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Habitat-Mediated Efficacy of 360 Degree Diver-Operated Video For Quantitative Surveys of California Reef Fishes

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HABITAT-MEDIATED EFFICACY OF 360 DEGREE DIVER-OPERATED VIDEO FOR QUANTITATIVE SURVEYS OF CALIFORNIA REEF FISHES

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ABSTRACT

Habitat-Mediated Efficacy of 360 Degree Diver-Operated Video For Quantitative Surveys of California Reef Fishes

by

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Master of Science in Marine Science

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Temperate rocky reefs feature a mosaic of complex macrohabitat features which host a variety of demersal fish species. Giant kelp forests add considerable vertical structure to rocky reefs, including macrohabitats extending from the reef to the upper water column. Much of what we know about temperate communities derives from shallow SCUBA surveys in which divers record observations using underwater visual census (UVC) techniques. Increasingly, these communities are being studied with video techniques first utilized in deeper water. While UVC provides immediate data on fish communities and requires no additional technology either for data collection or post-processing, imagery captures the fine-scale associations between fish specific habitat features that elude UVC techniques. While traditional video cameras constrain the field of view available to a UVC diver, 360˚ cameras record everything in all directions, eliminating the need to selectively survey one direction underwater. However, questions remain as to how data derived from 360˚ video transects compare to the more well-established UVC transects, particularly in complex environments. My primary research objective was to examine the trade-offs associated with 360˚ video and UVC when quantifying attributes of the demersal fish community across multiple sites and macrohabitat types. I performed SCUBA dives at four sites around the Monterey Peninsula in central California. Pairing UVC and 360˚ video, I recorded fish counts along 30 meter demersal transects. Richness, diversity, abundance, and density of fishes from UVC and 360˚ video were compared statistically with two-way analysis of variance (ANOVA) and non-metric multidimensional scaling (NMDS). Results indicate that within fish-habitat guilds, counts of species were similar between methods at all macrohabitats and at most sites. 360˚ video and UVC produced similar results with respect to species richness and diversity. At every scale, UVC density was always significantly greater than 360˚ video density. Count per meter independent of volume was greater when measured from 360˚ video for all fish combined, but this result was less clear when fish were separated into habitat guilds. Both methods were plotted similarly and revealed comparable site-specific trends in community structure when ordinated via nMDS. These results suggest that despite higher research costs and some data caveats, 360˚ video transects can be incorporated into temperate subtidal reef monitoring without compromising data quality. 360˚ video techniques can supplement traditional survey methods within nearshore environments to monitor shallow marine protected areas and fisheries resources.

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ACKNOWLEDGEMENTS

I applied for graduate school fresh out of my undergraduate degree, just before news COVID-19 was making national headlines. I feel incredibly fortunate to have succeeded during my Master's degree, but I could not have done this work without the help of many key individuals. I am enormously grateful to CSUMB's diving safe officer Andrew Morgan and my advisor James Lindholm for facilitating the beginning of my fieldwork despite in-person pandemic restrictions. Wearing facemasks until the moment we were underwater, their support allowed me to begin fieldwork during the first semester of graduate school. Similarly, I owe much of my fieldwork to Jordan Velasco, a fellow CSUMB scientific diver, who assisted on a majority of my SCUBA dives. Sometimes collecting data, sometimes simply acting as a dive buddy – Jordan budgeted time for over 30 dives to support my project. I am tremendously thankful for my family and friends who have listened to me vent about this project for three years.

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INTRODUCTION

Before researchers were able to directly observe the underwater environment in which marine fishes occur, data on community attributes such as relative abundance, size structure, and species composition were first collected incidentally, and later were derived primarily from fishing activities. Fisheries landings data provide some of the earliest documented records of fish abundances and spatial distribution, particularly for commercially important species (Pauly et al. 2003; Pauly and Zeller 2016). These data were valuable for studying broad trends, such as how species composition patterns changed with shifting environmental conditions and population declines due to overfishing.

There are, however, several challenges associated with relying primarily on fisheries techniques to collect data. Most trawl surveys result in high levels of mortality (Thrush and Dayton 2002; Boldt et al. 2018). Even non-consumptive fishing (i.e. catch and release) causes stress to fish (Campbell et al. 2010), reducing their ability to avoid predators, find prey, or allocate energy towards reproduction once released back into the environment (Campbell et al. 2010; Davis 2010). Fish that use swim bladders to control te particularly susceptible to barotrauma during rapid ascents to the surface and often require human intervention to descend (Kerwath et al. 2013). Further, fishery-derived data cannot resolve questions about the temporal and spatial scales of demersal fish-habitat associations with the seafloor, a critical factor in understanding fish ecological paradigms (e.g., settlement, post-settlement survivorship, and ontogenetic shifts in habitat utilization) and successfully managing communities (Yoklavich et al. 2000; Laidig et al. 2009).

Shallow rocky landscapes are traditionally monitored via SCUBA surveys (Van Dykhuizen 1983; Hallacher and Roberts 1985; Bodkin 1988; Carr 1989; Carr 1991). SCUBA diving allows scientists to enter the marine environment and make direct observations on abundance, size structure, and community composition. This is helpful for better describing behavior, habitat associations, and position in the water column. A review by Allen and Pondella (2006) revealed that out of all the potential survey methods, “kelp bed/rock reef” habitats were overwhelmingly sampled using visual surveys led by SCUBA divers.

Underwater visual census (UVC) is a common non-extractive technique for surveying fish. It is best described as divers writing observations on slates and waterproof datasheets. The

trade-offs associated with the use of UVC have been reviewed extensively (Harmelin-Vivien ML and Francour 1992; Samoilys and Carlos 2000; Pelletier et al. 2011; Lowry et al. 2012; Holmes et al. 2013; Grane-Feliu et al. 2019). UVC is an appealing technique because it does not require expensive hardware beyond SCUBA equipment. It is a quick method for generating data as it does not require post-processing beyond data entry. Cohorts of divers can be trained to replicate UVC methods, as is common in subtidal monitoring efforts among universities (e.g., Partnership for Interdisciplinary Studies of Coastal Oceans; www.piscoweb.org), federal agencies (e.g., the Channel Islands National Park Kelp Forest Monitoring Program; www.nps.gov/im/medn/kelp-forest-communities.htm), and citizen science groups (e.g., Reef Check Worldwide; www.reefcheck.org). Such data have been used to create baseline ecosystem datasets, detect range shifts in shallow species, and quantify the efficacy of marine protected areas (Beck et al. 2007; Gillet et al. 2012; Witman et al. 2013; Di Lorenzo et al. 2016; Menge et al. 2019).

Yet challenges associated with studying fish via UVC persist. Diver training requirements, can be considerable, including factors such as prolonged exposure to cold water, air management, and communications amongst divers in low-visibility. Underwater task loading can overwhelm inexperienced divers, potentially compromising data quality and precluding sufficient data collection. It can be difficult to accurately count large schools of fish and estimate size of particularly large individuals (K. Strickland, *personal observation*). And since fish encounters are often brief, divers must have identification expertise on all possible species of the fish community, including species' temporal changes in appearance. The resulting dataset may be limited by underwater distractions, specific dive objectives, or even the datasheet used to record observations. Analyses of UVC data are constrained to the specific notation divers make on their slates, with no definitive way to revisit the field observations that lead to those data. UVC solely generates *in situ* data and removes the option to review the dive as it occurred. Methods that capture additional information beyond the task of the dive could be helpful for this reason.

Improvements in camera and underwater housing technologies have made imagery-based platforms for research increasingly more accessible. Past studies have introduced methods for surveying marine environments using video and still photographs (Auster et al. 1989; Auster et al. 1991; Norcross and Mueter 1999). Non-scientists are also increasingly recording undersea environments with cameras. Imagery provides researchers with a permanent record of fish

observations in the environment in which they occur, records which assist with categorizing fine scale habitat utilization (Lindholm et al. 2008; Smith and Lindholm 2016; Basset et al. 2018). Recorded imagery also frees researchers, whether they are a submersible observer or a SCUBA diver, from needing to make split second data decisions. Footage can be analyzed *post hoc* by pausing and examining individual frames, which is helpful for accurately counting large numbers of quickly moving organisms. Additionally, imagery also allows new questions, unanticipated at the time of capture, to be explored in the future and by additional researchers (Lindholm et al. 2008, Basset et al. 2017). Revisiting imagery can calibrate generations of scientists with shifting baselines to past ecological states. More knowledge can be gained from past field work efforts if recorded with video and analyzed by new researchers.

However, using cameras underwater for data collection presents new challenges. Water refraction narrows the field of view (FOV) that a camera records, resulting in a tighter image than that of a SCUBA diver. Dome ports, which can be expensive, are necessary to counter the effects of refraction and expand the FOV back to what it would be if recording through air. Also, organisms bisected by the edge of the image frame may not be possible to identify to the lowest taxonomic level due to defining characteristics falling outside of the FOV, a problem non-existent with UVC methods. If a camera is unmanned, there is no solution to the above challenges. And there may be interesting features present just outside of the camera's FOV that a diver could have noted, but would never be captured by video. Stationary video landers are particularly impacted by the inability to reframe or "look around" since a video platform can drift away from its intended settlement position if deployed from a boat (Kilfoil et al. 2017; Hemery et al. 2022). If the camera is operated, the operator could reframe the field of view to include the observation, but depending on the research protocol this could result in a change to the volume of water surveyed. Thus, it is difficult to select for habitat features of interest and truly estimate densities of fishes. In response to limitations in a camera's field of view, many imagery-based studies have adopted metrics such as MaxN, the greatest number of uniquely identifiable individuals in a deployment (Denney 2017; Campbell et al. 2018). This conservative measurement of fish abundance eliminates double-counting individuals that swim out of the frame and return, but also fails count new non-conspicuous individuals of the same species. MaxN counts are influenced by the volume of water sampled, so it is likely that MaxN is correlated with FOV.

Visibility can severely hinder imagery work in California and other temperate regions. Like other western continental boundaries, the Eastern Pacific Ocean has areas of strong upwelling which bring nutrients towards surface waters to stimulate primary production (Ramp et al. 2005; Rykaczewski and Checkley 2008; Booth et al. 2012). These conditions can lead to plankton blooms which worsen visibility and inhibit sunlight penetration at the surface. At its poorest, visibility can fall to a meter or less. These conditions present challenges for cameras, particularly those with smaller sensors. At low light levels, cameras record at higher ISO values and slower shutter speeds, often resulting in grainy, blurry imagery. Autofocus performance also decreases in dark conditions, reducing the usability of the footage. The lights used to illuminate subjects can also illuminate particulates, causing distracting backscatter in the final footage. Combined, these challenges can lead to problems with species identification and inaccurate counts of fishes recorded on video. Because there are tradeoffs associated with using imagery instead of visual census, video should be included when the technique is required to meet project objectives.

Cost can also be a significant barrier to imagery-based surveys because beyond the cameras themselves, there are several additional expenses. The water proof housings required for undersea research can sometimes exceed the value of the camera. Bright video lights or strobes are often required to expose an image and see the full visible color spectrum at depth. Other hardware includes the batteries for cameras and lights, as well as the media that imagery is recorded to. Once field work is complete, powerful computers may be required to view and process high resolution video. Although time spent in the field may stay the same as with UVC, post processing and data extraction can take much longer than a method like (UVC Willis et al. 2000; K. Strickland, *personal observation*). Video analysis can take upwards of five times longer than *in situ* data collection (Stephens et al. 2006), though machine learning may resolve some of these challenges in the future (Marrable et al. 2022). Researchers must also decide how they will archive their video fieldwork for themselves and others to access in the future. Safe, redundant backups could come in the form of multiple external hard drives as well as cloud backups. If there is intent for subsequent viewers to analyze and ask future questions from the imagery, there will likely be long-term costs in physical or online storage as well.

We have learned a great deal about California's shallow underwater environments from previous studies, both work with divers in the water and imagery-based studies. A variety of fish

taxa occupy coastal reefs in California, displaying a wide diversity in body shapes and life history strategies. Notable are members belonging to the family Scorpaenidae, particularly the rockfishes of the genus *Sebastes*, which are economically important for recreation and tourism. There are also several species of surfperch (Embiotocidae), greenlings (Hexagrammidae), and sculpins (Cottidae) associated with temperate rocky reefs. Besides these residents, there are also visitor fish species that can be observed on rocky reefs (Allen and Pondella 2006). This results in diverse fish communities which interact with many aspects of their environment. Subtidal reefs add heterogeneity to low relief, unconsolidated habitats, and provide structure for algae, fish, and invertebrate communities. It has been estimated that kelp forests and rocky reefs support up to 15 times the density of fishes of comparable soft substrate (Bond et al. 1999). Giant kelp (*Macrocystis pyrifera*) and Bull kelp (*Nereocystis leutkeana*) are two of several macroalgae that occur along the shallow California coastline (Schroeder et al. 2019). Both require hard substrate for holdfast attachment, making kelp forests limited to rocky reefs that are shallow enough for adequate light penetration (Schiel and Foster 2006).

The vertical relief and habitat complexity generated by rocky reefs and kelp forests provide various fine-scale habitat opportunities for fishes. Stephens et al. (2006) list at least 15 different fish microhabitats found on rocky reefs from California and Baja California. Many species occur in multiple of these microhabitats at various life stages (Stephens et al. 2006). These fine-scale microhabitats (or positions within the water column) within broader kelp forest habitats include elevated positions within blades of the kelp forest, high relief rocky ledges, and crevices between reef structures. Species may also shift habitat utilization strategies as they mature, leaving their place of recruitment for later-life positions that better serve their foraging and reproduction needs (Love et al. 1991; Nelson 2001; Bassett et al. 2017). Thus, it is important to examine all water column positions within structurally complex reefs to better understand life history strategies within the environment.

Recent innovations in 360˚ video have made possible a much wider field of view than other imagery-based platforms (Kilfoil et al. 2017, Denney 2017, Whitmarsh et al. 2018, Campbell et al. 2018). Video studies to-date using 360˚ video or other expanded FOV solutions have exclusively utilized stationary methods, often in warm water (Kilfoil et al, 2017; Campbell et al. 2018; Whitmarsh et al. 2018; Auster and Giacalone 2021; Hemery et al. 2022). Increasing FOV to 360˚ has allowed for better understandings of fish-habitat interactions. Count accuracy

can increase as FOV increases (Kilfoil et al. 2017). Recording in all directions and being able to reframe *post hoc* captures observations that are less commonly seen from traditional video landers, such as shy species (Hemery et al. 2022). Less is known about how this technology works in temperate environments, typically characterized by poorer visibility and light penetration. No published literature to-date has used 360˚ video cameras to perform mobile, swimming transects, and important questions remain about the extent to which it captures common metrics such as abundance, density and species composition Further, it is unknown how any of those metrics may vary depending on the relief and/or presence of macro algae in the area being studied.

My primary goal in this study was methodological, driving me to answer two questions: 1) What are the similarities and differences between how UVC and 360˚ video capture fish counts, densities, richness, and diversity between sites? I predicted that there would be significant differences in fish counts, densities, species richness, and species diversity between sites and survey methods. Specifically, I anticipated all numeric statistics describing fish populations and communities would be greater when sampled from 360˚ video transects compared to UVC transects. 2) What are the similarities and differences between how UVC and 360˚ video capture fish counts, densities, species richness, and species diversity between habitats at the transect level? Similarly, I predicted significant differences in fish counts, densities, species richness, and species diversity between macrohabitat treatments and survey methods, and that these metrics describing fish populations would be greater from 360˚ video. My secondary goal was to test if differences in fish community composition occur between 360˚ video transects and UVC transects. I predicted there would be distinct fish communities between sites and macrohabitats, and that the two survey techniques would yield similar results between sites. This project contextualizes the use of 360˚ video transects to study demersal marine fishes in Central California. Findings are intended to provide alternate sampling options to managers seeking to survey complex rocky reefs for monitoring purposes.

MATERIALS AND METHODS

Study locations

The Monterey Peninsula represents an interesting laboratory for marine science. More than 80 years after Ed Ricketts described the Eastern Pacific's intertidal fauna in *Between Pacific Tides*, many institutions conduct interdisciplinary marine research out of the Monterey Bay. The Monterey Submarine Canyon is a nearshore canyon which intersects the shallow continental shelf within the Monterey Bay. Compared to nearby substrate, the canyon's steep walls bring access to deep water close to shore. Northerly winds drive upwelling processes and supply nutrients rich water to shallow environments along much of the California Current System (Huyer 1983; Ramp et al. 2005). The peninsula's granodiorite composition resists erosion, providing rugose and rocky habitat (Eittreim et al. 2002). Both *Macrocystis pyrifera* and *Nereocystis luetkeana* form kelp forests on the peninsula.

I conducted a field study at three sites in Carmel Bay and one site in Monterey Bay (Figure 1). These dive sites were selected for their consistent access to shore diving, probability of encountering fish, and presence of the following macrohabitat treatments: high relief with macroalgae, high relief without macroalgae, low relief with macroalgae, and low relief without macroalgae (Table 1). Within each site, multiple habitat types were present.

The Monterey Breakwater (BW) wall is an artificial reef created from large boulders piled up a steep slope. Its construction was completed in 1934 and serves as protection from waves to vessels within the Monterey harbor (Lennox 1969). A patchy forest of *Macrocystis pyrifera* exists year-round between approximately 3 – 10 meters seawater (msw). The site is located within the Edward F. Ricketts State Marine Conservation area, where fishing is allowed. Butterfly House (BFH) features a rocky reef that descends offshore. The site is characterized by high relief rock features (several to tens of meters) and patchy kelp forests. Butterfly House is located within the Carmel Bay State Marine Conservation area, where fishing for finfish is allowed. North Monastery (NMON) features a very high relief and highly rugose rocky reef that rapidly descends into a wall at some locations. The Carmel Canyon is visible from the outside of the reef, descending to greater than 50 m depth. The kelp forest is dense with a thick canopy and occurs between approximately 5 – 20 msw. Relief and rugosity are less extreme at the shallower, inshore edge of this site. Here the substrate is flat with low relief boulders and reef

providing hard substrate for macroalgae to attach. South Monastery (SMON) is separated from North Monastery by approximately 400 m of rippled sand waves. This site does not feature the vertical wall that is present at North Monastery. Instead, the reef has gradually sloping features over a longer distance. The overall relief and rugosity of South Monastery varies between low and high. A 2019 increase in sea urchin populations (primarily the Purple sea urchin *Stronglyocentrotus purpuratus*) was correlated with an almost complete destruction of the kelp forest at South Monastery. The kelp forest existed in a limited spatial range from approximately 5 – 12 msw, and the kelp forest has started to regrow since data collection ceased. Both North Monastery and South Monastery are located within the Point Lobos State Marine Reserve, where no extraction of organisms is permitted.

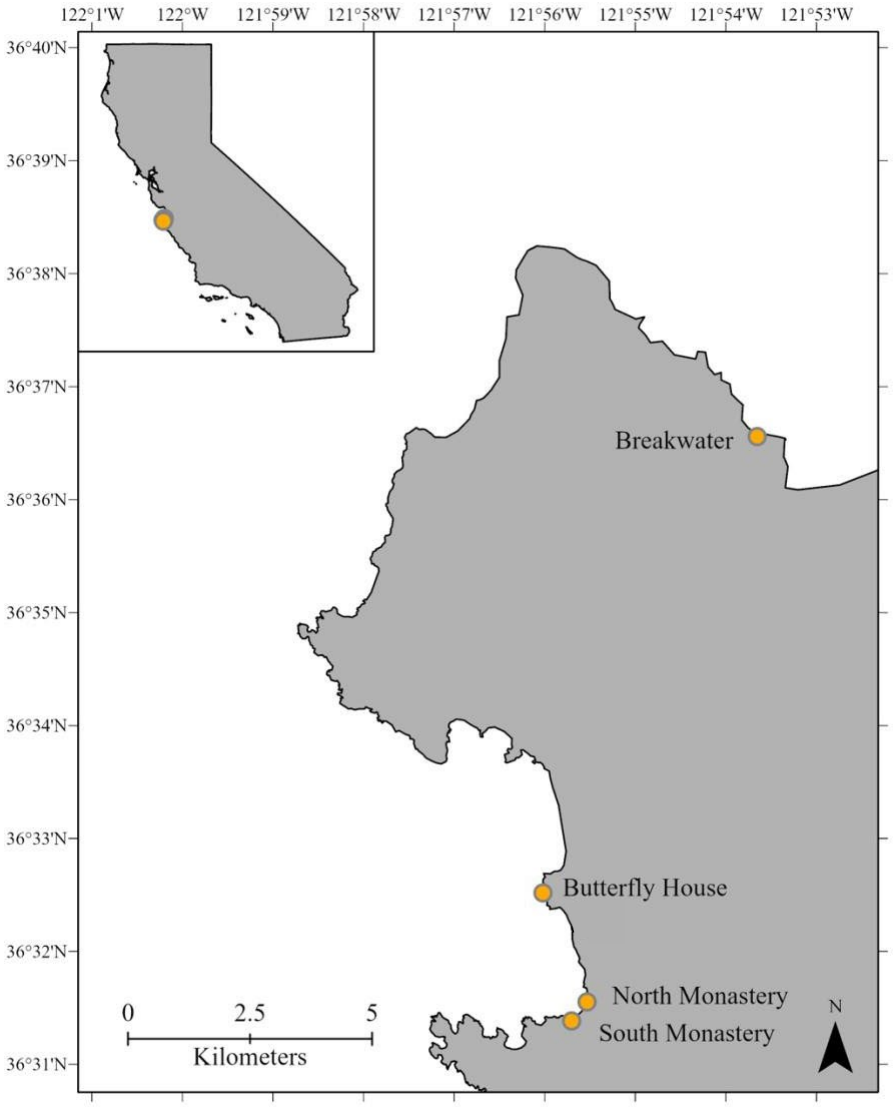

Figure 3 – Four sites were distributed along Carmel Bay and Monterey Peninsula in Central California. The inset map marks region's location within California, U.S.

Materials

I recorded 360˚ video with Insta360 ONE X and Insta360 X2 cameras (Insta360, Irvine CA, US). These models were selected for their cost, ease of use, and image quality. Both models are dual lens compact cameras which record 5.7K 360˚ video (5760 x 2880 pixels) at 30 frames per second. The presence of only two lenses, each recording one hemisphere of footage, results in only one stitch line in the final video. Differences between the two models are

primarily related to usability (battery life, encoding, etc.), and thus there are unlikely to introduce variability. Dive housings allow the ONE X and the ONE X2 to descend to depths of 98' and 147.5', respectively. Due to their design, the base of the dive housing is visible in the final footage.

Cameras were mounted to divers' slates using GoPro adhesive mounts. The camera lenses were oriented with one looking in the forward direction and one looking at the diver in the backwards direction. This minimized stitching artifacts in important areas of the frame where fish may be found. When mounted onto slates, the camera was angled so that the base of the dive housing obscured the diver and slate rather than any of the sampling volume (Figure 2). I used wide angle dive lights to illuminate the seafloor and fish in the forward direction (Light & Motion, Marina, CA). Beyond aiding with fish identification, bright wide-angle lights helped balance exposure of the dark seafloor with the bright surface of the water. I found this important due to the inability to monitor and adjust exposure settings when the cameras were in their dive housings. Divers also carried 30 m fiberglass transect tapes, which were the sampling unit used to constrain transects.

Figure 2 – Insta360 X2 attached to a PVC dive slate with a datasheet. This configuration allowed UVC and 360˚ video data to be collected simultaneously.

Field methods

All diving occurred within 70' depth on SCUBA whilst breathing air. Using 100 cf SCUBA cylinders, I usually completed six transects per dive. The beginnings and ends of transects were separated by at least ten horizontal meters. Before data collection, two divers measured visibility by swimming apart and extending a transect tape, writing the distance at which the second diver was no longer visible. The slate-mounted 360˚ camera recorded this process so that analysts could estimate visibility as rendered from video. At the beginning of each transect, the lead diver recorded time of day and depth, and started a video recording on their slate-mounted camera. Then they swam a straight line while unspooling the 30 m transect, only diverting their heading if there was a tall obstacle that would require more than a 3 m change in depth. Swimming speed was fixed at approximately 10 $m*min^{-1}$, so each 30 m transect was three minutes in duration. As the 360˚ camera recorded fish observations in all directions, the diver wrote species names and counts for all identifiable fish within a 2x2 m swath. This volume was chosen to match the level of effort that divers from PISCO undertake. Only fish within the diver's swath in the forward direction were included. An assumption of the UVC data collection was that individual fish did not swim around the diver and return to the front of the swath. Unlike many UVC methods, divers did not estimate fish length because there is no way to also derive length from monoscopic 360˚ video.

Lab methods

360˚ video was edited using Insta360 Studio and Adobe Premiere Pro. I first used Insta360 Studio to convert camera files into a format that Premiere Pro could edit. I exported videos from Insta360 Studio in the highest native resolution and bitrate to reduce the loss of data. With the converted files in Premiere Pro, I added title cards before the start of each transect to display pertinent information such as the transect number, time of day, and depth. Using the *VR Rotate Sphere* effect, I manually keyframed rotational changes to keep the video's direction stable and pointed forward. I added *Lumetri Color* to correct exposure and white balance with the intent of preserving natural conditions of the dive. This usually involved raising the shadows slider and pushing the tint slider towards magenta. The color corrected video had less contrast and more realistic colors.

I exported two versions of 360˚ transects: equirectangular planar video and full-sphere 360˚ video. The only difference between these two formats was viewing projection. Equirectangular planar (EP) video is a projection that fits 360˚ video onto a flat 2:1 aspect ratio plane. Similar to challenges associated with projecting a globe onto a flat surface, EP video suffers from distortion at the top and bottom edges of the frame (Figure 3). The benefit of EP video is the ability to see the entire 360˚ view at once without needing to reframe. Full-sphere 360˚ (FS) video is a spherical video format where the viewers watch from "inside" the sphere. It features minimal projection distortion but only shows a limited FOV at a time. Viewers must use computer inputs to rotate the sphere and reframe the video. While appearing more natural, reviewing video this way is significantly slower and does not utilize the benefits of 360˚ video.

Figure 3 – Equirectangular planar (EP) 360˚ video (above) and full-sphere (FS) 360˚ video (below) provide different viewing experiences. EP video was primarily used for video analysis, switching to FS video if fish were at the extreme edges of the frame.

I extracted data from EP video using SeaGIS EventMeasure software (SeaGIS Pty Ltd, Victoria, Australia). EventMeasure can record three-dimensional information as points in space and time while reviewing video. During video review, EventMeasure did not have capabilities to review 360˚ video in 360˚ projections, so footage was automatically displayed as a 2:1 equirectangular planar projection. Within EventMeasure, I placed points on every fish in the forward direction of transects, similar to how fish were counted *in situ* via UVC. EventMeasure

points are non-spatial placeholders of information that cannot be used to estimate distances or sizes, but are helpful for keeping running counts of observations.

While reviewing video, each 30 m transect was assigned into a macrohabitat category: High_Kelp, High_None, Low_Kelp, or Low_None (Table 1). I paused video transects at 15 second intervals and estimated the general relief ("High", "Low") and macroalgal cover ("Kelp", "None") at that point. Vertical relief less than 2 m was quantified as "Low relief", and vertical relief greater than 2 m was quantified as "High relief". The most commonly occurring relief and macroalgae codes during the 30 m transect were assigned as the macrohabitat treatment to the entire 30 m transect. If a tie occurred, I assigned relief as "high" rather than "low", and macroalgae as "present" rather than "not present". This is because structure forming, high relief features can attract and harbor organisms from afar. Thus, I believe the fish community on transects with equal parts high relief and low relief were more representative of high relief. This treatment, as determined from video, was also applied to the corresponding UVC data from that transect.

Table 2 – The presence of macrohabitats at each study site. Gray boxes represent macrohabitats that were unavailable or unsampled at the site. Due to high habitat heterogeneity along the Monterey Peninsula, each site contained several macrohabitats.

	Sites			
	BW	BFH	NMON	SMON
Macrohabitats	High_Kelp	High_Kelp	High_Kelp	High_Kelp
	High_None	High_None	High_None	High_None
	Low_Kelp	Low_Kelp	Low_Kelp	Low_Kelp
	Low_None	Low_None	Low_None	Low_None

I identified each individual to the lowest possible taxonomic level. If I believed an individual was a certain species based on intuition, but the identification could not be verified, a "best guess" identification was recorded in a separate data column next to the conservative, higher taxonomic identification. One example of this is the species *Chromis punctipinnis*, a damselfish species that often forms active schools in the water column and kelp canopy layer. Although often silhouetted on camera, their position in the water column and behavior strongly suggested that they were *C. punctipinnis.* Similar to the assumptions of UVC data collection, I

assumed that observed fish did not swim back to the front of the camera's view, and instead remained in their parcels of water in which they were first observed. 360˚ video allows me to confirm by following the path of a fish to the edge of visibility after its initial time of encounter. This benefit reduced the chances of double counting individuals. I used VLC Media Player to view the FS version of the transects when individuals were in the extreme top and bottom of the frame and affected by distortion. After confirming the identification in the FS view, I returned to the EP view in EventMeasure and created the respective points.

After video analysis in EventMeasure, data were exported as text files and formatted in Microsoft Excel. To understand the similarities and differences with which UVC and 360˚ video survey different zones of temperate rocky reefs, I binned species *post hoc* into habitat guilds based on their understood habitat associations within temperate rocky reefs in Central California (Table 2). These habitat guilds ("Canopy", "Demersal", and "Benthic") were based on published life history information for each species, augmented by my direct observations. Canopy species were defined as those that are likely to be found swimming in the upper ½ of the water column. Demersal species were defined as those found in the lower ½ of the water column. Benthic species were defined as those likely to be found on or very near the substrate. Binning species into these guilds allowed comparisons with broader appeal beyond any one species that I observed.

Table 3 – Species were binned into guilds based on their anticipated position within the water column.

Guild	**Species**
Canopy	Black rockfish; Blacksmith; Blue rockfish; Kelp perch; Opaleye
Demersal	Black perch; Copper rockfish; Kelp rockfish; Olive rockfish; Pile perch; Striped perch
Benthic	Black and yellow rockfish; Blackeye goby; Cabezon; Gopher rockfish; Kelp greenling; Lingcod; Painted greenling; Treefish

Statistical framework

It was expected that UVC and 360˚ video would survey different volumes of water. Density (individuals * m^{-3}) for UVC and 360˚ video was calculated using the volume of water sampled by each technique. UVC data was collected within a 2 m * 2 m * 30 m swath (120 m^3 * $transect^{-1}$). More challenging, the volume measured by 360˚ video transects was calculated as a 30 m cylinder with a half sphere at the end (Figure 4). I used the visibility that I measured at the beginning of each dive to serve as the radius of both the 30 m cylinder and the half sphere for all transects during the dive. Because transects occurred at one meter elevation above the seafloor, this volume was multiplied by 0.6 to prevent inflating the volume with space below the seafloor that was not studied. I created the following equation to estimate the volume of 360˚ video transects:

$$V_{360} = (6/10)[(30\pi r^2)+((1/2)(4/3)\pi r^3)].$$

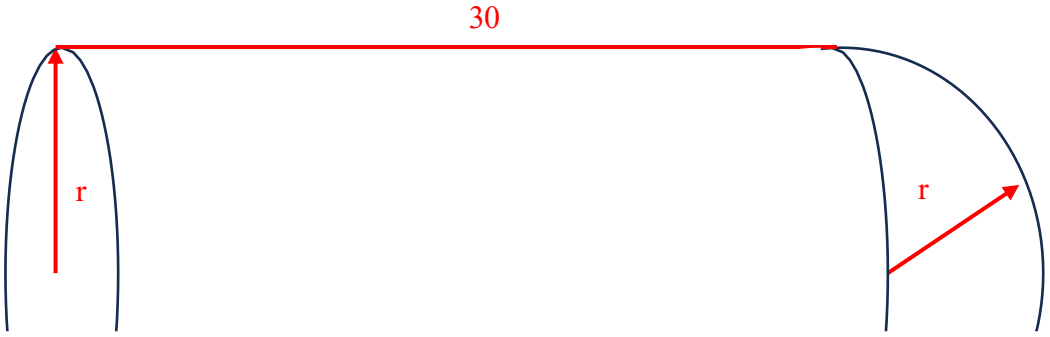

Figure 4 – Graphic representation of the volume of water surveyed sampled during a 30 m 360˚ video transect. The length of the cylinder was 30 m, and the radius (r) of the both the cylinder and the sphere was the visibility as measured with a transect tape.

I also represented density as count per meter (CpM) by dividing the total number of individuals per transect by 30 meters. CpM did not account for the true volume of water sampled by either tool, but instead provided a relative estimate of abundance standardized by the same linear distance of seafloor covered by either technique.

The differences in density and CpM of all taxa combined across sites and macrohabits, as well as between methods, were examined with Mann-Whitney U tests. Subsequent analyses only used CpM when an unforeseen challenge arose with density calculations. CpM was also rank transformed using the datawizard package in RStudio to achieve homogeneity of variances amongst residuals, an assumption of the two-way ANOVA tests I later performed. Species richness was calculated as the maximum number of unique species per transect. Diversity was calculated in RStudio with the vegan package using the Shannon-Weiner index based on counts of individuals for each transect and each technique.

To answer Question 1 (what are the similarities and differences with which UVC and 360˚ video transects survey fish across sites), I performed two-way analysis of variance (ANOVA) tests (one each for species richness, Shannon-Weiner diversity, density, and count per meter) to test how UVC data and 360˚ video data differ between sites. I included the effect of site, the effect of survey method, and the interaction between site and survey method. When the interaction between site and survey method was greater than $p = 0.25$, I removed the interaction term and reran the two-way ANOVA. Significant results were explored with Tukey's Honestly Significant Difference test (Abdi and Williams 2010).

I also investigated the similarities and differences with which UVC and 360˚ video transects survey fish across macrohabitats with a series of two-way ANOVAs (one each for species richness, Shannon-Weiner diversity, density, and count per meter). I included the effect of macrohabitat treatment, the effect of survey method, and the interaction between macrohabitat treatment and survey method. The interaction term was dropped and the two-way ANOVA rerun without it if it was greater than $p = 0.25$. Significant results were explored with Tukey's Honestly Significant Difference test.

I plotted CpM and density against visibility to test whether visibility affected counts from UVC or 360˚ video. To address my second goal (are the observed fish communities a result of sites or the macrohabitats within sites), I used CpM calculated for each method to create Bray-Curtis non-metric multidimensional scaling ordination (nMDS) plots which helped visualize relationships between species abundances, macrohabitat treatments, and sites (Clarke 1993; Dexter et al. 2018). I used the 'envfit' function within the vegan package to quantify which species drove the patterns observed between sites and between macrohabitats, referred to as intrinsic variables. I plotted significant taxa as vectors on the nMDS plot results to visually determine which species drove the observed differences in CpM.

RESULTS

Overall, a total of 149 transects were completed across the four study sites – 44 at BW, 11 at BFH, 55 at NMON, and 39 at SMON. Each of the four macrohabitats were surveyed by at least one transect at BW and SMON. Three out of the four macrohabitats were surveyed at BFH and NMON. Across the four sites, a total of 3462 fish observations (from 26 species and 4 species complexes) were made with UVC, and 4820 fish observations (across 25 species and 8 species complexes) were made with 360˚ video (Table 3). The range of fishes observed per 30 m transect ranged from 0 individuals to 297 individuals. UVC methods surveyed a total volume of 16,000 m^3, and 360˚ video methods surveyed 1,149,737.5 m^3. The average visibility across all transects was 9.8 m.

Table 3 – Mean count per transect of each fish taxa across sites and between survey methods. Most individuals were identified to the species level, although some were only identifiable to genus or family.

Fish ID	Taxonomic level	Site and method							
		BFH		BW		NMON		SMON	
		360˚	UVC	360˚	UVC	360˚	UVC	360˚	UVC
Black and yellow rockfish	Species	0	0	0	0	2	1	1	1
Black perch	Species	1.333	1.333	2	1.467	2	2	1	1
Black rockfish	Species	1	1	0	0	0	1	1	1
Blackeye goby	Species	0	2	6	3.5	1	1	5	2
Blacksmith	Species	0	0	28.519	15.583	0	0	0	0
Blue rockfish	Species	32.667	9	8.167	12.111	15.481	6	6.933	3.111
Cabezon	Species	0	0	0	1	0	0	1	1
California sheephead	Species	0	0	1	1	0	0	0	0
Canary rockfish	Species	0	0	0	0	0	0	0	1
Copper rockfish	Species	0	0	0	0	1	1	1.5	1.333
Gopher rockfish	Species	0	0	0	0	1	1.2	1.167	1.167
Kelp bass	Species	0	0	1.333	1.5	0	0	0	0
Kelp greenling	Species	0	0	0	0	1.25	1	1	1
Kelp perch	Species	0	0	3	2	3	1.75	1	0
Kelp rockfish	Species	0	1	0	0	2.694	2.029	1	1.111
Lingcod	Species	1	0	1	1	1	1	0	0
Olive rockfish	Species	1	1	2.571	1.8	1.125	1	2	1.545
Opaleye	Species	0	0	3.333	1	0	0	0	0
Painted greenling	Species	1	1	3	2.737	2.133	2.095	2	1.833
Pile perch	Species	1.333	1	3.1	2.667	1.857	2.182	0	1
Pink perch	Species	0	0	0	0	1	0	0	0
Pipefish	Genus	0	0	0	0	0	1	14	0
Rubberlip perch	Species	0	0	0	1	0	0	0	0
Sargo perch	Species	0	0	0	1	0	0	0	0
Senorita wrasse	Species	0	0	0	0	0	0	5.5	0
Striped perch	Species	0	1.25	1	1.571	1.182	1.609	1	1.429
Treefish	Species	0	0	0	0	0	0	1	0
Tube snout	Species	0	0	0	0	0	0	0	5
Unidentified fish	N/A	1	0	24.167	0	1	0	29	0
Unidentified greenling	Family	0	0	0	0	0	0	1	0
Unidentified perch	Family	1.25	0	1.667	0	1.091	1.333	1.333	0
Unidentified prickleback	Family	0	0	0	0	1	0	0	0
Unidentified rockfish	Genus	3.5	0	5	0	14.64	0	18.4	0
Unidentified sculpin	Family	0	0	0	1	1	1	0	0
Vermilion rockfish	Species	0	1	0	0	0	0	1.5	1.5
Wolf eel	Species	0	0	0	0	0	0	1	1
YOY rockfish	Genus	18	18.111	14.958	17.667	27.429	20.308	14.56	14.424

A two-way ANOVA demonstrated significant differences in total species richness between sites ($F_{3,272} = 4.251$, $p = 0.0059$), but not between methods ($F_{1,272} = 0.016$, $p = 0.90$). The most significant differences in species richness occurred between SMON and NMON (Tukey's $p < 0.05$) followed by differences between SMON and BW (Tukey's $p = 0.054$). These data suggest species richness was significantly lower at SMON compared to the other sites (Figure 5A). Differences in Shannon-Weiner diversity were neither significant between sites ($F_{3,272} = 2.449$, $p = 0.064$), or between methods ($F_{1,272} = 0.890$, $p = 0.35$) (Figure 5B).

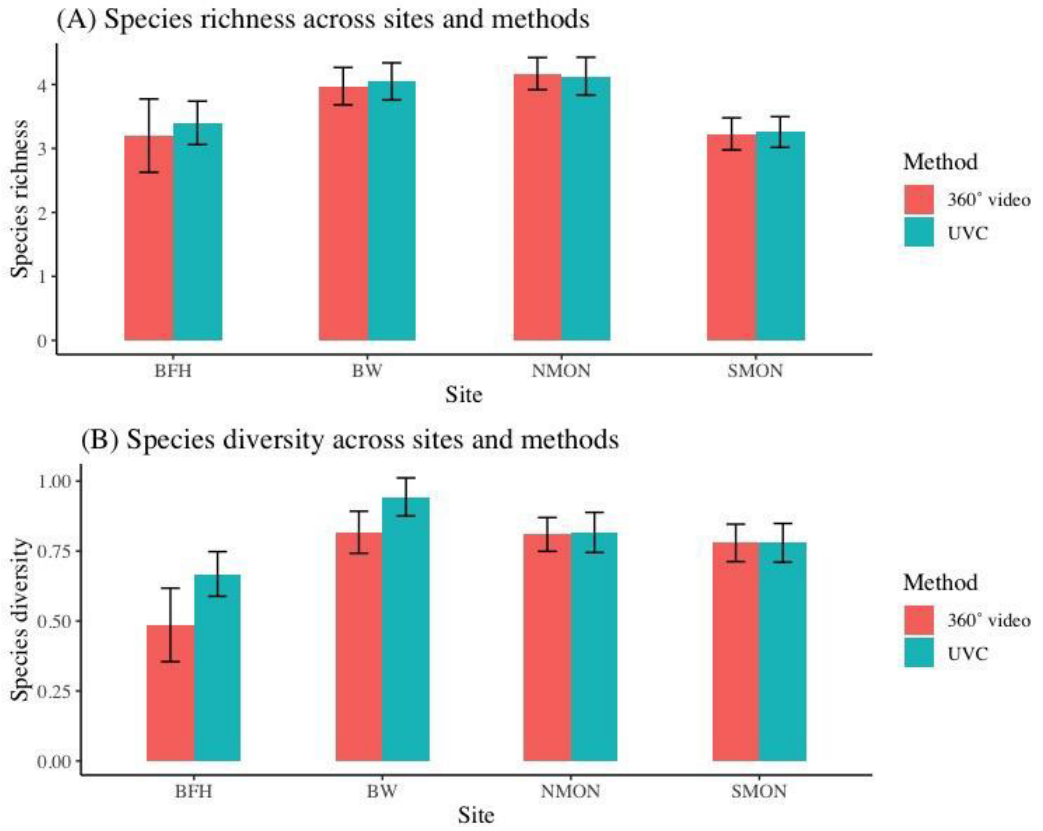

Figure 5 – Species richness (A) and Shannon-Weiner diversity (B) across sites and between methods. Error bars represent ± 1 standard error.

There were significant differences in total species richness between macrohabitats ($F_{3,272} = 11.845$, $p < 0.001$), but not methods ($F_{1,272} = 0.005$, $p = 0.94$). A Tukey's Honest Significant Difference test revealed significant differences in species richness between High_None and High_Kelp macrohabitats (Tukey's $p < 0.01$), Low_Kelp and High_Kelp macrohabitats (Tukey's $p < 0.001$), and Low_None and High_Kelp macrohabitats (Tukey's $p < 0.001$). These results

indicate that High_Kelp macrohabitats, where species richness was significantly greater, was the driver for these differences (Figure 6A).

There were also significant differences in Shannon-Weiner diversity between macrohabitats ($F_{3,272} = 7.138$, $p < 0.001$), but not methods ($F_{1,272} = 0.653$, $p = 0.42$). There were significant differences in mean Shannon-Weiner diversity between the High_None and High_Kelp macrohabitats (Tukey's $p < 0.01$), between Low_Kelp and High_Kelp macrohabitats (Tukey's $p < 0.05$), and between Low_None and High_Kelp macrohabitats (Tukey's $p < 0.01$). Similar to species richness, the High_Kelp macrohabitats drove the differences in Shannon-Weiner diversity (Figure 6B). High_Kelp had the greatest mean Shannon-Weiner diversity (0.95) and Low_None had the lowest mean Shannon-Weiner diversity (0.61).

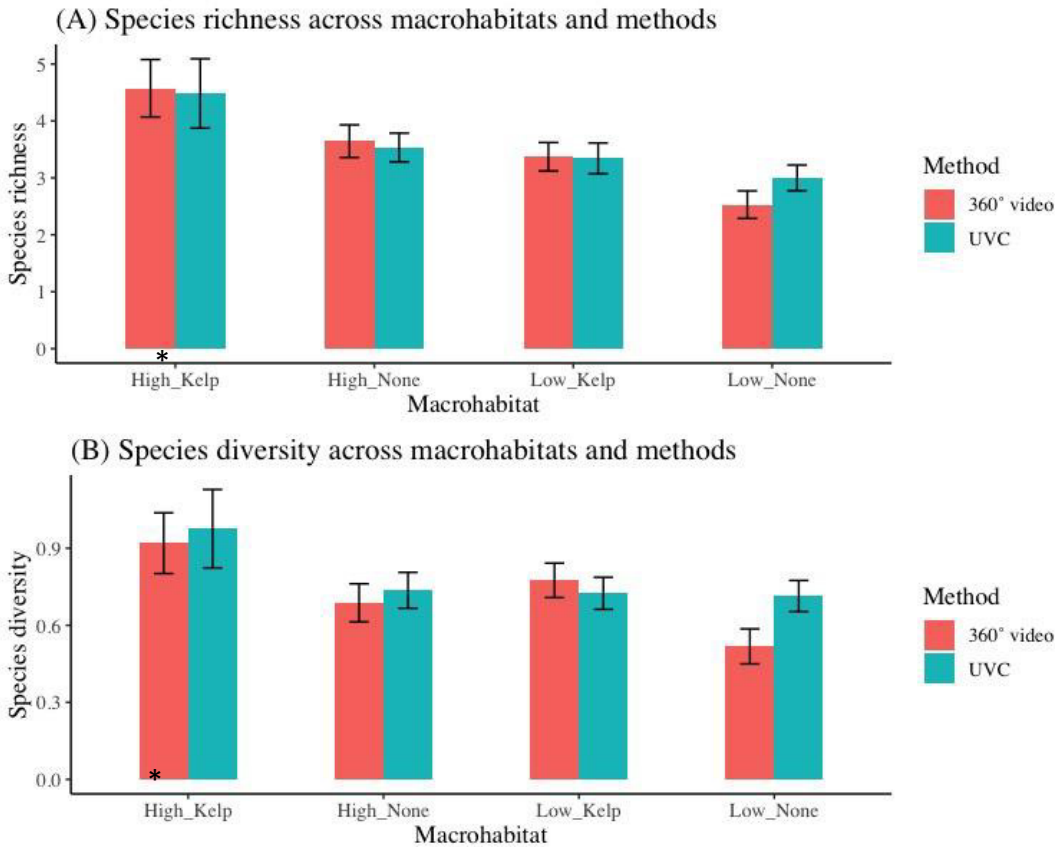

Figure 6 – (A) species richness and (B) Shannon-Weiner diversity between sites. Bars are colored by method. Error bars represent ± 1 standard error.

Marked differences were observed in density between UVC and 360˚ video. Always, there were significantly greater densities from UVC compared to 360˚ video, even though counts

between the two methods were similar (Figure 7). This trend held true while investigating the effects of both site ($F_{1,1069} = 108.143$, $p < 0.001$) and macrohabitat ($F_{1,1069} = 108.27$, $p < 0.001$). This result halted the progress of using density to compare the two methods because the difference was so extreme. Thus, subsequent analyses were instead considered with count per meter (CpM) for 360˚ video and UVC analyses.

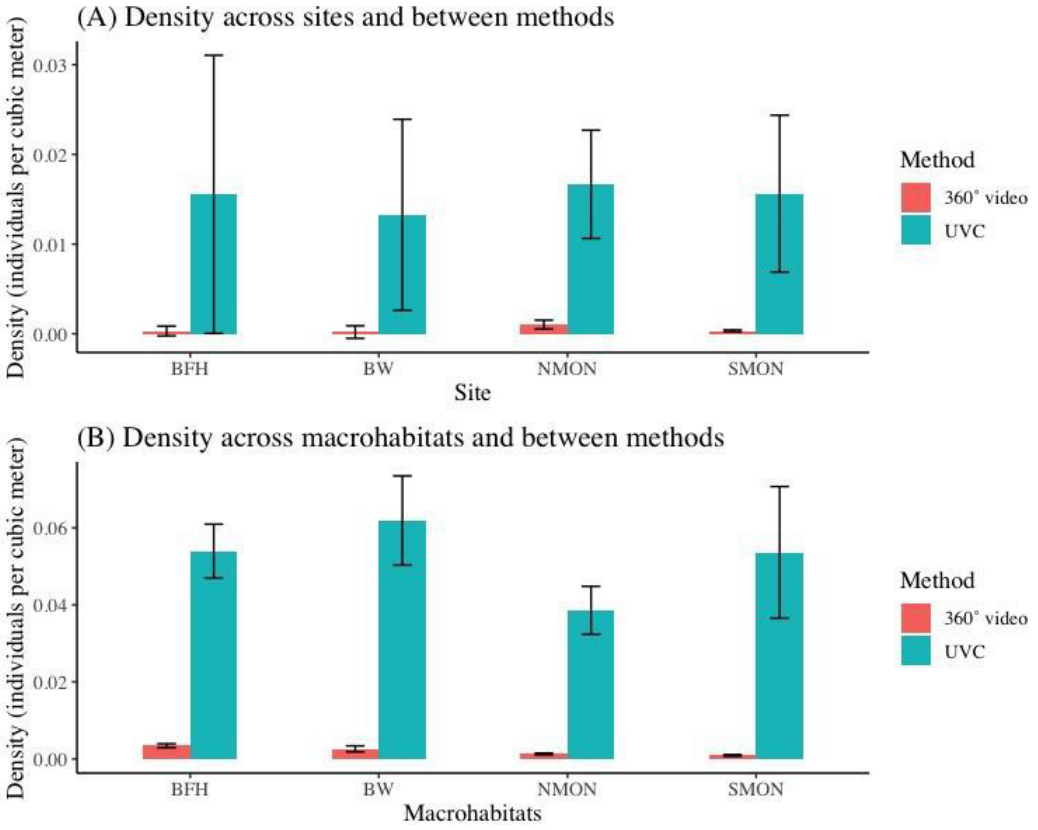

Figure 7 – Density of fishes (A) between sites and (B) between macrohabitats. Bars are colored by method. Error bars represent ± 1 standard error. Density measured via 360˚ video was so small that it was almost imperceptible when plotted with UVC density.

CpM was greater from 360˚ video for nearly all taxa (Table 4). For example, mean Blacksmith CpM was 0.951 from 360˚ video and 0.519 from UVC. The largest differences in mean CpM were observed with Blacksmith (0.431 more via 360˚ video) and unidentified rockfish (0.448 more via 360˚ video).

Table 4 – Mean CpM of fish taxa between methods.

Fish ID	360˚ video	UVC	Fish ID	360˚ video	UVC
Black and yellow rockfish	0.053	0.038	Pile perch	0.088	0.079
Black perch	0.061	0.049	Pink perch	0.033	0.000
Black rockfish	0.033	0.033	Pipefish	0.467	0.033
Blackeye goby	0.122	0.068	Rubberlip perch	0.000	0.033
Blacksmith	0.951	0.519	Sargo perch	0.000	0.033
Blue rockfish	0.437	0.240	Senorita wrasse	0.183	0.000
Cabezon	0.033	0.033	Striped perch	0.038	0.051
California sheephead	0.033	0.033	Treefish rockfish	0.033	0.000
Canary rockfish	0.000	0.033	Tube snout	0.000	0.167
Copper rockfish	0.044	0.038	Unidentified fish	0.683	0.000
Gopher rockfish	0.036	0.040	Unidentified greenling	0.033	0.000
Kelp bass	0.044	0.050	Unidentified perch	0.045	0.044
Kelp greenling	0.040	0.033	Unidentified prickleback	0.033	0.000
Kelp perch	0.094	0.061	Unidentified rockfish	0.448	0.000
Kelp rockfish	0.082	0.061	Unidentified sculpin	0.033	0.033
Lingcod	0.033	0.033	Vermilion rockfish	0.050	0.047
Olive rockfish	0.060	0.046	Wolf eel	0.033	0.033
Opaleye	0.111	0.033	YOY rockfish	0.662	0.589
Painted greenling	0.076	0.077			

After species were binned into their functional guilds, a Mann-Whitney U test showed that mean CpM from 360˚ video was significantly greater than UVC within the canopy guild ($U = 6250.5$, $p = 0.0077$). Mean CpM of the canopy guild from 360˚ video was nearly double that of UVC (Table 5). The differences in mean CpM between 360˚ video and UVC for the demersal guild ($U = 14736$, $p = 0.71$) and the benthic guild ($U = 3355$, $p = 0.83$) were not significant.

Table 5 – Mean CpM of fish guilds between methods.

Guild	**360˚ video**	**UVC**
Canopy	0.560	0.294
Demersal	0.069	0.057
Benthic	0.062	0.061

Across all taxa, there were significant differences in CpM both across sites ($F_{3, 1069}$ = 5.787, $p < 0.001$) and between methods ($F_{1, 1069}$ = 4.749, $p = 0.030$). Across sites, significant differences in CpM occurred between SMON and BW (Tukey's $p = 0.0055$) and between NMON and BW (Tukey's $p < 0.01$). These significant differences were driven by greater CpM at BW compared to the other sites (Figure 8). Between methods, 360˚ video recorded significantly greater counts per meter than UVC.

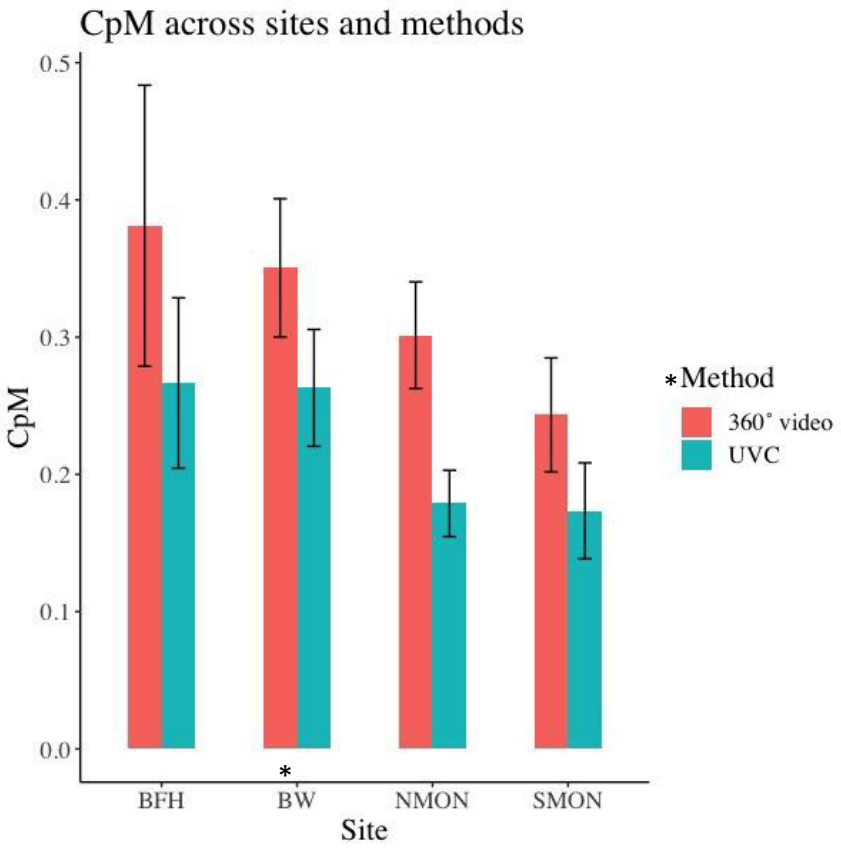

Figure 8 – Bars represent CpM for all species combined across four sites and are colored by method. Error bars represent ± 1 standard error.

Canopy guild CpM was significantly different between sites ($F_{3, 198}$ = 5.385, $p < 0.005$) and almost significantly different between methods ($F_{1,198}$ = 3.669, $p = 0.056$). Significant differences occurred between SMON and BFH (Tukey's $p < 0.05$) and between SMON and BW (Tukey's $p < 0.005$). Canopy guild CpM was significantly lower at SMON compared to these other sites (Figure 9A). There were significant differences in the CpM of demersal guild species

between sites ($F_{3,337} = 3.540$, $p = 0.015$), but not between methods ($F_{1,337} = 0.267$, $p = 0.606$). CpM of demersal guild species at BW was significantly greater than at SMON (Figure 9B). It is important to qualify that the rank-transformed CpM did not yield homogeneity of variances between CpM of the demersal guild. (Levene's test, $F_{3,338} = 3.5479$, $p = 0.0148$). And benthic guild species experienced significant differences in the CpM between sites ($F_{3, 165} = 4.523$, $p = 0.0045$), but not between methods ($F_{1,165} = 0.659$, $p = 0.42$). Significant differences in rank-transformed CpM occurred between NMON and BW (Tukey's $p < 0.05$) and between SMON and BW (Tukey's $p < 0.05$). CpM of benthic guild species were significantly greater at BW than these other two sites (Figure 9C).

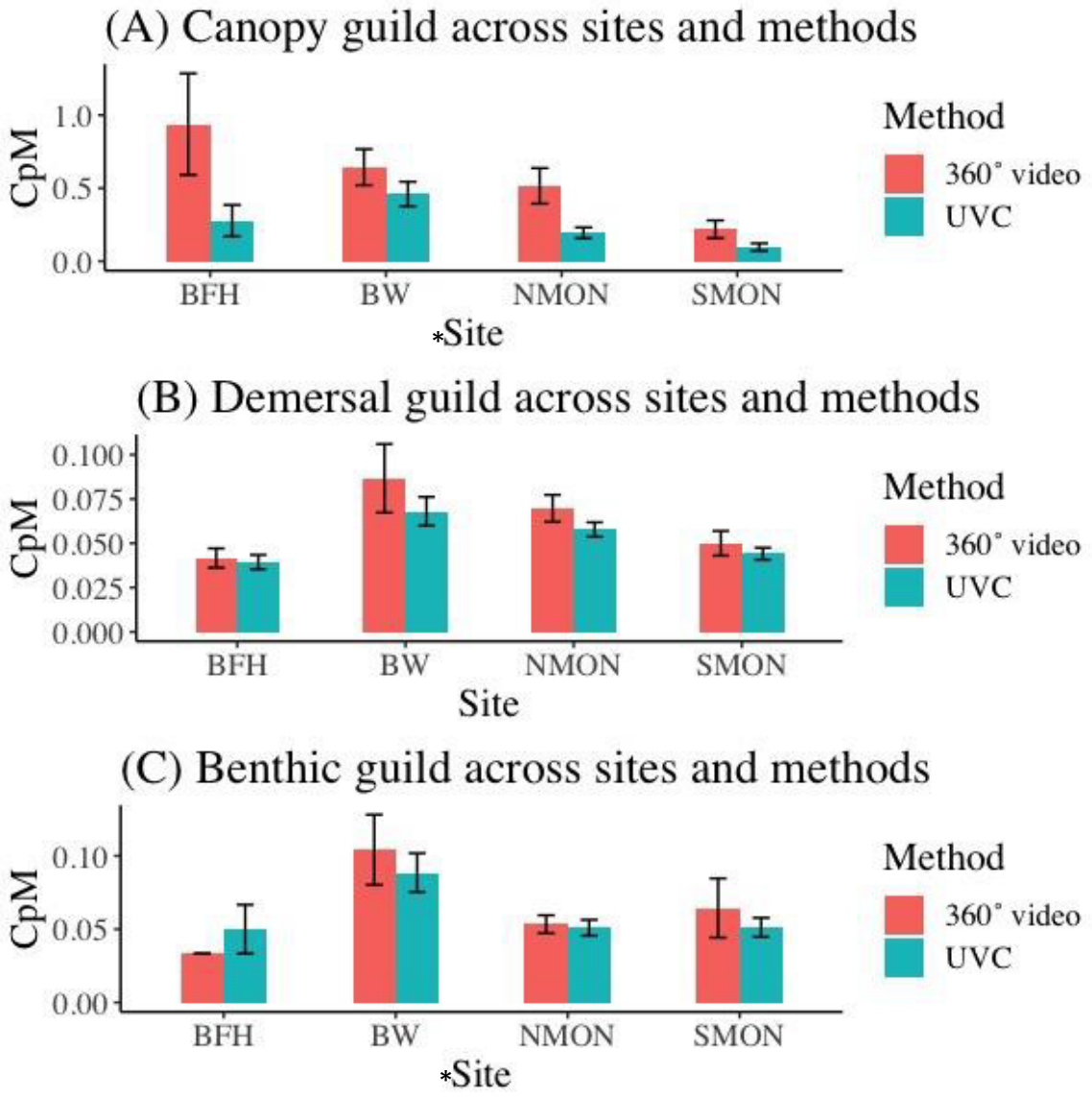

Figure 9 – Bars represent CpM across sites for (A) canopy-guild species, (B) demersal-guild species, and (C) benthic-guild species. Bars are colored by method. Error bars represent ± 1 standard error.

There were no signifcant differences in total CpM of all species across macrohabitats ($F_{3,1069} = 1.059$, $p = 0.37$), but were significantly different again between methods ($F_{1,1069} = 4.668$, $p = 0.031$). CpM was significantly greater from 360˚ video methods than UVC methods (Figure 10).

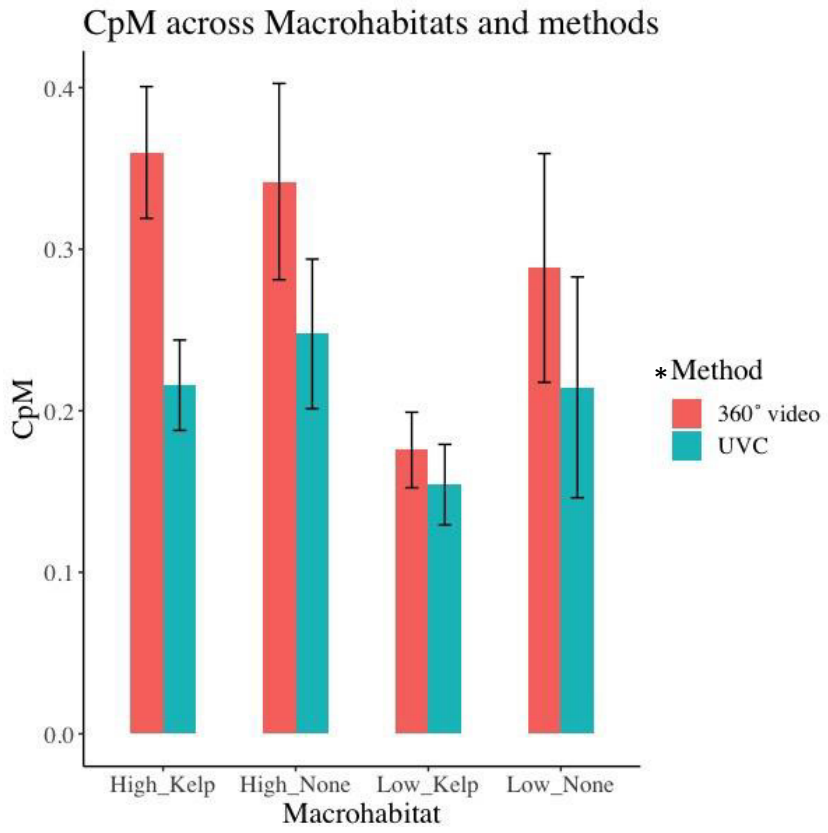

Figure 10 – Bars represent CpM for all species combined across four macrohabitats and are colored by method. Error bars represent ± 1 standard error.

There were marginally non-significant differences in canopy fish CpM between methods ($F_{1,198} = 3.657$, $p = 0.057$), and no significant differences in canopy fish CpM between macrohabitats ($F_{3,198} = 0.535$, $p = 0.66$) (Figure 11A). Another two-way ANOVA showed no significant difference in CpM of demersal fish between macrohabitats ($F_{3, 337} = 0.379$, $p = 0.77$) or methods ($F_{1, 337} = 0.279$, $p = 0.60$). Like the canopy-guild, CpM was similar across methods and macrohabitats for the demersal guild (Figure 11B). Finally, there were no significant differences in CpM of benthic-guild species between macrohabitats ($F_{3, 165} = 0.911$, $p = 0.44$) or

methods ($F_{1, 165} = 0.070$, $p = 0.79$) (Figure 12C). These combined results indicate that habitat features do not contribute to significant differences in CpM.

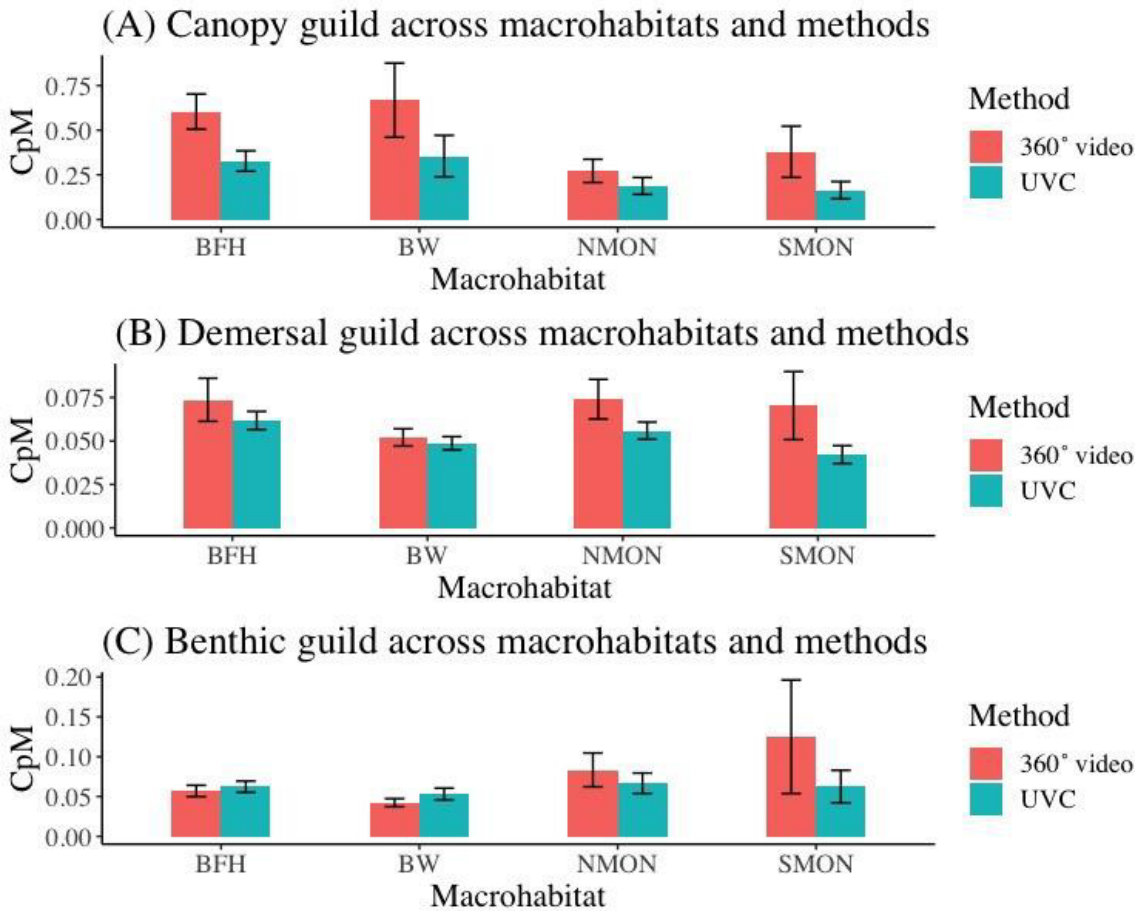

Figure 11 – Bars represent CpM across habitats for (A) canopy-guild species, (B) demersal-guild species, and (C) benthic-guild species. Bars are colored by method. Error bars represent ± 1 standard error.

With all sites combined, CpM from 360˚ video was negatively correlated with visibility while CpM from UVC was positively correlated with visibility (Figure 12). However, a linear regression suggessts these correlations were not significant ($F_{1,275} = 0.3224$, $p = 0.56$). R^2 values for both methods suggest that the generated trendlines were poor fits for the data.

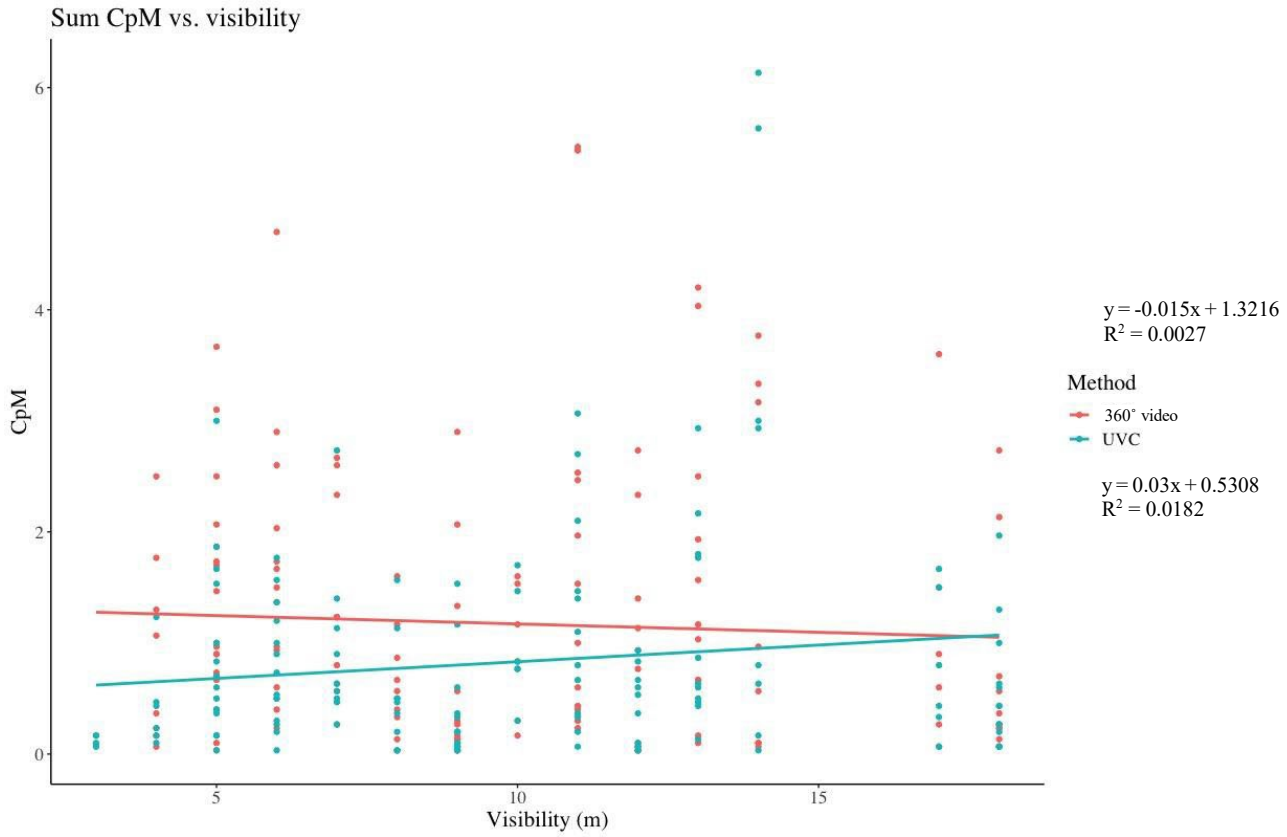

Figure 12 – CpM plotted against visibili1ity for 360˚ video transects and UVC transects.

Ordination patterns can be deduced visually from the nMDS plots. At the scale of the Monterey Peninsula, there were many similarities in the community composition of transects between methods. The vast majority of UVC transects and 360˚ video transects overlapped within their counterpart's 95% confidence intervals (Figure 13), suggesting that both methods surveyed the same fish community structure.

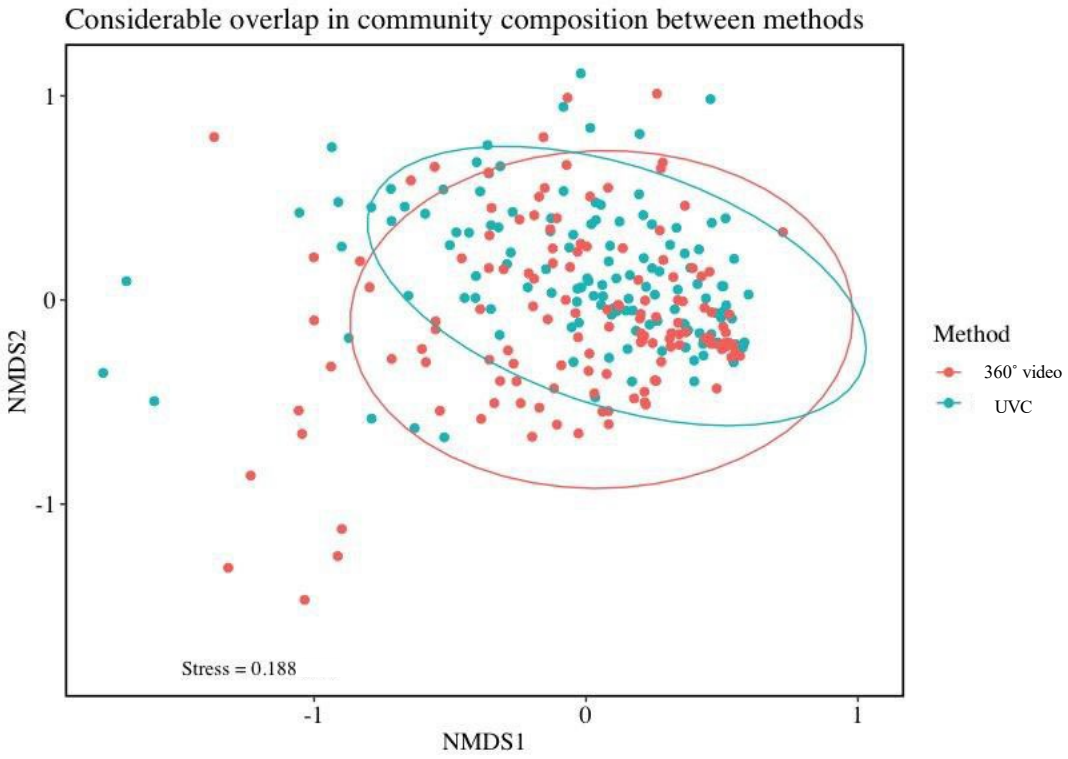

Figure 14 – Results of nMDS analysis for CpM of all species across without dinstinguishing between site or macrohabitat. Points represent individual transects and ellipses represent 95% confidence intervals. Data were ordinated in three dimensions and plotted as (x, y) coordinated for NMDS1 and NMDS 2. Transects are colored by method.

With the data parsed at finer scales, transects still showed a high amount of overlap in community composition between sites and between macrohabitats (Figure 14). Still, there were strong similarities in the way species that were significant drivers of the nMDS ordination are listed in Table 6 and Table 7. The species most responsible for driving UVC transect ordination were Pile perch and Blackeye gobies. Ordination of 360˚ video transects, on the other hand, were most influenced by Blacksmith and Kelp rockfish. The most abundant species between both methods was Blue rockfish, followed by Blacksmith and Kelp rockfish. There wasn't any one species that was a strong driver of community composition over the rest, suggesting that the communities at these four sites and habitats were robust.

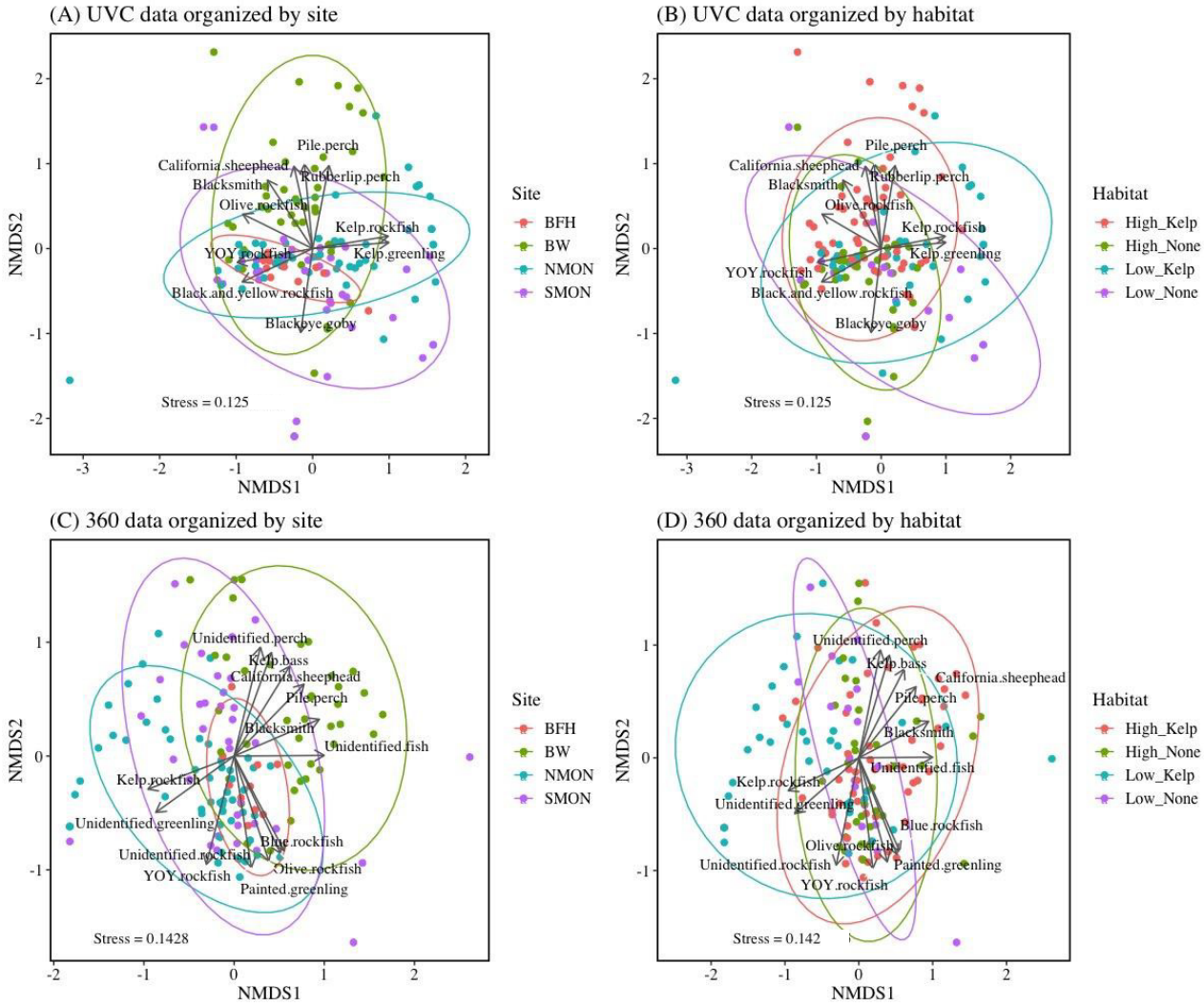

Figure 14 – Results of nMDS analysis for CpM of fish species. Points represent individual transects and ellipses represent 95% confidence intervals. Transects are colored by A) UVC site, B) UVC macrohabitat, C) 360˚ site, and D) 360˚ macrohabitat. All plots were ordinated in three dimensions and plotted as (x,y) coordinates for NMDS 1 and NMDS 2. Vectors with longer lengths indicate species that are strong predictors.

Table 6 – Taxa that significantly contributed to the ordination of UVC transects across sites and macrohabitats.. The r^2 value describes the correlation between species CpM and the transects in which they were present.

Species	r^2	p - value
Black and yellow rockfish	0.0782	0.007
Blackeye goby	0.1370	0.002
Blacksmith	0.0929	0.007
California sheephead	0.0530	0.036
Kelp greenling	0.0448	0.045
Kelp rockfish	0.1246	0.002
Olive rockfish	0.0719	0.008
Pile perch	0.1459	0.001
Rubberlip perch	0.0661	0.019
YOY rockfish	0.3325	0.001

Table 7 – Taxa that significantly contributed to the ordination of 360˚ video transects across sites and macrohabitats. The r^2 value describes the correlation between species CpM and the transects in which they were present.

Species	r^2	p - value
Blacksmith	0.2571	0.001
Blue rockfish	0.0635	0.010
California sheephead	0.0737	0.010
Kelp bass	0.0536	0.028
Kelp rockfish	0.1631	0.001
Olive rockfish	0.0552	0.023
Painted greenling	0.0721	0.008
Pile perch	0.0570	0.027
Unidentified fish	0.0930	0.002
Unidentified greenling	0.0544	0.022
Unidentified perch	0.0642	0.011
Unidenfitied rockfish	0.0816	0.004
YOY rockfish	0.3732	0.001

DISCUSSION

This study indicated that 360˚ video surveyed components of rocky reef communities similarly to traditional underwater visual census SCUBA surveys. At the fish-habitat guild level, counts of species were similar between methods at all macrohabitats and most sites. 360˚ video and UVC produced similar results with respect to species richness and diversity. Differences between the methods arose by looking at density at any scale, as well as total count per meter of all fishes. These results suggest that with some caveats, 360˚ video transects can be incorporated into temperate subtidal reef monitoring without compromising data quality.

In the context of the methodological comparison, species richness and diversity are useful information for comparing spatial and temporal community trends (Danet et al. 2021). There were significant differences in species richness between sites, species richness between macrohabitats, and Shannon-Weiner species diversity between macrohabitats. But survey method, whether from 360˚ video or diver-collected UVC, never had a significant impact on species richness or diversity. So, 360˚ video transects can complement visual surveys on temperate subtidal reefs. Based on my results, species richness and diversity data collected from future 360˚ video transects can be compared to historic long-term datasets collected via UVC. Now that the efficacy of 360˚ video has been demonstrated for richness and diversity of demersal fishes, future work can investigate its use for other taxa. Whereas long-term monitoring practices usually separate fish, invertebrate, and algae censuses across different divers, 360˚ video could be a rapid all-encompassing method that surveys entire communities.

My study found significant differences in the total density of all species between the two methods. Despite counting less fish overall, UVC always, for every species, reported far greater densities than 360˚ video. The suggested reason for these results is the difference in volume calculations between methods; when performing transects, divers estimated a conservative survey volume in the forward direction (here, 2 m * 2 m * 30 m) and excluded observations outside of that volume. This increases precision in density estimates because it is difficult both to consistently scan far distances in the water and to count all of the fishes within larger volumes. UVC volumetric subsampling can lead to an underestimate of fish density on subtidal rocky reefs (Figuero-Pico et al. 2019), but I believe this study's 360˚ video transects reported enormous underestimates of true fish density. My 360˚ video transects could not, with precision, be

constrained to any survey volume other than the extent of visibility that was measured at the start of each dive. Thus, the only measurement to use for calculating volume was visibility. I tested 360˚ video transects in the environment I intended to survey, without manipulation of the environment or equipment trials. Visibility, however, is likely not an accurate representation of the distance from the camera at which video analysts can accurately identify fish to the species level. Future studies can improve density estimates by measuring the effective volume of water sampled across a range of visibilities, contributing to an estimate of effective strip width (ESW) of the transect. This may be achieved by swimming life-size models of representative taxa away from the camera along a transect tape and determining the distance at which *in silico* identification is no longer possible. Then these measurements, likely less than the full extent of visibility, could be substituted into the volume equation. Such an effort would reduce estimated volume, thereby increasing density for the same abundance of organisms. By determining the detectable distance at which fishes can be identified, researchers could gain a better sense of how far away fish should be counted and more appropriately calculate density along moving transects (Hyrenbach et al. 2007).

The greater abundances of fish observed from 360˚ video were not homogenously distributed throughout the additional volume of water that 360˚ video sampled. Rather, 360˚ video transects surveyed great quantities of water without fish, resulting in far smaller density estimates. My 360˚ video transects suggest that central Californian reef fish are not uniformly distributed in the water column from surface to substrate. Most individuals were observed near the substrate, positions in which demersal and benthic species were anticipated to occupy. Even within complex kelp forests that provide more vertical structure, Central Californian species are mostly associated with either the substrate or the canopy (Carr 1989; Nelson 2001).

As a workaround, I believe count per meter (CpM), to be an appropriate alternative for counts of organisms from 360˚ video transects. Unlike density calculated as individuals per cubic meter, CpM does not consider the volume of water surveyed. CpM, when reported with visibility, can still be used to qualitatively estimate effort. It benefits from including taxa that UVC transects at an equivalent depth would miss, while not suffering the significant density underestimation. For entire subtidal communities, I found that CpM interprets 360˚ video transects similarly to UVC transects, which can be helpful for comparing 360˚ video methods with long-term datasets collected via UVC. It is clear from this project, as well as others, that increasing effort via

survey area increases the frequency of organisms observed (Denney 2017; Campbell et al. 2018). For most species, CpM was greater from 360˚ video transects compared to UVC transects. These results were not entirely unexpected; 360˚ video transects surveyed more seawater than UVC transects because of visibility and the elevation at which transects occurred. This is why the canopy guild CpM was approximately double when measured from 360˚ video compared to UVC.

CpM from 360˚ video was similar to CpM from UVC for demersal guild species and benthic guild species, but nearly double for canopy guild species. This suggests that although the effective detectability radius for 360˚ videos is close to UVC's 1 m near the seafloor, it is greater futher up into the water column. Most of the fish observed were at eye level or below the 360˚ camera. However canopy associated species, such as Blacksmith and Blue rockfish, were less commonly observed from UVC because they less frequently visited the demersal zone. They were observed in greater numbers from 360˚ video transects since *post hoc* observations could be made in the water column above the UVC survey volume. CpM is much more equivalent between method for demersal and benthic species because the area surveyed is much more equivalent. On days with high visibility, individuals occupying the upper water column (such as the canopy guild species) would likely benefit from increased detection probability compared to individuals occupying lower areas of the reef (such as the demersal and canopy guild species). My experience indicates that 360˚ video transects have the additional capability of surveying upper water column fishes when swam at demersal depths. UVC divers may be able to match the survey volume of 360˚ video by expanding the survey distance beyond 1 m in all directions, but this comes with additional challenges. Even in a small survey volume, counting large schools of mobile fish with precision is a difficult task to untrained divers.

Still, CpM for some species was higher from UVC transects rather than 360˚ video transects. There are a few explanations for this. Firstly, inconspicuous species were difficult to identify from 360˚ video unless they were well illuminated. Many of the perches and rockfishes appeared as silhouettes on 360˚ video, while identification was possible from the UVC transect. Thus 360˚ video transects resulted in individuals identified to higher taxonomic levels (i.e., *Sebastes sp.*, Embiotocidae, etc) instead of exact species. Next, some species were too small to see in 360˚ video even if they were also sampled within the UVC survey. The 5.7k 360˚ video, although sufficient for larger organisms, is not detailed enough to observe small fishes in

California's challenging conditions. Finally, most species were not distributed uniformly throughout the water column to see an increase in CpM from 360˚ video. All transects were swam at an altitude of one meter above the substrate – close proximity to benthic and demersal species. It was these species, fish typically observed on or near the seafloor, that could have greater UVC CpM. These results demonstrate that from a fixed altitude, 360˚ video transects can capture taxa characteristic of the kelp forest canopy, demersal, and benthic zones.

At the fine-scale macrohabitat level, 360˚ video transects and UVC transects produced similar CpM results from sampling canopy guild, demersal guild, and benthic guild fishes. From flat, simple substrata to complex vertical environments, both methods produced comparable results. This suggests that both methods could be used interchangeably in heterogeneous environments. Temperate rocky reefs are often very complex and include many different habitat features and microhabitats. My results demonstrate that 360˚ video transects can be as robust as UVC transects at surveying fishes in complex environments. On some transects there were differences in CpM between methods within the canopy guild, both at the site level and macrohabitat level. Similarly to UVC, a solution to this would be to stratify 360˚ video transects by depth to give the method the most fair opportunity to detect species at all depths of the environment. UVC and 360˚ video could benefit from being stratified by depth, but would both require additional effort to swim multiple elevation passes.

Not all fish were able to be identified from 360˚ video, which differed from UVC in which divers were able to identify every fish to the species level. This was particularly true for fish occupying the kelp forest canopy and upper water column; they were often darkly silhouetted and lacked body orientation cues. In fact, the taxonomic group with the greatest differences in mean CpM between methods (greater from 360˚ video) was unidentified rockfish, primarily due to video's reduced capabilities at identifying species. I think it is unlikely that brighter lights would have made a substantial difference in identifying these fish from video. The limited dynamic range of cameras is a shortcoming that is not specific to just 360˚ video, but will likely always be present in imagery-based research. Researchers may be able to couple *in situ* observations with silhouetted individuals to arrive at a species identification. 360˚ video could better survey an entire reef by swimming at a higher elevation in the water column to prioritize swimming in-line with canopy-dwelling fishes.

My results indicate that both density and CpM were not significantly affected by visibility for both 360˚ video and UVC. Other studies have demonstrated clear negative impacts that poor visibility has on imagery-based research (Assis et al. 2013; Figuero et al. 2019). Visibility varied rapidly during this project and reflected typical conditions in Monterey Bay. Poor visibility may not have affected 360˚ video CpM because of the experience that I (the only video analyst for the project) have identifying and counting fish in temperate waters. Swimming behavior, general shape, and site-specific knowledge were helpful for arriving at least a genus or family identification for unknown individuals. 360˚ data coming from a less experienced analyst may be more greatly hindered by the effects of poor water clarity. Luckily though, the permanent record of observations provided by all imagery techniques could allow multiple analysts to review 360˚ video transects.

Future work should compare from stereoscopic 360˚ video transects to from UVC transects, a technology which was unavailable to me. By recording in stereoscopic formats, these cameras could estimate volume far more accurately than a monoscopic 360˚ video camera or a human *in situ*. Stereoscopic 360˚ cameras would also allow video analysts to measure the length of fishes using a software such as EventMeasure. Collecting size information is helpful for studying the health of habitats and the effectiveness of closures (Duffy et al. 2021). Precise volume and length measurements would lead to more precise reports of fish biomass.

NMDS plots of the CpM metric showed considerable overlap in fish communities between sites and between macrohabitats. Their ordination suggests more similarities than differences between sites and the macrohabitats within the sites. Both UVC transects and 360˚ video transects suggest that BW was the most dissimilar of the four sites. Vectors of significant species plotted over transects showed that the species typically characteristic of southern California accounted for the differences in the site-specific nMDS plots.

The fish community at BW more closely resembles that of Southern California and the Channel Islands than local sites immediately adjacent to it, and has for at least the last three years (K. Strickland, *personal observation*). At BW, observations of Blacksmith damselfish (*Chromis punctipinnis*), California sheephead (*Semicossyphus pulcher*), Kelp bass (*Paralabrax clathratus*), and other fishes characteristic of Southern California reefs are common. Reasons for this unique fish community were not investigated in this study, but it is possible that water circulation patterns transport retain warmer surface water and transport the larvae associated with it to this

location. The presence of small female and large male California sheephead, a conspicuous protogynous hermaphrodite, indicates reproduction and local recruitment of this species and likely others.

The transects I performed at SMON were representative of the site, with generally lower reef complexity than BW. There were some exceptions at deeper depths; boulders several meters tall towered above the rest of the seafloor and provided great microhabitat opportunities for fishes and invertebrates. Macroalgae was sparse to non-existent during many SMON transects, resulting in fewer vertical microhabitat opportunities for kelp forest species.

With its steeply sloping rocky walls and dense kelp forests, NMON included the most complex habitats of all sites. Fishes at NMON had a variety of low and high relief rock and kelp microhabitats to utilize. Unlike BW, fishes characteristic of Southern Californian reefs were not present at NMON during the time of data capture. Blacksmith damselfish were observed in the water column and kelp at NMON in previous years (K. Strickland, *personal observation*), but none were present during this study. For years, sea surface temperature has been noticeably warmer at BW compared to NMON and SMON (K. Strickland, *personal observation*). Temperature is an important physical condition which affects the range of species and fine-scale positioning of individuals (Baltz et al. 1987). Despite similar habitat opportunities as BW, the colder temperature may be a reason Southern Californian species are absent or rare encounters at NMON.

The canopy-guilds, demersal-guilds, and benthic-guilds were not equally abundant between sites. SMON had significantly fewer canopy-guild fish than both BW and BFH. For the duration of this project, SMON had very scarce abundance of giant kelp. Additionally, there were few high relief features such as rocky outcrops and pinnacles sampled at SMON. As a result, it is unsurprising that canopy-guild fishes were not as commonly observed here compared to BW – a site with dense giant kelp coverage, and BFH – a site with high-relief rock. Some species have high site fidelity to particular habitat features such as kelp forest canopies or rock structure, suggesting that alterations in the environment could affect future community dynamics (Bodkin 1988; Hartney 1996; Nelson 2001; Freiwald 2012).

Similarly, there were greater counts of benthic-guild fish at BW compared to SMON and NMON. The substrate at BW is nearly continuous rocky bottom with interstitial spaces for fishes of all sizes to occupy. Transects at SMON often ran over patches of sand that interrupted

continuous rock. NMON featured both continuous rocky transects with interstitial spaces and transects comprised of sandier substrate. Rugose rocks and lots of interstitial spaces at BW likely contributed to it supporting the highest abundances of benthic-guild species. Both the canopy-guild and benthic-guild results suggest that BW supported more fishes than other sites. A diver at BW can easily look up and see schools of Blacksmith and rockfishes in the upper layers of the water column, or look down and see ample bottom dwellers between rocks.
Like the site factors, macrohabitat was not responsible for significant differences in fish count per meter. Fish were not as segregated into zones as expected when going into this project. Species characteristic of the kelp forest canopy and upper water column, such as Blue rockfish, were present in low and high relief habitats, both supporting and lacking giant kelp. Counts of demersal species that occupy the lower zones of reefs, and benthic species that occupy the substate, were not significantly affected by vertical relief or the presence of giant kelp. My decision to bin species into guilds based on expected vertical position in the water column may contribute to these results. The brief moment in time that researchers glimpse at individuals may not be a complete representation of the species' true habitat utilization patterns (Love et al. 1991; Freiwald 2012).

CONCLUSIONS

While commonly deployed below the effective depth of SCUBA to study demersal fishes, image-based surveys have only recently been engaged for surveys in the shallow depths typically monitored by SCUBA divers using UVC techniques. Understanding that method for surveying subtidal communities has associated strengths and weaknesses, my goal was to assess the trade-offs between UVC transects and 360˚ video transects.

The primary conclusion of my research indicated that 360˚ video transects sampled shallow temperate reef fish communities similarly to UVC methods. More to the point, data derived from 360˚ video transects did not compromise the quality of data collected by the more well-established UVC techniques. The next, and perhaps greater, challenge is to determine what the implications of these results are for surveying fish communities moving forward.

In my experience, the placement of scientists *in situ* to study temperate reef fishes is vital to our understanding of how these complex communities function, and to how that understanding

can be translated into management, notably including spatial management regimes such as marine protected areas (MPAs). The field of view of a SCUBA diver exceeds that of any traditional video platform. Fish identifications, which can be particularly nuanced in low-visibility, are demonstrably more precise when made by a trained diver *in situ* rather than a video analyst *in silico*. That said, UVC data are constrained by what a diver can be expected to quantify live while swimming a transect. The introduction of traditional imagery-based techniques, while narrowing the field of view underwater, creates a permanent record of fish-habitat interactions that researchers can leverage to ask questions unanticipated at the time of video recording. Adding even more value, the novel application of 360˚ transect video offers researchers the greatest possible field of view with which to rewatch transects and extract data both planned and unplanned.

Any researcher with experience in the analysis of video imagery will be familiar with the fact that post-processing and data extraction can take a considerable amount of time. That investment of time is indeed a potential barrier to the widespread adoption of 360˚ video approaches, particularly when compared to rapid results of UVC data. Yet the future holds even more promise for the use of 360˚ video. Automation of video analysis via machine learning is already showing great promise for both fish ID and fish length estimation, which will likely enhance the productivity of imagery-based research. Considered together, and taking into account the variety of challenges facing any subtidal field research program (including available personnel, tight research budgets, and widely variable visibility underwater), I suggest that both 360˚ video and UVC have a place in temperate reef fish surveys, and both should be engaged as circumstances allow. Now with an understanding of how the technology fares in shallow Californian rocky reefs, I welcome new researchers to apply 360˚ video transects to other environments such as coral reefs and the deep sea.

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