



Optimizing remote underwater video sampling to quantify relative abundance, richness, and corallivory rates of reef fish

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Abstract Remote underwater videos (RUVs) are valuable for studying fish assemblages and behaviors, but analyzing them is time-consuming. To effectively extract data from RUVs while minimizing sampling errors, this study developed optimal subsampling strategies for assessing relative abundance, richness, and bite rates of corallivorous fish across eight geographically dispersed reef sites on the Great Barrier Reef and in the Torres Strait. Analyzing 40 frames per 60-min video yielded precise and accurate estimates of the mean number of individuals per frame (i.e., MeanCount), with systematic sampling (one frame every 90 s) proved as effective as or better than random sampling, depending on the survey sites. However, this approach underestimated species richness by ~40%, missing the less common species. For estimating bite rates, 30 min or 15 feeding events were optimal, with no significant gains in precision and accuracy with further effort. These strategies enhance data standardization and process efficiency, reducing the time required for MeanCount and bite rate estimates by nine and two times, respectively, compared to full video annotation.

Keywords Tropical reefs · Coral reef fish · Corallivory · Unbaited RUV · Relative abundance · Species richness estimate

Introduction

Coral reefs are facing increasing threats due to anthropogenic-induced climate change characterized by mass bleaching, reductions in the cover of scleractinian corals, increases in the cover of other benthic taxa (e.g., macroalgae), and flattening of the reef structure (Alvarez-Filip et al. 2009; Darling et al. 2017; Hoegh-Guldberg et al. 2017; Hughes et al. 2017). The loss of coral cover and the physical structure they provide have important implications for associated fish assemblages, with the magnitude of the effect varying among trophic groups (Ferrari et al. 2018; Wilson et al. 2006). Species that are directly dependent on live corals for food and/or shelter are generally the first and most adversely affected by the loss of live corals (Pratchett et al. 2012; Wilson et al. 2006). Reliable and robust ecological surveys are therefore essential to explore the structure of fish assemblages and quantify corallivory, which may further improve the understanding of future reef trajectories.

Underwater Visual Census (UVC) techniques are commonly used to survey fish population dynamics and assemblage structure in shallow coastal habitats (Benthuisen et al. 2022; Clynick et al. 2008; Hsu et al. 2023). There are three main types of UVC: transects, point counts, and rapid visual techniques (Caldwell et al. 2016; Murphy and Jenkins 2010). All UVC techniques involve divers directly counting and identifying fish underwater, providing estimates of richness, abundance/density, and fish length. These techniques produce quantitative measures with minimal post-survey processing; however, a range of potential limitations

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exists. Firstly, the presence of divers in UVC surveys and the generated bubbles/sound can lead to avoidance by fishes (Lindfield et al. 2014) and declines in estimations of fish abundance and/or richness with the magnitude varying among fish families (e.g., 35–70% in Dickens et al. 2011 and 24–73% in Emslie et al. 2018). Importantly, it can take several hours for the abundance and composition of fish assemblages to recover from the disturbance of divers conducting UVC (Emslie et al. 2018). Moreover, divers conducting UVC surveys must also be highly experienced in species identification (Williams et al. 2006), and length/distance estimation by divers can be highly variable (Harvey et al. 2004). Lastly, data validation is unavailable once the survey is completed.

To address limitations of traditional visual surveys, imaging systems have been developed to quantify fish assemblages post-hoc. Image-based surveys using single or stereo cameras offer more precise fish length and distance estimates than UVC (Harvey et al. 2001, 2004). Diver-operated videos (DOVs) are videos recorded along transects, eliminating the need for underwater species identification and providing accurate length estimates. Divers conducting DOV can still impact fish behavior (Hellmrich et al. 2023), likely leading to underestimation of the number of fish with responses varying among species as in UVC (Emslie et al. 2018). Baited remote underwater videos (BRUVs) attract and sample fish using animal or algal bait (Cheal et al. 2021; Hoey and Bellwood 2009), but results vary with bait types and are influenced by environmental conditions (Dorman et al. 2012; Loffler et al. 2015). Unbaited remote underwater videos (RUVs) capture natural underwater scenes with minimal disturbance, making them ideal for behavioral studies (Eggertsen et al. 2020; Knoester et al. 2023). Feeding activities are typically quantified using focal individual observations, where divers follow fish and record the number of bites and prey items (Eggertsen et al. 2020; Hoey et al. 2016). This method requires intensive underwater observations and can be challenging when predation rates are high (T. Hsu's personal observation). Recording videos while following individuals helps (Zambre et al. 2018), but diver presence may still alter fish behaviors. RUVs offer a better alternative to study coral reef fish feeding by quantifying total bites of all individuals within a set period (Magneville et al. 2024). However, no study has provided information on the optimal video length for precise and accurate individual bite rate estimates at either species-specific or community-wide scales. Both scales are important, as species within the same functional group often adopt different foraging strategies due to competition and resource partitioning (Berumen and Pratchett 2006; Fox and Bellwood 2012). Corallivorous fish, especially the obligate corallivores, is ideal for testing RUVs to quantify bite rates due to their frequent feeding activities, likely linked to coral's lower nutritional values compared to

small mobile invertebrates (Gregson et al. 2008). Moreover, these fishes play key functional roles in coral growth and species distributions (Cox 1986) and potentially in facilitating algal symbionts dispersal (Grupstra et al. 2021).

Unlike UVC, BRUV and RUV surveys cannot provide abundance and density estimates because of the higher probability of double counting the same individuals on stationary videos. As fish enter and leave the camera view, it is impractical to distinguish individuals, so 'relative abundance' is used. The most commonly used metric to assess relative abundance is 'MaxN', defined as the maximum number of individuals of a species at any timepoint across the video (Whitmarsh et al. 2016). Another common metric used is 'MeanCount', the average number of individuals over a given number of time points or frames sampled from the video (Whitmarsh et al. 2016). While both metrics are routinely quantified, there is ongoing debate over which index is more representative. Some users promote MeanCount due to its linear relationship with true abundance in a laboratory experiment, which is not the case for MaxN (Schobernd et al. 2014). Others support MaxN because of its higher precision and discourage the use of MeanCount for its tendency to overinflate zero observations (Campbell et al. 2015).

While video recording in the field is efficient, annotating videos is time-consuming. With advancements in artificial intelligence (AI), deep learning (DL) algorithms now enable automation of fish detection and tracking (Connolly et al. 2024; Ditria et al. 2020; Lopez-Marcano et al. 2021). However, challenges remain due to the dynamic underwater environment, model generalization, and dataset limitations (Saleh et al. 2024), necessitating manual annotations and subsampling strategies. Most studies focus on optimizing video collection and soak time (Garcia et al. 2021; Wong et al. 2019). Only two studies examined the precision and accuracy associated with subsampling videos for relative abundance and species richness. Bacheler and Shertzer (2015) recommended analyzing BRUVs using 50 frames per 20-min video for species richness and MeanCount on shelf-edge reefs, though its applicability to longer unbaited videos is unclear. Erickson et al. (2023) found that analyzing richness and MaxN in real-time is the best, while a 60-s sampling interval is optimal for MeanCount on oyster reefs. The optimal subsampling method for RUVs on coral reefs remains unknown. We used MeanCount for its linear relationship with abundance (Schobernd et al. 2014) and superior precision and accuracy in subsampling, compared to MaxN (Erickson et al. 2023).

This study used RUVs to develop optimal sampling strategies for fish assemblages and corallivorous bite rates on coral reefs. The specific objectives were to (1) identify the optimal sample size (instantaneous counts of individual video frames) required for precise and accurate MeanCount

estimates, (2) compare MeanCount estimates derived from systematically versus randomly sampled frames, (3) explore the effect of the above optimal sampling on species richness, and (4) determine the optimal feeding events/video lengths for precise and accurate estimates of corallivore bite rates. Overall, this study aimed to provide guidelines on efficient and standardized data extraction from RUVs across eight geographically dispersed reef sites, which can further contribute to advancing artificial intelligence (AI) techniques by curating training datasets more effectively.

Materials and methods

Remote underwater video collection

To optimize the sampling strategy to assess reef fish relative abundance, richness, and bite rates using remote underwater videos (RUVs), we collected videos from different geographically dispersed reef sites to develop sampling guidelines broadly applicable regardless of reef types. RUVs were recorded at eight reef sites spanning > 1,700 km across the Great Barrier Reef (GBR) and Torres Strait. Study sites included eight inshore and offshore (mid- and outer-shelf) reefs: Aukane Reef and Masig Island in the Torres Strait, Lizard Island on the offshore northern GBR, Pelorus Island of the inshore Palm Island group, Davies and Chicken reefs on the offshore central GBR, Halfway Island of the inshore Keppel Island group, and Heron Island on the offshore southern GBR (see further site location and benthic composition in Table S1 and Table 3 in Gordon et al. 2023). One GoPro camera (1080p, 60fps, wide view) was deployed at 5 m depth to record one > 70 min video between 10 am and 3 pm at each site from April 2021 to Jan 2022, resulting in eight videos (total of ~ 10 h). Cameras were mounted 1 m above the benthos on pre-existing star pickets and set to capture two-thirds reef habitat and one-third water column in the video frame.

Video analysis

RUVs were analyzed using EventMeasure (SeaGIS, Australia) with annotations restricted to two-thirds of the video comprised of reefs (~ 15 m²; 3 m in width and 5 m in length). The first 10 min of each video were discarded to minimize any potential effects of diver presence on fish behavior (Nanninga et al. 2017). Three videos were selected and analyzed for the MeanCount and richness of reef fish assemblages due to the intensive sampling required (see details below). Selected sites were Aukane Reef (Torres Strait), Chicken Reef (central GBR), and Heron Island (southern GBR) based on their latitudinal distribution, differences in benthic composition, and a ~ threefold geometric gradient of fish

densities quantified by UVC transects (Table S1) to capture the uncertainty across a broad range of variability. Moreover, fish densities at the three selected sites spanned the range available, being in the first, third, and fourth quantiles of all eight sites. Additional videos from six sites, Masig and Davies Reefs, and Lizard, Pelorus, Halfway, and Heron Islands were used to assess bite rates of corallivores on account of the high variability of corallivorous fish assemblages associated with benthic communities across shelf position (Emslie et al. 2010).

Establishing the best estimates for MeanCount and species richness

The three selected videos were first intensively sampled every 10 s per 60-min video (hereafter referred to as ‘S10’), resulting in 360 annotated frames per video. This process took ~ 30 h for each 60-min video. This S10 dataset served as a reference for evaluating reduced sampling designs using bootstrapping techniques. We acknowledged that this intensive sampling might not reflect the true fish counts and richness when analyzing the whole video exhaustively but acted as a practical and best estimate in this context. All fishes in each frame were labeled and identified to species level where possible. Cryptobenthic species (e.g., gobbies and blennies) (Goatley and Brandl 2017) that were difficult to detect were excluded from annotations. Raw counts of S10 were normalized and compared among sites using ANOVA followed by the Tukey’s HSD test. MeanCount was calculated as the mean number of fish per frame (Erickson et al. 2023), and species richness was the total number of species.

MeanCount

Optimal sample size

We assessed the optimal number of frames needed for precise MeanCount estimates by randomly subsampling the S10 dataset with replacement at varying intensities (from 1 to the maximum of 360 frames), calculating MeanCount for each. Each sample intensity was repeated 1,000 times to generate precision and accuracy. Precision (%) was defined as the relative standard error (RSE), the standard error divided by the mean of the 1,000 bootstrapped MeanCount estimates for each sampling intensity, expressed as a percentage. Accuracy (%) was defined as the percentage of absolute (unsigned) deviation from the MeanCount estimated using all sampled frames (S10), which was the best estimate possible. Logarithmic regressions were applied to model the absolute deviations as a function of the number of random frames. There are no common threshold values for associated sampling errors, so the optimal number of frames was determined by analyzing the trend of curve deceleration to identify the point of diminishing

returns (Bacheler and Shertzer 2015; Erickson et al. 2023). In this study, the inflection point was identified as the sampling intensity (number of frames) at which precision and accuracy dropped below 0.5% or the slope change became less than 0.05% frame⁻¹ (see results). This process was completed for each of the three videos separately.

Systematic versus random sampling

We next compared the effect of systematic (at fixed intervals) versus random sampling on precision and accuracy for Mean-Count estimates using the optimal number of frames identified in the previous analysis (40 frames over the 60-min video, see results). A challenge to this comparison is that while there is a very high number of potential unique samples that can be derived from randomly sampling 40 of the 360 total frames available over the 60 min of each video, there are only nine unique samples when sampling systematically, which involves picking one frame every 90 s (we refer to this sampling strategy as S90). Our approach for each video was therefore to generate one estimate of the mean and RSE for systematic sampling (based on those nine unique samples of 40 frames at 90-s intervals) and compare this to estimates generated from drawing 9 samples of 40 frames randomly (with replacement). To allow for assessment of significance, the random strategy was repeated 1,000 times to generate a distribution of values against which the estimate from systematic sampling could be compared. Where the single estimate from the systematic approach fell outside the 95% confidence interval of the random sampling, the two methods were determined to provide statistically significantly different estimates of MeanCount.

Fish species richness

The effect of optimal sampling on richness

Since systematic sampling 40 frames (S90) generally outperformed random sampling for MeanCount (see results), we explored the accuracy of richness estimates derived from different levels of systematic sampling, specifically using frames every 10, 30, 60, and 90 s (S10, S30, S60, and S90, respectively). Species accumulation curves were constructed (Hsieh et al. 2016), and species richness at each accumulated frame for each sampling interval was expressed as a percentage of the best estimate from each video (that derived from S10).

Bite rates

Feeding events and bite rates

Six videos were analyzed to investigate the optimal video length and the number of feeding events required for

estimating bite rates of obligate corallivorous fishes (as defined by Cole et al. 2008). The time an obligate coral-livorous fish entered and left the field of view (FOV) was recorded, and any bites taken were counted. This defined a feeding event, and events with zero bites were excluded from the analyses. If a fish moved to an area where it could no longer be seen (i.e., out of the FOV or obscured by a coral or other structure), the observation was ended. A new feeding event started if, and when, the fish reappeared. If a fish entered the FOV, took bites, stopped, swam away but still in the FOV, and resumed feeding, this was still counted as a single feeding event (note that event duration was short, averagely ~ 30 s, see results). Bite rates per feeding event were calculated as the number of bites divided by the event duration (bites min⁻¹). Mean bite rates per feeding event were computed for all fish and the most dominant fish species, which had the highest feeding events, to assess the application at both assemblage and species-specific levels.

Optimal video length and number of feeding events

A series of simulations was conducted to examine precision and accuracy of mean bite rates per feeding event from the first 10 min and every following 30 s up to 60 min for each video per site. Specifically, mean bite rates per feeding event were calculated over the video length analyzed. Precision (%) was defined as the RSE of bite rates per feeding event over the video length analyzed. Accuracy (%) was defined as the percentage of absolute deviation from the mean bite rate per feeding event estimated using all events recorded across the 60 min of video. Similarly, precision and accuracy of mean bite rates with accumulated feeding events were examined from two events to the total number of events for each video per site. Precision and accuracy were measured for all species pooled together and for the most dominant fish species only. The optimal video length and the number of feeding events were determined by inspecting the trend of curve deceleration, where precision and accuracy dropped below 20% and 10%, respectively (see results).

Data analyses

Data wrangling and calculations of all metrics were completed using the base built-in functions and *dplyr* 1.1.2 (Wickham et al. 2023), *reshape* 0.8.9 (Wickham 2007), and *stringr* 1.5.0 (Wickham 2023) packages in R v4.3.2 (R Core Team 2023). Species accumulation curves were generated using the *iNEXT* 3.0.0 (Hsieh et al. 2016) package. All figures were prepared using *cowplot* 1.1.1 (Wilke 2020), *ggplot2* 3.5.1 (Wickham 2016), and *ggpubr* 0.6.0 (Kassambara 2023).

Results

MeanCount

Optimal sample size

Raw counts of the 360 intensively sampled frames were significantly different among sites (ANOVA, $F = 509.6$, $p < 0.001$), and all pairwise comparisons were significant (Tukey's HSD test, $p < 0.001$), with MeanCount (\pm SE) being 27.10 ± 0.78 at Aukane, 3.87 ± 0.10 at Chicken, and 9.62 ± 0.50 at Heron. RSE and absolute deviations were generally low, ranging from 0.08% to 3.34% and 0 to 3.03%, respectively, across sites (Fig. 1). There was an initial sharp increase in precision (RSE decreased) for estimating MeanCount of reef fish assemblages with increasing sampled frames across all videos, but gains in precision for sampling with > 10 frames were minimal (i.e., changes in RSE $< 0.05\%$ per frame) (Fig. 1a). RSE dropped below 0.5% at 12 frames, 10 frames, and 37 frames at Aukane, Chicken, and Heron sites, respectively. Absolute deviations for estimating MeanCount of reef fish assemblages were quite variable, but it generally decreased (i.e., accuracy increased) with increasing sampled frames (Fig. 1b) (logarithmic regressions: slope = -0.06 , -0.09 , and -0.14 at Aukane Reef, Chicken Reef, and Heron Island, respectively; all $p < 0.001$). However, the declining trend in deviation was not as sharp as the trend for precision and was

highly variable at lower sampling (i.e., frames). Therefore, the inflection points were determined by where the slope change was less than 0.05% frame $^{-1}$ instead of 0.5% of absolute deviations. It was not until 15 frames, 17 frames, and 31 frames at Aukane, Chicken, and Heron sites, respectively, that the slope changes of absolute deviation fell below 0.05% per frame. Overall, the optimal sampling frames appeared to be 40 frames over a 60-min video, which could report both precise and accurate MeanCount estimates across all sites.

Systematic versus random sampling

The precision of systematic sampling was generally better than the average random approach (Fig. 2a–c, systematic means were all lower than the mean of the random sampling) but was only significantly better at Aukane, where the systematic mean was smaller than the lower bound of the 95% CI of random sampling RSE values. This was not the case for accuracy where there was no apparent difference between the two sampling approaches (Fig. 2d–f).

Fish species richness

The effect of optimal sampling on richness

Systematically sampling 40 frames (S90) recorded 34, 19, and 41 species at Aukane, Chicken, and Heron sites, respectively. The majority of the species ($> 60\%$) were generally

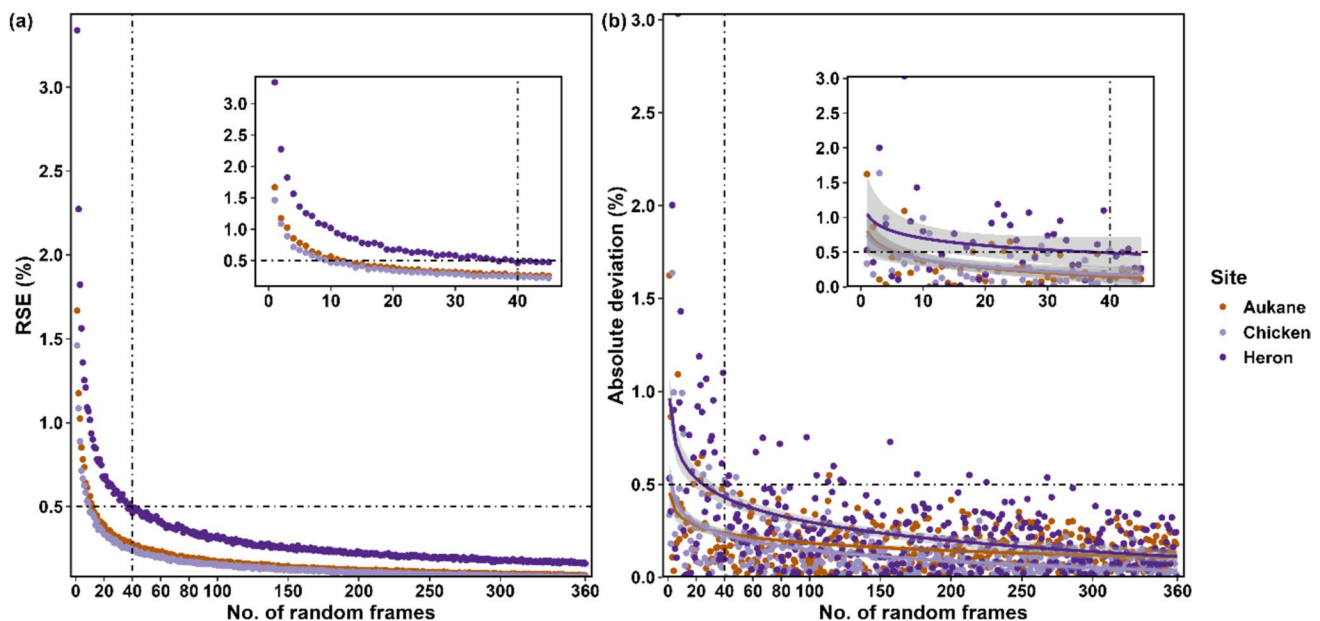


Fig. 1 Precision (a) and accuracy (b) of MeanCount estimates of reef fish assemblages from each of three videos (sites indicated by different colors, see legend) which were intensively sampled (every 10 s, 360 frames in total). Estimates were calculated by randomly subsampling (with replacement) 1 to 360 frames of each dataset.

Insets represent zoom-in views of the x-axis (0–45 frames). Vertical and horizontal dashed lines mark the values at 40 frames and RSE/absolute deviation of 0.5%, respectively. Logarithmic regressions were fitted on the absolute deviation (b) to visualize the declining trend with the 95% confidence interval shown in shades

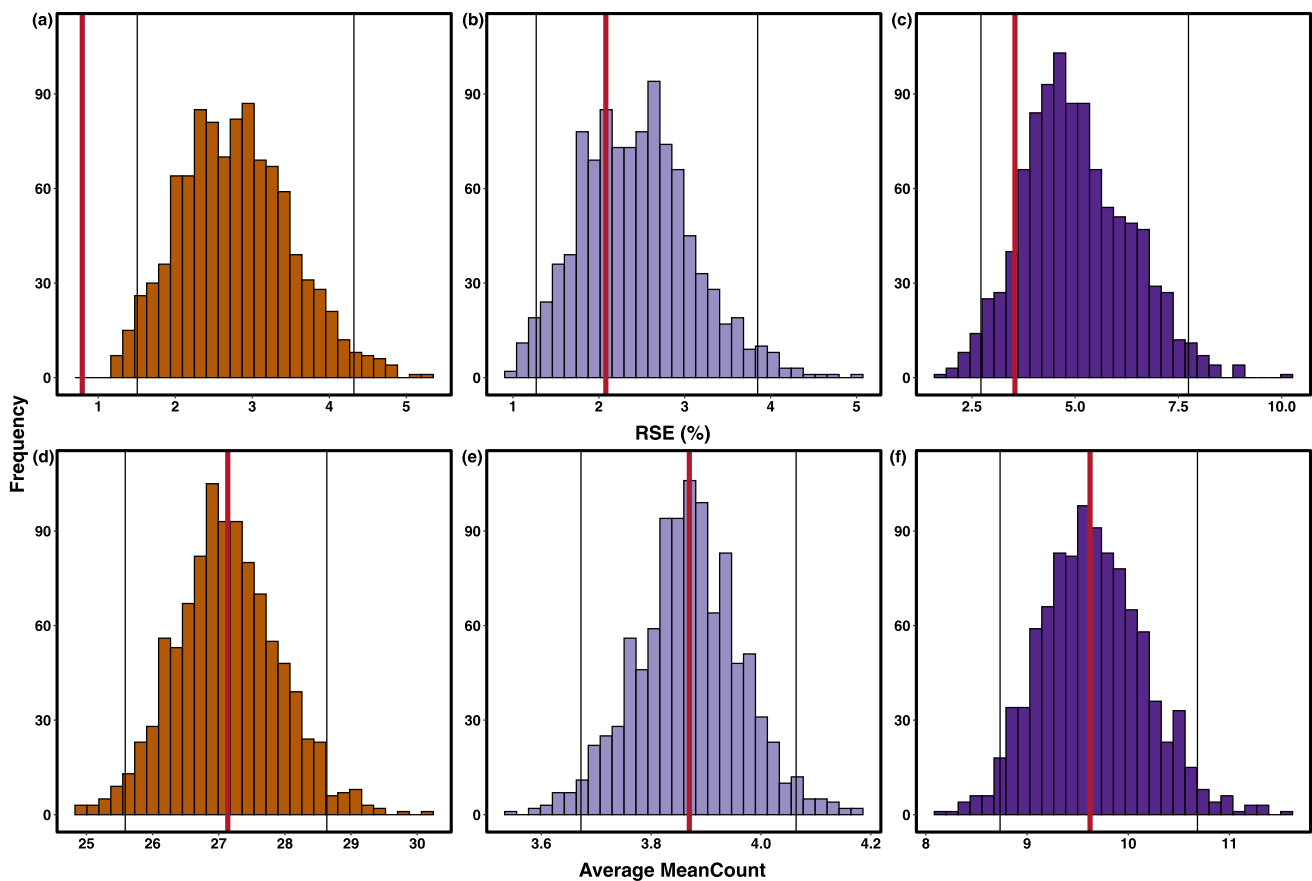


Fig. 2 Comparison of precision (a–c) and average (d–f) MeanCount estimates of reef fish assemblages derived from systematic (red vertical line) versus random (distribution) sampling of 40 frames from each video; Aukane Reef (a and d), Chicken Reef (b and e), and Heron Island (c and f). Systemic estimate is derived from the nine

unique sets of 40 frames per video while the random distribution represents the outcome of 1,000 such random samples (nine sets of 40 random frames per video, with replacement). Black vertical lines mark the upper and lower bound of the 95% CI of the random (bootstrapped) samples

small to medium bodied, ranging from 3 to 65 cm (estimated by UVC), comprising families such as wrasses (f. Labridae), surgeonfishes (f. Acanthuridae), parrotfishes (f. Labridae; Tribe: Scarinae), damselfishes (f. Pomacentridae), and butterflyfishes (f. Chaetodontidae). However, reducing the systematic sampling intensity generally had a very strong negative effect on the richness estimates at all sites (Fig. 3), and none of the curves reached the asymptote. Relative to S10, the average percent of species captured across all sites was 77%, 64%, and 58% at S30, S60, and S90, respectively. These drops in richness were driven by the rare species present in ≤ 10 frames among the total 360 frames (probability $< 3\%$, Table 1).

Bite rates

Feeding events and bite rates

The number of feeding events, bite rates, and event duration are summarized in Table 2. Seven obligate corallivorous

species were observed to consistently feed on live corals, including six butterflyfishes (*Chaetodon aureofasciatus*, *C. trifascialis*, *C. rainfordi*, *C. lunulatus*, *C. unimaculatus*, and *C. baronessa*) and one mucus-feeding wrasse, *Labrichthys unilineatus* (Online Wrasse). Feeding events increased linearly through time at most of the sites but were less common at Masig and Davies (Fig. S2) where the first feeding event was at 20 and 33 min of the videos, respectively. The dominant corallivorous species were *Chaetodon aureofasciatus* at Masig, Lizard, Pelorus, and Halfway, *C. baronessa* at Davies, and *C. trifascialis* at Heron. Moreover, *C. aureofasciatus* was the only corallivorous species that preyed on coral at Masig, Pelorus, and Halfway (Table 2).

Optimal video length and number of feeding events

Precision and accuracy curves for estimating bite rates were similar between all corallivorous fishes (Figs. 4a, b, 5a, b) and the dominant species (Figs. 4c, d, 5c, d), and the curves were the same at Masig, Pelorus, and Halfway

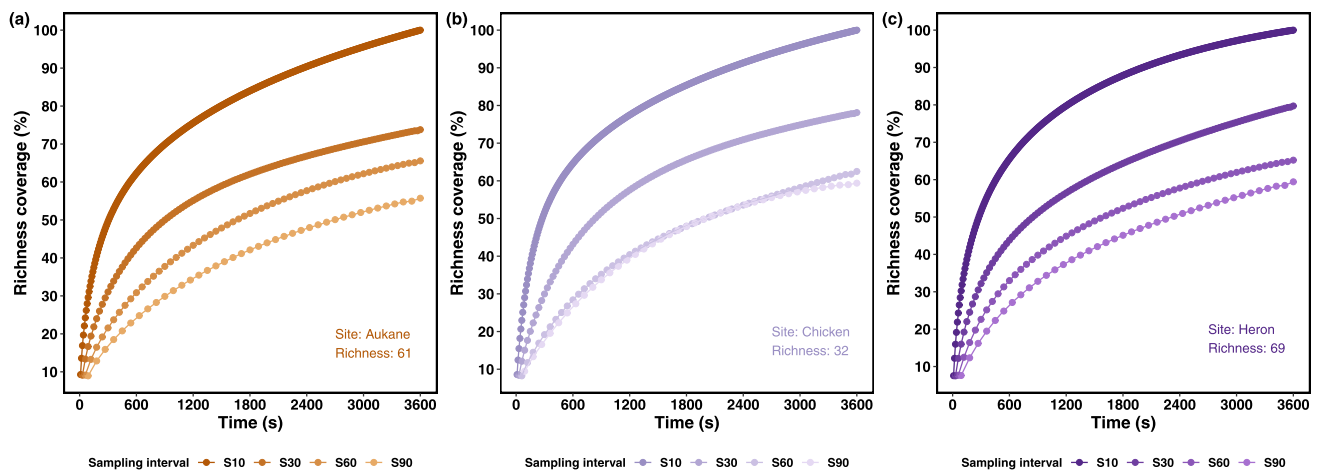


Fig. 3 Species rarefaction curves for reef fish assemblages at Aukane Reef (a), Chicken Reef (b), and Heron Island (c) sites where richness presented as the percentage of the best estimate (using all sample points per video, S10; value indicated on each panel). Color shades

represent different sampling intervals: S10, S30, S60, and S90 (standing for systematically annotating each frame every 10, 30, 60, and 90 s over a 60-min video)

sites with *C. aureofasciatus* being the only species foraging. The precision curves for bite rates did not show the same strong decelerating nonlinear pattern apparent for the MeanCount data, but RSE was at least 10–20 times higher in estimating bite rates. Diminishing returns were evident after about 20–30 min at all sites and for all species groups. RSE values ranged from 10 to 20% for most sites after 30 min except Masig and Davies which were much higher due to the relative rarity of events in the video from these two sites (Fig. 4a, c). Absolute deviations (accuracy) did not change strongly as sample time increased, being roughly 10%, though variability in estimates was considerably lower for periods of 30 min or more (Fig. 4b, d). However, on some occasions, either RSE or absolute deviations increased in a short period of time (e.g., RSE at 13.5 min at Halfway and absolute deviation at 14 min at Heron). The pattern when considering feeding events was quite similar to that of overall bite rates (Figs. 4 and S2). The point of diminishing returns for RSE was at about 15 events, after which RSE values ranged between 10 and 15% for all sites and species groupings (Fig. 5a, c). Similarly, for accuracy, variability dropped after about 15 events, though mean absolute deviations did not vary substantially across video sample lengths, being about 10% (Fig. 5b, d). Bite rates across sites with the top 15 events highlighted are presented in Fig. S3.

Discussion

Among many fish survey methods, RUV stands out for surveying fish assemblages without major disturbances to fish behavior as in UVC (Emslie et al. 2018) and documenting natural feeding activities compared to the use of

bait in BRUV. Furthermore, video surveys save time spent underwater and alleviate the need for highly trained divers to survey fish assemblages in situ, but processing videos is labor-intensive and time-consuming (e.g., taking ~30 h to annotate a 60-min video every 10 s in this study). Still, there is very limited information to guide how videos are sampled to document abundance proxies, richness, and behavior, and what accuracy and precision such sampling can deliver for each (but see Erickson et al. 2023). In this study, we evaluated the optimal subsampling strategies for RUVs from coral reefs across the GBR and the Torres Strait to inform video annotation processes and still ensure precise and accurate MeanCount and bite rate estimates from a 60-min video. Our results suggest that 40 frames over a 60-min video enable both precise and accurate MeanCount estimates of reef fish assemblages during the survey period. While systematic sampling (1 frame every 90 s) didn't overall provide significantly different estimates compared to random sampling, it resulted in slightly higher precision. Systematic sampling is thus recommended because it is logistically simpler. However, our analysis indicated that such sampling would lead to underestimates of species richness by ~40% due to the less common species being present in approximately 3% of the frames. This work has also provided firm guidance on the use of RUV for documenting corallivore feeding rates, suggesting that 30 min or 15 feeding events per 60-min video are sufficient to generate both precise and accurate mean bite rates at most of the sites surveyed in this study.

Precision is measured as the RSE, which is inversely related to the sample size. As such, precision in estimating MeanCount increased (RSE decreased) with increasing sampled frames in this study, a common finding as in a similar study conducted on oyster reefs (Erickson et al. 2023). The

Table 1 Summary of species which were not captured in sampling using 90 s systematic sampling (S90) at each site. Frame occurrence was the number of frames where the species was present. MeanCount was the average number of individuals over 360 frames

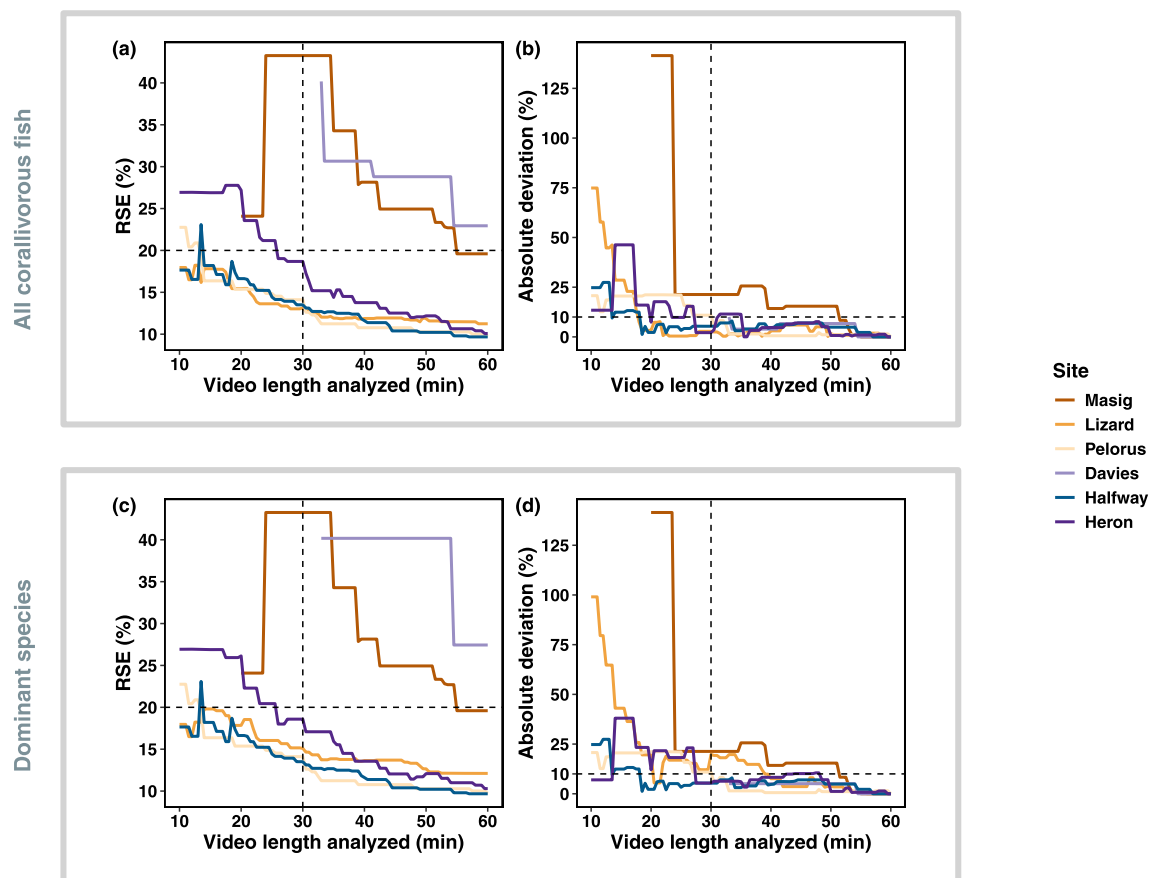
Aukane Reef			Chicken Reef			Heron Island		
Species	Frame occurrence	Mean count	Species	Frame occurrence	Mean count	Species	Frame occurrence	Mean count
<i>Aeoliscus strigatus</i>	2	0.014	<i>Anampses neoguinaiicus</i>	1	0.003	<i>Acanthochromis polyacanthus</i>	4	0.011
<i>Caesio caerulea</i>	1	0.011	<i>Cephalopholis cyanostigma</i>	2	0.006	<i>Acanthurus grammoptilus</i>	1	0.003
<i>Carangoides fulvoguttatus</i>	1	0.003	<i>Cheilinus oxycephalus</i>	1	0.003	<i>Acanthurus nigrofuscus</i>	2	0.006
<i>Centrophorus moluccensis</i>	1	0.003	<i>Chlorurus spilurus</i>	10	0.028	<i>Acanthurus xanthopterus</i>	3	0.008
<i>Cephalopholis nigripinnis</i>	2	0.006	<i>Chromis margaritifer</i>	8	0.022	<i>Chaetodon flavivostris</i>	3	0.011
<i>Cephalopholis</i> sp.	1	0.003	<i>Epinephelus merra</i>	2	0.006	<i>Chaetodon kleinii</i>	8	0.028
<i>Chaetodon baronessa</i>	4	0.011	<i>Halichoeres chrysus</i>	1	0.003	<i>Forcipiger longirostris</i>	1	0.003
<i>Chaetodontoplus duboulayi</i>	2	0.006	<i>Neoglyphidodon melas</i>	3	0.008	<i>Halichoeres hortulanus</i>	2	0.006
<i>Cheilinus chlorourus</i>	6	0.017	<i>Scarus globiceps</i>	1	0.003	<i>Halichoeres marginatus</i>	2	0.006
<i>Cheilinus oxycephalus</i>	8	0.022	<i>Scarus schlegeli</i>	1	0.003	<i>Halichoeres</i> spp.	1	0.006
<i>Cheilodipterus</i> spp.	10	0.042	<i>Scarus</i> spp.	1	0.003	<i>Heniochus varius</i>	7	0.036
<i>Chlorurus microrhinos</i>	3	0.008	<i>Synodus variegatus</i>	2	0.006	<i>Kyphosus vaigiensis</i>	1	0.003
<i>Choerodon schoenleinii</i>	2	0.006	<i>Thalassoma hardwicke</i>	1	0.003	<i>Labrichthys unilineatus</i>	6	0.017
<i>Epibulus insidiator</i>	3	0.008				<i>Naso</i> spp.	2	0.006
<i>Halichoeres argus</i>	1	0.003				<i>Naso vlamingii</i>	2	0.006
<i>Halichoeres melanurus</i>	1	0.003				<i>Oxycheilinus digamma</i>	2	0.006
<i>Labridae</i> spp.	3	0.008				<i>Pomacanthus semicirculatus</i>	1	0.003
<i>Lethrinus harak</i>	1	0.003				<i>Pseudocheilinus evanidus</i>	1	0.003
<i>Neotrygon australiae</i>	1	0.003				<i>Pterocaesio marri</i>	4	0.422
<i>Oxycheilinus digamma</i>	1	0.003				<i>Scarus frenatus</i>	2	0.006
<i>Pomachromis</i> spp.	1	0.003				<i>Scarus spinus</i>	3	0.008
<i>Pterocaesio digamma</i>	1	0.136				<i>Scolopsis bilineata</i>	2	0.006
<i>Scarus chameleon</i>	2	0.006				<i>Siganus corallinus</i>	4	0.011
<i>Scarus dimidiatus</i>	2	0.006				<i>Siganus fuscescens</i>	1	0.003
<i>Scarus niger</i>	1	0.003				<i>Siganus punctatus</i>	3	0.008
<i>Stethojulis strigiventer</i>	1	0.003				<i>Siganus vulpinus</i>	1	0.003
<i>Triaenodon obesus</i>	1	0.003				<i>Zanclus cornutus</i>	1	0.003

optimal number of frames for calculating the MeanCount was 40, where the RSE of MeanCount dropped below 0.5% at all sites, and deviation from truth fell within $\pm 0.5\%$. This value is similar to the 50 frames suggested in a study using

BRUV to estimate the MeanCount of three reef fish species on shelf-edge reefs (Bacheler and Shertzer 2015) and the 60 frames suggested when subsampling RUVs on oyster reefs to keep the coefficient of variation (CV) and deviation below

Table 2 Summary of the total number of feeding events, mean bite rates, and event duration of all corallivorous fish and the most dominant species

	All species			Dominant species		
	No. of feeding events	Bite rates (bites min ⁻¹ ; mean ± SE)	Event duration (min; mean ± SE)	No. of feeding events	Bite rates (bites min ⁻¹ ; mean ± SE)	Event duration (min; mean ± SE)
Masig	16	11.22 ± 2.20	0.39 ± 0.05	16	11.22 ± 2.20	0.39 ± 0.05
Lizard	63	10.20 ± 1.15	0.47 ± 0.04	51	8.96 ± 1.08	0.45 ± 0.04
Pelorus	34	6.17 ± 0.60	0.53 ± 0.06	34	6.17 ± 0.60	0.53 ± 0.06
Davies	6	12.17 ± 2.79	0.47 ± 0.14	4	14.11 ± 3.87	0.48 ± 0.22
Halfway	58	5.71 ± 0.55	0.53 ± 0.04	58	5.71 ± 0.55	0.53 ± 0.04
Heron	38	13.83 ± 1.39	0.52 ± 0.04	30	14.66 ± 1.51	0.49 ± 0.04

**Fig. 4** Relative standard error (RSE; **a** and **c**) and absolute deviations (**b** and **d**) of the mean bite rate estimates of all corallivorous fishes (**a** and **b**) and the dominant species (**c** and **d**) derived from analysis of increasing video length (x-axis) at each site (represented by different colors, see legend). The deviation is calculated as the percentage

of absolute difference from the mean bite rate when analyzing videos for 60 min. Vertical and horizontal dashed lines mark the values at 30 min and RSE of 20% or absolute deviation of 10%, respectively. Not all values started at the first 10 min because no feeding events were recorded at Masig and Davies until at the 20 and 33 min

10% (Erickson et al. 2023). Although the authors did not have actual precision estimates between 30 and 60 frames, interpolation from their presented data would suggest that the CV for MeanCount was near 10% at ~44 frames, further supporting our result and highlighting the power of scrutinizing precision by increasing frames one by one. A reduced

number of frames required in this study are not surprising given that MeanCount was calculated at the assemblage level instead of species-specific level and that the number of fish present in the camera view is less variable and typically greater on coral reefs compared to oyster reefs, where there were relatively low abundance and many zero observations

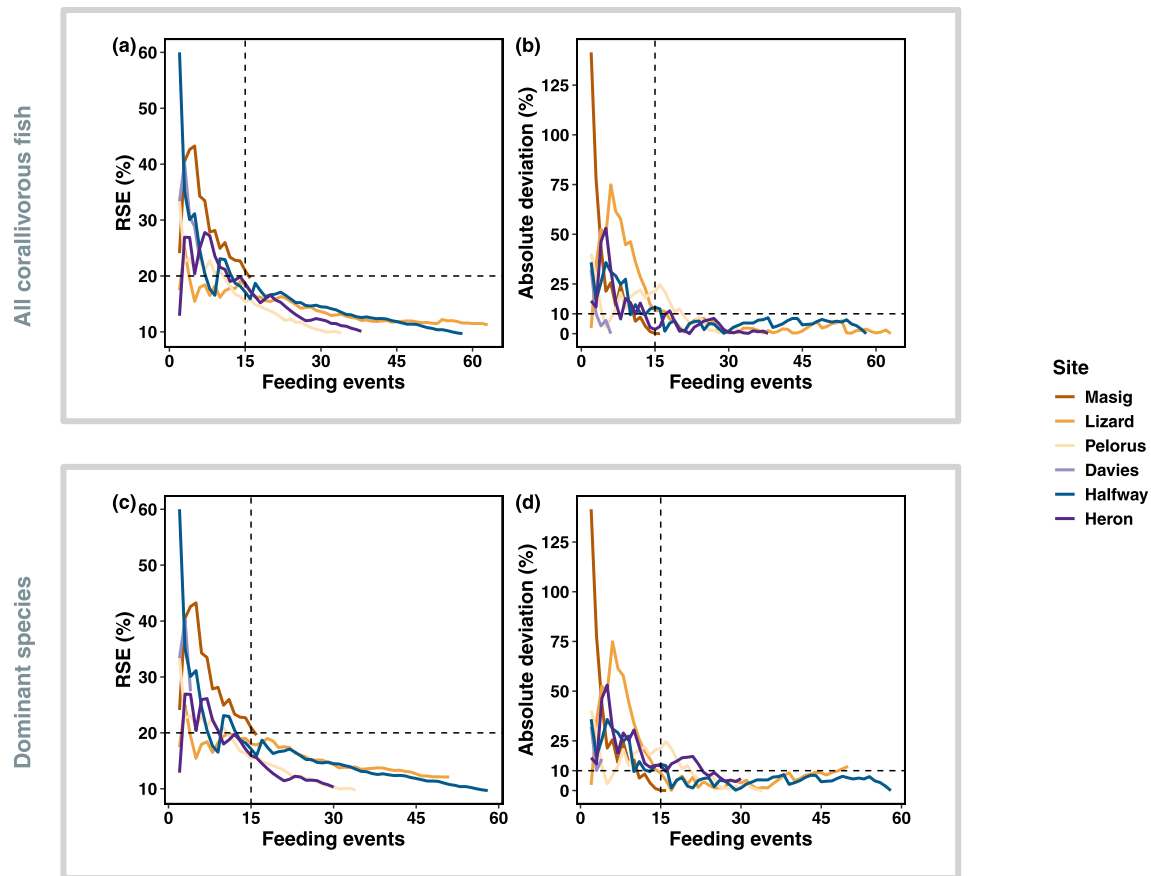


Fig. 5 Relative standard error (RSE; **a** and **c**) and absolute deviations (**b** and **d**) of the mean bite rates per event estimated for all corallivorous fishes (**a** and **b**) and the dominant species (**c** and **d**) as a function of the number of events considered (x-axis) at each site (represented

by different colors, see legend). Vertical and horizontal dashed lines mark the values at 15 feeding events and RSE of 20% or absolute deviation of 10%, respectively

(Erickson et al. 2023). Aside from the sample size effect, precision is subject to the relative abundance and dynamics of the observed taxa. The stationary video can capture most of the site-attached species (e.g., lemon damselfish, *Pomacentrus moluccensis*, and whitetail damselfish, *P. chrysurus*) in each frame. However, we hypothesized that the higher richness at a site, the more likely new transient or cryptic species that are less common can be snapshotted, inflating the sampling error. This is a potential reason why precision was the lowest at the most diverse site, Heron, compared to the other two sites. If the aim is to target less abundant or rare taxa, more sampling effort is required (Lechene et al. 2019). In summary, we recommend subsampling 40 frames from a 60-min video on coral reefs similar to those used here for precise and accurate estimates of the number of common species (i.e., MeanCount) on RUVs.

Sampling effort is just one element to be considered in optimizing the sampling strategy, but how this is done is also important, whether completely at random or some other more systematic approaches. In this study, we showed that

both techniques produced similar precision and accuracy in estimating MeanCount of coral reef fish assemblages. Previous studies applied either method (Bacheler et al. 2013; Bacheler and Shertzer 2015), but the optimal sampling method remained unknown. A notable recent exception is the study of Erickson et al. (2023) which found systematic sampling was more precise and accurate than random sampling for assessing fish assemblages on oyster reefs because large schools of fish that gathered in a specific time period were missed using random sampling. The swift pass of large schools of fish was also observed in this study. For example, MeanCount from intensive sampling at Heron was 9.62 ± 0.50 (mean \pm SE), but counts exceeded 80 individuals in some frames (Fig. S1) mainly composed of bigtail and doubleline fusilier (*Pterocaesio marri* and *P. digramma*). However, this did not lead to any significant difference in precision or accuracy between systematic and random sampling at this site owing to the infrequency of these events. There was one exception where systematic sampling was more precise than random sampling. Raw counts at Aukane

were examined and exhibited a more variable pattern compared to counts at Chicken and Heron (Fig. S1), which may explain why sampling at a fixed interval can result in a more precise estimate by capturing both high and low values more easily. Overall, we conclude that either method is appropriate for subsampling RUV on coral reefs, but systematic sampling is recommended owing to the logistic easiness of video annotations.

Systematic 40 frames have been proved optimal for estimating MeanCount. We further investigated how such sampling strategy applied to species richness. Overall, richness decreased as the sampling frequency decreased, a result of smaller sample size and less sampling effort. There was a consistent ~40% reduction in estimated species richness across all sites when reducing the sampling frequency from 1 frame every 10 s to 1 frame every 90 s. These underestimated species (Table 1) included those with great mobility and large home range such as whitetip reef shark (*Triaenodon obesus*), yellow spotted trevally (*Carangoides fulvoguttatus*), and many labrids. In contrast, some species are more site-attached and often hide among the complex reef structures such as bluespotted rockcod (*Cephalopholis cyanostigma*) and birdwire rockcod (*Epinephelus merra*). This trade-off is acceptable if the aim is to capture the common species because of the low detection probability (<3%) of the missed species. Furthermore, the species richness recorded per video using the current optimal sampling strategy is similar to those per sampling unit surveyed by UVC (26.5 ± 1.0 ; mean \pm SE) or BRUV (26.6 ± 0.8 ; mean \pm SE) on the central GBR (Cheal et al. 2021). However, if the objective is to scrutinize fish diversity and to detect rare species that often support unique and vulnerable functions (Mouillot et al. 2013), subsampling videos are not recommended. To aid in this, software using DL algorithms has been developed to automatically detect, count, and track fish individuals in the video (Ditria et al. 2020; Lopez-Marcano et al. 2021). Nevertheless, several challenges remain to be solved (Saleh et al. 2024, 2022). Underwater images are subject to a changing environment, where changes in light, depth, and turbidity affect image quality. Another challenge is the ability of DL models to differentiate between training and testing data (i.e., model generalization). Moreover, one of the bottlenecks is the limit of training datasets. Thousands of annotated points/segmentations are required for a single species (Lopez-Marcano et al. 2021), impeding the fast development of models. This study provides guidelines on effectively extracting important fish metrics without compromising precision and accuracy, and the resulting annotated images could further be used as a training dataset for AI models.

RUVs are useful for assessing fish abundance, diversity, and foraging behaviors (Eggertsen et al. 2020; Knoester et al. 2023), though the optimal video length for precise

and accurate bite rate estimates is uncertain. Using obligate corallivorous fish as a case study, we found that mean bite rates across species from RUVs (5.71–14.66 bites per min) align with previous diver-based observations at Lizard Island (7.80–12.29 bites per min; Gregson et al. 2008). Precision and accuracy in estimating mean bite rates generally increased with increasing video length analyzed due to more feeding events recorded (Fig. S2). However, occasional drops in precision or accuracy were linked to sudden changes in activities. Feeding success can be inhibited when coral polyps withdrawn (Gochfeld 2004) or where interspecific competition or aggression occur (Gregson et al. 2008). We observed that some species, such as *C. baronessa* and *C. trifascialis*, showed aggressive behaviors toward subordinate species, which is subject to territories, resource availability, dietary overlap, and specialization (Berumen and Pratchett 2006; Blowes et al. 2013, 2017). Precision and accuracy in bite rate estimation were much lower than individual counts, reflecting the high variability in foraging behaviors which are associated with quantity, quality, and accessibility of food. However, this discrepancy may stem from methodological differences, as MeanCount was calculated by bootstrapping frames from the intensively sampled dataset, while bite rates were recorded over time.

Although this study provides guidelines on sampling strategies with strong support from empirical and simulated data, there are several limitations. First, initial camera deployment can still alter fish behaviors, necessitating an acclimation period. We used 10 min, though some species may not fully recover (Emslie et al. 2018). Additionally, RUVs were collected during a single period at each reef site, which may not be representative of the overall fish assemblages as abundance can change with season (Vaughan et al. 2021), time of the day, and tidal state (Mallet et al. 2016). Fish activities also fluctuate within the day [e.g., herbivores (Zemke-White et al. 2002) and corallivores (Gregson et al. 2008)]. Moreover, the feeding rates of corallivores peaked between 10 am and 2 pm (Gregson et al. 2008), coinciding with our camera deployment. Furthermore, RUVs have a limited field of view. Our cameras captured a reef area of ~15 m², much smaller than a typical UVC belt transect (250 m²), making it difficult to document large, roaming species. One solution is to fast screen the video to find the taxa of interest and record the time of first arrival, which can reflect abundance (Willis and Babcock 2000). Alternatives are to deploy more replicates to cover a wider area at each site, use 360° cameras to obtain a holistic field of view (Mallet et al. 2021), or switch to BRUVs to attract highly mobile and predatory fish (Cheal et al. 2021). Second, intensive sampling was performed by analyzing one frame every 10 s (360 frames) from three sites, where the hypothetically best estimates for MeanCount and species richness were derived. While the recommendations in this study should

be robust and adequate for most shallow Indo-Pacific reefs (the selected reefs were in the first, third, and fourth quantile of fish density across all sites), we acknowledge potential underestimation of true values, and it may not apply across all reef systems and habitats. Specifically, caution should be applied if surveying reefs with few fish. Yet, further increases in sampling effort beyond 40 frames did not significantly improve precision and accuracy for MeanCount; therefore, more frames or longer videos are not suggested. Future studies might examine how relative abundance and richness change if sampling frequency doubles, total video length shortens to 30 min, and the sampling frames remain 40. Lastly, though our sampling strategy yields precise and accurate bite rates of obligate corallivores, it may be challenging to apply this approach to herbivores, which have high bite rates and often swim in groups (Bonaldo et al. 2014). Herbivores can be harder to track when groups consist of a mix of species with very similar appearance (e.g., juveniles or subadults of parrotfish and surgeonfish) (Reinthal and Lewis 1986; Robertson et al. 1976). Optimizing sampling for herbivore bite rates should consider schooling effects and may require breaking observations into shorter intervals.

The optimal sampling strategies developed in this study were systematically sampling 40 frames over an hour of video for MeanCount and analyzing 30 min of the video or 15 feeding events for corallivorous bite rates. Following this guideline, researchers can have a nine-fold and two-fold reduction in video analysis time and reduce the processing time to 3–4 h and ~2 h for MeanCount/species richness and bite rates of corallivorous, respectively. Regarding the field deployment, future studies aiming at assessing bite rates could record 30 min of videos plus an extra 10 min to minimize the disturbance during deployment, which enables the collection of double the number of spatial or temporal replicates. However, it is yet to be explored if sampling 40 frames from a 30-min video still ensures precise and accurate estimates of MeanCount. The current findings are especially important for studies that aim to monitor population or community dynamics and to understand foraging behaviors. The emerging datasets generated by following the guidelines in this study can be further used as training datasets for AI models.

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Hsu conducted the video annotations and prepared the first draft of the manuscript. T-H.T. Hsu and W.F. Figueira completed the statistical analyses. T-H.T. Hsu, A.S. Hoey, and W.F. Figueira revised the initial manuscript. All authors contributed to the finalization of the manuscript.; Corresponding author - Correspondence to Tsai-Hsuan Tony Hsu.

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Data availability Data along with an R markdown (Hsu et al. 2025) are available at the Sydney eScholarship (<https://hdl.handle.net/2123/33520>) and GitHub (<https://github.com/THTonyHsu/SamplingRUV.git>) to replicate all the analyses.

Conflict of interests The authors declare no competing interests.

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