and is reflected in our finding that large predators were more common, speciose and abundant in BRUVS videos compared to UVC counts. Many predators fed directly on the bait bags while others were obviously attracted into the camera's field of view by the bait plume, even if they were hesitant to feed directly on the bait: the coral trout *P. leopardus* and the wrasse *C. fasciatus* being prime examples (AJC pers. obs.). Additionally, once BRUVS have settled on the sea floor they are relatively inert and not likely to discourage the presence of large predators, unlike the bubbles and movement of scuba divers while

surveying UVC transects (Lindfield et al., 2014; Emslie et al., 2018).

The less frequent occurrences and often lower relative abundances of damselfishes from BRUVS compared to UVC highlights the restricted ability of BRUVS to record small site-attached species (Colton and Sweare, 2010; Watson et al., 2010; Gilmour et al., 2014) and the associated influence of fine-scale habitat. Most damselfishes are site-attached, so the number of damselfishes recorded by BRUVS is largely restricted to those resident in the camera's field of view; more so than for large mobile fishes that often randomly entered video frames during 1 h soaks. In contrast, the mobile nature of UVC surveys along 50m transects allowed a greater area of damselfish habitat to be surveyed and thereby more of these site-attached fishes to accumulate during transect counts. The fine-scale placement of sampling units can also be critical in capturing the presence of damselfishes. The suite of damselfish species that were particularly abundant on UVC transects but relatively depauperate on BRUVS, were typically associated with rugose reef habitat. For example, two species that had especially low numbers in BRUVS relative to UVC were the planktivorous *N. azysron* that typically schooled and fed alongside steep reef drop-offs on UVC sites, and *P. lacrymatus* that farmed algae in defined territories between coral structures. Such rugose habitats are difficult to survey effectively with BRUVS as the remotely deployed units rarely sit flat, resulting in variation in the field of view, and random reef structures may obstruct the view. Accordingly, a number of BRUVS videos in our study were unusable and a proportion of those used were from deployments on sand and rubble patches among or alongside reef structures; habitat that was less commonly incorporated in UVC transects (Fig. S4). This could explain the relatively low abundances of reef-associated damselfishes in BRUVS and the particularly high abundances of *P. amboinensis*, a species that preferentially inhabits areas of mixed rubble, sand and coral

(McCormick and Hoey, 2006). However, a number of BRUVS were effectively deployed within the UVC sites in rugose reef habitat (particularly all three BRUVS at Chicken Reef: Fig. S4), but different overall fish assemblages still resulted from the two methods. So, while fine-scale variability in habitat sampling between methods almost certainly influenced inter-method comparisons, BRUVS and UVC appear to fundamentally sample the same fish communities in different ways.

Differing results from UVC and BRUVS could have been influenced by variability in sampling locations. While there were few clear differences in total species richness, total abundance and assemblage structure from BRUVS inside and outside the UVC sites, it is possible that “outside” BRUVS landed amongst fundamentally different fish communities. However, all “outside” BRUVS were deployed on reef contiguous with the UVC sites on habitat that was generally of very similar appearance, aspect and depth to that surveyed by UVC; gauged during deployment by use of a bathyscope and depth sounder, and confirmed later by the appearance of video images. Additionally, fish assemblages from UVC sites 1, 2 and 3 at survey reefs were often similar despite these sites being separated by up to 900 m (Fig. S5). This implies that long stretches of contiguous habitat on our survey reefs mostly harboured similar fish assemblages. Based on this and our assessment of BRUVS data in and out of UVC sites, we suspect that our use of “outside” BRUVS data from habitat contiguous with UVC sites should not have compromised UVC versus BRUVS comparisons.

BRUVS were also deployed two months after surveys of UVC transects with unknown influences on inter-method comparisons. However, it is doubtful that fish communities had fundamentally changed over that period. Recruitment is unlikely to have boosted fish numbers in BRUVS surveys as most recruitment occurs over the spring/summer season, well prior to the UVC surveys. Un-replenished mortality of fishes over the 2-month period between UVC and BRUVS surveys could have influenced comparisons. Typical fish mortality rates on our UVC sites are unknown, but we suspect that the interim period between surveys was short enough for factors other than mortality (discussed earlier) to have had more influence on the fish data. Disturbances to coral reef habitat are another major driver of change in reef fish communities (Bell and Galzin, 1984; Wilson et al., 2006; Emslie et al., 2014). Coral-eating crown-of-thorns starfish (COTS: *Acanthaster planci*) were present in low numbers at Rib Reef during UVC surveys and had caused scattered deaths of coral heads that can particularly impact coral feeding butterflyfishes and resident damselfishes (Pratchett, 2001; Pratchett et al., 2012). However, there was no evidence from BRUVS videos two months later that COTS numbers had considerably increased or had caused major impacts since UVC surveys. No other signs of recent disturbances were evident on survey reefs. In such relatively stable circumstances, UVC counts of fish taxa on the GBR made months apart generally add little variation to the considerable error typically recorded from standard day to day sampling (Thompson and Mapstone, 2002). They also showed, however, that UVC counts of a few damselfish genera that were abundant in our surveys (*Acanthochromis*, *Chromis*, *Neopomacentrus* and *Pomacentrus* in particular) substantially increased in variation from daily to monthly scales. It is therefore possible that the two-month delay between UVC and BRUVS surveys influenced relative abundance patterns of damselfishes. However, Thompson and Mapstone (2002) tested the influence of different observers in collecting UVC samples and implicated observer bias between months as a possible contributing factor, while we tested UVC vs diver-less BRUVS, so it is uncertain whether their findings are directly applicable to damselfish patterns in our study.

In general, our study suggests that there is limited scope to directly compare ecologically important reef fish measures derived from UVC and BRUVS. While similar estimates of species richness between methods suggest each provides an understanding of a large component of the same fish communities, particularly of herbivores, the inconsistencies in the relative occurrences and abundances of constituent species between UVC and BRUVS raised concerns. To allow confident broad-scale comparisons of data from either method, with or without

correction factors, a more expansive study would be required to distinguish whether the differences and similarities we documented hold true more generally. However, we believe that while certain reef fish measures may prove directly comparable between UVC and BRUVS it is doubtful that the spatial scale of reef fish monitoring on the GBR can be generally expanded in this way.

While direct comparability of reef fish data from UVC and BRUVS is limited, the two methods are highly complementary, together providing a more complete understanding of reef fish communities. Species accumulation curves showed that when the two methods are combined, a substantially higher number of species are recorded than by UVC alone. Greater combined richness resulted from the unique species recorded by each method, and the steeper trajectory of the BRUVS species accumulation curve indicated that further unrecorded diversity existed. Importantly, our direct inter-method comparisons highlighted fish species and focal groups best suited to sampling by each method. For example, utilising the two methods together will provide the best suite of indicator species; large herbivores and damselfishes were better sampled by UVC and large predators by BRUVS. The capacity of BRUVS to record so many more species of large predatory fishes than UVC is particularly significant as their status and distributions are often of great interest to reef managers due to their generally high commercial and recreational value. The complementarity of the two methods is of particular benefit when considering that BRUVS can survey exposed reef areas and deeper waters that are logistically difficult or impossible to survey by UVC. Likewise, including shallow BRUVS deployments in habitats surveyed by UVC can better quantify whole fish assemblages, and predatory fishes in particular. As such, BRUVS can be utilised in monitoring programs to provide greater spatial/depth coverage within reef systems. This would allow better assessments of species distributions; of relevance given predicted changes in the geographic range of fishes due to climate change (Munday et al., 2008). Stereo BRUVS deployed deeper than maximum UVC depths would also help elucidate any depth-related differences in fish population size structures (after testing that the two methods are equally effective in sampling the range of size classes of each species), and by association, overall population fecundity (Carter et al., 2015). BRUVS document entire fish communities, not just the 218 species subset listed within the AIMS UVC program, providing the option to examine patterns in a greater array of taxa. However, it is likely that the AIMS UVC program will upgrade to all-species counts in the future (AJC comment), including cryptic species, which are preferentially quantified using UVC but are currently excluded from the monitoring program. Overall, combining UVC and BRUVS in reef fish monitoring programs, particularly with full species lists, would provide a more comprehensive picture of fish communities than by using either method alone (see also Colton and Sweare, 2010; Lowry et al., 2012; Schramm et al., 2020).

There are practical challenges though in how to most effectively integrate UVC and BRUVS in reef monitoring programs. Given that both methods together provide a better categorization of fish communities, it would be beneficial to apply both methods in the same habitat as one aspect of field sampling if logistical considerations allow. Differences in the efficiency of sampling and the effort required by each method could also be used to advantage. BRUVS sampled species richness more efficiently, capturing greater species richness with fewer replicate deployments (albeit with partially different species complements) than from a complete reef survey of 15 UVC transects: on average around 10 BRUVS deployments accumulated a similar number of species as 15 transects. This contrasts with the speedier accumulation of temperate reef fish species by UVC than by BRUVS in Colton and Sweare (2010). However, their individual UVC transects sampled a far larger area (average of 1790 m<sup>2</sup>) than ours (250 m<sup>2</sup>) and we targeted a restricted species pool rather than the entire community they targeted, so results from the two studies are not directly comparable. In our study, BRUVS were far more time-efficient in gathering the same proportion of the 218-species pool: 10 BRUVS were deployed in half a day compared to

the full day typically required for a full UVC reef survey due to safe-diving limitations. So, on the day of any given UVC reef survey, two sets of 10 BRUVS could be deployed to expand the spatial extent of local reef fish knowledge. For example, the first set could directly complement UVC surveys in shallow habitat while the second could be deployed on other habitats (e.g. back reef), or at depths too deep for UVC. Alternatively, complimentary BRUVS sampling could focus on key reefs more intensively, with greater replication to further capture the latent diversity of species yet to be recorded.

There would be also challenges in reporting fish data from an integrated UVC and BRUVS monitoring program given the difficulties in making direct comparisons. However, comparisons of *change* in reef fish measures between the two methods at different locations could be more valid and would extend the spatial knowledge of fish community stability, declines and recovery. The argument for directly comparing change between methods, despite different relative abundances of taxa, rests with the fact that many species were common to both methods. These species may be expected to show similar responses to the same forcing circumstances (disturbances, recruitment pulses etc.) irrespective of survey method or recorded abundance; acknowledging that interpretation of such responses should consider the possible influence of density-dependent processes. Valid comparisons of the temporal trajectories of reef fish measures from UVC and BRUVS in different locations would more comprehensively inform where reef fish communities are doing well and poorly, and over what spatial range. To assess change in this way UVC and BRUVS should ideally be integrated into a monitoring program under the same sampling regime: both methods applied over the same dates with the same inter-survey intervals.

In conclusion, while there are limits to the comparability of reef fish data from UVC and BRUVS, the complementarity of the two methods would allow for more comprehensive reporting of the status of reef fish communities, of species distributions and of the spatial extent of declines or recovery within reef ecosystems. Provision of such improved estimates of ecological status and condition would boost the ability of reef managers to implement conservation measures that are most likely to be effective. In addition, better quality information provides clearer justification for reef managers to apply bold remedial decisions which may be socially, commercially and politically unwelcome: fishing closures being a prime example (Emslie et al., 2015).

## Author contributions

Alistair J Cheal: Conceptualization, Methodology, Project administration, Visualization, Writing - original draft, Writing - review & editing. Michael J Emslie: Conceptualization, Formal analysis, Methodology, Visualization, Writing - original draft, Writing - review & editing. Leanne M. Currey-Randall: Conceptualization, Formal analysis, Methodology, Visualization, Writing - review & editing. Michell Heupel: Conceptualization, Funding acquisition, Methodology, Project administration, Writing - review & editing.

## Declaration of competing interest

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

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## Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.jenvman.2021.112375>.

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