





ORIGINAL RESEARCH

Underwater robots provide similar fish biodiversity assessments as divers on coral reefs

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Abstract

Coral reefs are under increasing threat, and the loss of reef-associated fishes providing valuable ecosystem services is accelerating. The monitoring of such rapid changes has become a challenge for ecologists and ecosystems managers using traditional approaches like scuba divers performing underwater visual censuses (UVC) or diver operated video recording (DOV). However, the use of small, low-cost robots could help tackle the challenge of such monitoring, provided that they perform at least as well as diver-based methods. To address this question, tropical fish assemblages from 13 fringing reefs around Mayotte Island (Indian Ocean) were monitored along 50 m-long transects using stereo videos recorded by a semi-autonomous underwater vehicle (SAUV) and by a scuba diver (Diver Operated stereo Video system, DOV). Differences between the methods were tested for complementary fish assemblage metrics (species richness, total biomass, total density, Shannon diversity and Pielou evenness) and for the number and size of nine targeted species. SAUV recorded on average 35% higher biomass than DOV which in turn recorded on average 12% higher species richness. Biomass differences were found to be due to SAUV monitoring larger fishes than DOV, a potential marker of human-related fish avoidance behaviour. This study demonstrates that SAUV provides accurate metrics of coral reef fish biodiversity compared to diver-based procedures. Given their ability to conduct video transects at high frequency, 100 m depth range and at a moderate cost, SAUV is a promising tool for monitoring fish assemblages in coral reef ecosystems.

Introduction

Coral reef ecosystems have been increasingly impacted by human activities for decades, and changes are now happening at unprecedented rates worldwide (Obura et al., 2019; Stuart-Smith et al., 2018). Such disturbances have markedly altered biomass, diversity and trophic structure of fish communities (Graham et al., 2017; Munday et al., 2008). As coral reef fishes provide key services to human populations (Woodhead et al., 2019), the ability to detect rapid changes in fish assemblages is critical for efficient management (Robinson et al., 2019).

Underwater Visual Censuses (UVCs) by divers performing on-site visual identification, count and sometimes measurements of fishes along a transect (Harmelin-Vivien et al., 1985) remains a classic approach (e.g. worldwide database used in Cinner et al., 2013; Edgar & Stuart-Smith, 2014). A camera-based extension of UVC, the diver operated stereo video (DOV), offers comparable approaches in fish surveys with the possibility for rapid and accurate measurements of fish size and distance to the camera (necessary for biomass and density estimates) as well as allowing permanent storage of raw data (Holmes et al., 2013; Letessier et al., 2015; Mallet &

Pelletier, 2014; Wartenberg & Booth, 2014). However, scuba divers are limited in depth (often 30 m), immersion duration and frequency (e.g. a maximum of two dives per day), which limits the yield of reef monitoring for a given effort (i.e. number of divers and days in the field).

As a solution to the limits of scuba-diving, robots have been increasingly used for the last decade to survey fish assemblages, mainly employing the transect approach to quantify fish abundances (Sward et al., 2019). Recent advances in underwater robotics have led to design of small (<1 m, <30 kg) and low-cost (<50k\$) vehicles, either remotely operated by a human from the surface (remotely operated vehicle, ROV), or with some autonomous embedded functionalities such as the automatic control of stability and 3D-motion (SAUV – semi-autonomous underwater vehicle). Such robots are well-adapted for complex navigation in shallow coral reefs (Dunbabin et al., 2005, 2019; Louis et al., 2017a, b) and they allow the embedding of stereo camera as well as sensors to monitor the environment (e.g. depth, current). This allows for monitoring coral reef ecosystems with a high rate of data acquisition over space and time. Several studies have compared UVC with ROV for surveying fish assemblages (Andaloro et al., 2013; Carpenter & Shull, 2011; Raoult et al., 2020; Wetz et al., 2020), and one study compared multiple video-based surveys, including ROV (Schramm et al., 2020). However, results across studies remains inconsistent concerning the relative efficiency of the different types of surveys. Furthermore, no study has compared these methods done along the same transects on the same sites with complementary metrics of fish biodiversity such as species richness, species density, biomass estimation and fish behavioural avoidance. Therefore, there is still no comprehensive comparison between the performance of robot surveys compared to DOV surveys for monitoring fish biodiversity (Somerton et al., 2017). In the present study, we aim to address this research gap by comparing DOV and SAUV methods for fish biodiversity surveillance on coral reefs.

Materials and Methods

Study sites

We surveyed fish assemblages in 13 sites located on fringing reef habitats from the lagoon of Mayotte (12°49'53.9"S 45°09'21.2"E, Fig. 1). Upon arrival at the sites, a marker, made of a dive weight, a string and a small buoy, was delicately dropped from the boat, and the GPS location of this marker was recorded. Next, the boat dropped anchor at a suitable distance from the site. At each site, four transects were performed parallel to the

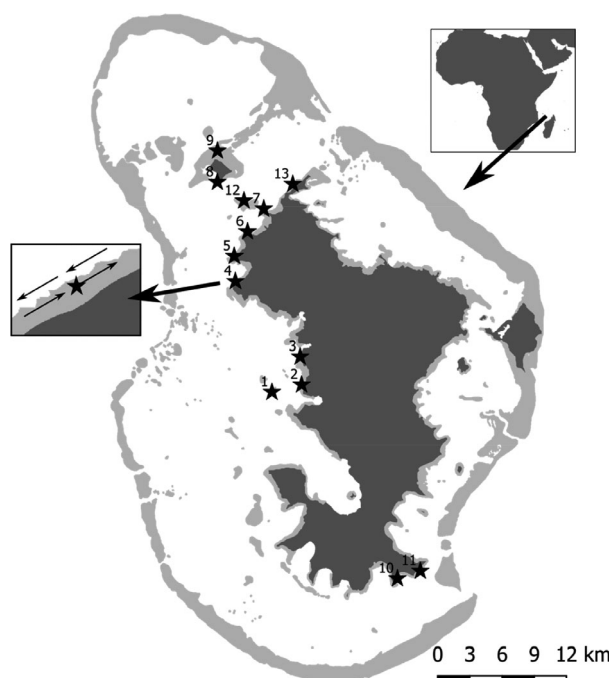


Figure 1. Study sites on Mayotte fringing reefs. Mayotte Island is located in the north-central part of the Mozambique channel off the coast of Eastern Africa. Dark grey areas represent land and light grey areas show extent of fringing, inner and barrier coral reefs. Stars indicate the 13 sites where four DOV and SAUV transects were performed parallel to the land. Zoom on site 4 illustrates how transects (arrows) were performed around the GPS-recorded mark. DOV, diver operated video; SAUV, semi-autonomous underwater vehicle.

shore on the reef crest and at the bottom of the reef slope (17 m max depth, Fig. 2). A distance of at least 10 m was kept among transects. Surveys were done in May 2017 with two sites surveyed per day.

Fish survey protocol

Each transect was surveyed by both the DOV and the SAUV. Running order was randomly assigned and the DOV and the SAUV procedures were separated by at least 20 min to allow fish communities to recover from potential perturbations (Somerton et al., 2017). Both DOV and SAUV moved at a speed of $0.2 \text{ m}\cdot\text{s}^{-1}$ (i.e. average of 4 min 10 s for a 50 m transect) and carried the same video system along the same course (i.e. same starting and ending points). Maximum transect overlap between SAUV and DOV was insured by (1) the GPS-located marker dropped earlier from the boat, (2) the record of starting depth of each transect and (3) the real-time video feedback from SAUV allowing the pilot to adjust the trajectory and follow the same noticeable landmarks as the

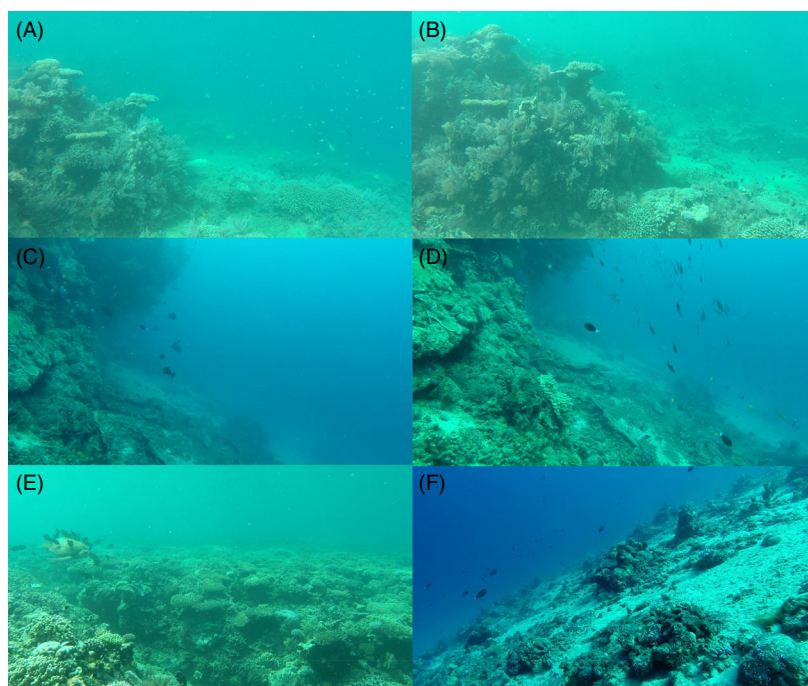


Figure 2. Pictures extracted from videos recorded at the top of the fringing reef for site 11 (A and B) and at the bottom of the reef slope at site 12 (C and D) from the same position but from the perspective of the SAUV (A and C) and the DOV (B and D) highlighting difference in altitude. Two other habitats encountered were reef flats, highlighting a turtle being cleaned (SAUV picture on site 11, E) and a slope with a mix of sand, coral rubble and coral colonies (the DOV pictured on site 8, F). DOV, diver operated video; SAUV, semi-autonomous underwater vehicle.

diver or the video recorded by SAUV allowing the diver to previsualize the path to follow (Figs. 1 and 2). Water visibility was assessed in the aftermath by measuring the distance to cameras for one of the furthest visible objects, and was found generally higher than 8 m. In four sites among the 13 surveyed, we only retained data of three replicates because DOV and SAUV followed too diverging paths or because water visibility changed between the two methods.

Semi-autonomous underwater vehicle

We used a prototyped SAUV, named ‘Ulysse,’ designed by the LIRMM laboratory to perform automated stabilized trajectories (Fig. 3). This SAUV measures $0.9 \times 0.5 \times 0.5$ m, is designed to work up to 100 m deep, is propelled by 12 vector thrusters (BlueRobotics T100) positioned to have 6 degrees of freedom, and is powered through embedded batteries. The SAUV is equipped with a GPS sensor to geo-localize the robot on the surface, a DVL (Doppler Velocity Log) sensor to monitor the position relative to the seafloor, a pressure sensor to monitor depth, an IMU (Inertial Measurement Unit) to monitor 3D orientation, and a forward-facing camera for real time streaming to the pilot (i.e. this camera was not used to

record fish transect). It was also equipped with four dimmable Lumen Lights, each one providing 1500 lumens (but not used in this experiment).

Embedded computers (Beaglebone black from Beagle-board for higher command computations and Dropix from Drotek for drivers and sensor actuators) ran the software architecture necessary to control the SAUV. A computer with a joystick was connected to the SAUV via a 200 m Ethernet cable to send command and display video flux. The SAUV could be controlled with two modes: (1) the manual teleoperation with the joystick to command depth, direction and speed using the forward camera and sensor readings to monitor the environment; (2) the autonomous mode allowing automatic transect execution, with five input parameters: the starting point coordinate, the direction to follow from this point, the length of the transect, the constant altitude to respect, and the constant speed to respect. Embedded control algorithms followed the automatic sequence: dive and reach the starting point of the first transect, execute that transect, move to the next transect starting point, repeat the sequence until the fourth transect, and reach the surface vertically after the mission. The transects were defined as moving at $0.2 \text{ m}\cdot\text{s}^{-1}$ on a straight line in the selected direction, at 1.5 m altitude and for a 50 m

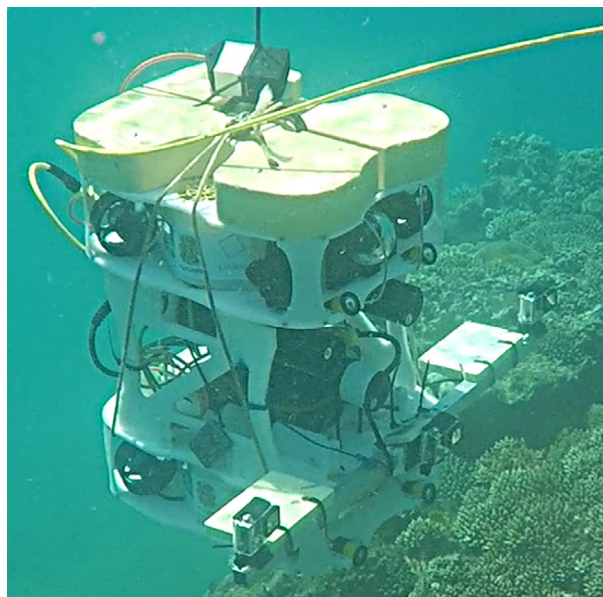


Figure 3. Picture of the semi-autonomous underwater vehicle (SAUV) used in this study. The stereo video apparatus is front-mounted on the bottom of the SAUV and is made of an aluminum bar carrying two GoPro cameras with two incompressible plates of foam to balance flotation (NB: camera in the middle of the bar was not used).

distance. The position of the SAUV was calculated with the initial surface GPS position of the SAUV, using depth and DVL information, which provided the motion of the SAUV relative to the seafloor.

During the transects, the SAUV was set to the autonomous mode, but a pilot ensured safety by monitoring for unforeseen obstacles through an HMI (Human Machine Interface) and ensuring as well the best match with the DOV surveys when necessary.

Diver protocol

Divers used classic air regulators and operated in pairs, one of them slightly in front of the other, carrying the stereo cameras and the second one unrolling a 50 m tape. The DOV was generally operated between 0.5 and 1 m altitudes (visually estimated). Swimming speed was slow and steady ($0.2 \text{ m}\cdot\text{s}^{-1}$). Depth was monitored with a hand-held dive computer (Aladin pro uwateck).

Recording apparatus

The stereo video apparatus (Fig. 3) was comprised of two digital cameras (GoPro Hero 3+) mounted on an aluminium bar, 80 cm apart and each oriented 8° inward to maximize picture overlap 5 m away (Letessier et al., 2015). The recording was made using medium view setting (127°

of horizontal field of view in air and 84° in water) and at full HD definition (1080p) with a frame rate of 30 fps. Calibration of the system was performed twice: before and halfway through the campaign using a $2 \times 2 \times 1 \text{ m}$ black cubic frame with white dots of known coordinates and situated 4 m from the system underwater. Distortion of cameras was calibrated with an $80 \times 50 \text{ cm}$ chessboard situated 1 m from the cameras underwater (Helmohoz et al., 2016; Neuswanger et al., 2016). Measurement accuracy was verified daily by filming a graduated ruler underwater with the system. Calibration calculation and 3D fish measurements were all performed using the open-source software Vid-Sync (www.vidsync.org).

Data processing

Video treatment consisted of measuring and identifying all individual fishes visible in the video to the lowest taxonomic level possible. Fish measurement was performed from snout to the caudal fork when fish were as close and as parallel to the camera as possible. For each individual fish, its closest distance to the camera system (range surveyed: 0.7–10 m) was measured as a proxy of species avoidance behaviour (Goetze et al., 2017; Lindfield et al., 2014). Biomass of each individual was estimated using species-specific length-weight relationships available in the literature (Kulbicki et al., 2005; Letourneur, 1998). For schools of more than 20 fishes (e.g. *Chromis viridis*), only five to 10 individuals among the closest to the camera were measured and the total number was estimated to the nearest 10 individuals. Fish weight was then averaged among the measured individuals and school biomass was computed by multiplying averaged mass by estimated number of individuals:

$$W = a \times L^b$$

with W being specimen weight, L being fork length, a and b being length-weight relationship parameters.

Each transect measured 50 m long and fish were counted on a 5 m wide band, thus covering a total surface of 250 m^2 . For each transect, the following calculations were made: the number of species, the total fish biomass (expressed in grams per 100 m^2), the total fish density (number of individuals per 100 m^2), the taxonomic diversity computed as $\exp(H)$ [i.e. Shannon diversity (H) expressed as an equivalent number of species; Jost, 2006] and the evenness of species biomass (Pielou, 1966). The dissimilarity between fish assemblages was measured using the Jaccard dissimilarity index that account only for species composition and using the Bray-Curtis dissimilarity index accounting for either species biomass or for density.

Statistical analyses

We first tested for detection bias between the two survey methods for the most common species (*Caesio xanthonota*, *Chromis ternatensis* and *Dascyllus aruanus*) and the most targeted by local fishers (*Caranx melampygus*, *Chlorurus sordidus*, *Chlorurus strongylocephalus*, *Lutjanus gibbus*, *Macolor niger*, *Naso brevirostris*, *Naso elegans*, *Naso unicornis*, *Cephalopholis argus* and *Variola louti*). Three metrics were selected to compare species detection by SAUV and DOV: abundance, maximal size and minimal distance to cameras. These three values calculated for each transect were compared between survey methodologies using Wilcoxon tests. To test for size-related distribution bias between survey methods for each of these species, we computed Kernel Density Estimates (KDE, Langlois et al., 2012). KDE were fitted on body length of all individuals from each survey method with bandwidth calculated by the Sheather-Jones selection procedure using the 'dpik' function in the package 'KernSmooth' (Wand, 2011). Finally, statistical comparison of KDEs between methods was performed using 10 000 permutations via the function 'sm.density.compare' in the package 'sm' (Bowman & Azzalini, 2010).

Subsequently, we compared species abundance, total biomass, species richness, Shannon diversity and Pielou evenness between methods (SAUV vs. DOV) using a linear mixed model framework. More specifically, models fixed arguments were method (DOV or SAUV) and order of the survey (which method was performed first) while the site and transect replicate were set as random factors [Full model: \sim method \times order + (1|site) + (1|transect)]. Candidate models were compared using the second order Akaike information criterion corrected for small or finite samples (AICc; Burnham & Anderson, 2002). Models with the lowest AICc value were considered to be the most significant drivers of assemblage variations. If the null model [M0: \sim 1 + (1|site) + (1|transect)] had the lowest AICc value, method and order had no influence on the quantification of tested assemblage. Candidate models were then compared against the null model (M0) and significant differences were evaluated with maximum likelihood ratio tests (χ^2 , $P < 0.05$). Models were computed using the function *lmer()* from the *lme4* package in R (Bates et al., 2015).

Finally, in order to test whether estimates of fish composition among assemblages were consistent between survey methods, station-nested PERMANOVA was run on both Jaccard and Bray-Curtis dissimilarity matrices. We also tested for correlation in the dissimilarity between SAUV and DOV methods using Mantel tests. A principal coordinate analysis (PCoA) was computed on each of these three dissimilarity metrics to illustrate

differences in fish assemblages across sites and between methods.

These analyses were performed using 'vegan' and 'beta-part' packages from R software (R Core Team 2020 V.4.0.3).

Results

A total of 9223 fishes belonging to 195 species and 33 families were identified on the 96 video-transects recorded in the 13 studied sites (see Data S1 for further details on species surveyed). One species (*C. melampygus*) was only observed with SAUV.

Density did not differ between survey methods for nearly all 13 selected species (Fig. 4). Maximal size of fishes estimated with DOV did not significantly differ from those estimated with SAUV for all but two species. *Naso elegans* and *Chlorurus sordidus* largest individuals were recorded by SAUV and were respectively 27 and 39% longer than largest individuals recorded with DOV (Fig. 4). Furthermore, KDE analyses for these two species revealed that more large fishes were surveyed by the SAUV (Fig. 4). Finally, minimal distance to the cameras for individuals of targeted species was significantly higher with SAUV than with DOV for three species: *C. sordidus*, *L. gibbus* and *C. ternatensis* (Fig. 4). These paired tests were not computed for the four species that were not recorded by both methods on the same transect (*C. melampygus*, *N. brevirostris*, *C. argus* and *V. louti*).

Total biomass and species richness showed significant differences between DOV and SAUV, with on average 35% higher biomass recorded with SAUV than with DOV, while on average three more species were recorded with DOV than with SAUV (Fig. 5 and Data S2).

No differences between survey methods were evidenced for fish density, Shannon diversity or Pielou evenness (Fig. 5 and Data S2).

The order of survey method did not have any significant effect on any of the diversity indices tested (Data S2).

PERMANOVA on Jaccard dissimilarity revealed a significant effect of method ($n = 9999$, $F_{1,95} = 2.29$, $P = 0.002$) but not of the site ($n = 9999$, $F_{12,95} = 3.72$, $P = 0.438$), nor of the interaction between those two factors ($n = 9999$, $F_{12,95} = 0.89$, $P = 0.770$), indicating some difference in species composition between sampling methods which is consistent among sites (Fig. 6). Similarly, PERMANOVA on Bray Curtis dissimilarity based on species relative biomass revealed only a significant effect of method ($n = 9999$, $F_{1,95} = 1.64$, $P = 0.027$). Finally, PERMANOVA on Bray Curtis dissimilarity based on species density revealed no significant effect of method ($n = 9999$, $F_{1,95} = 0.91$, $P < 0.541$), site ($n = 9999$,

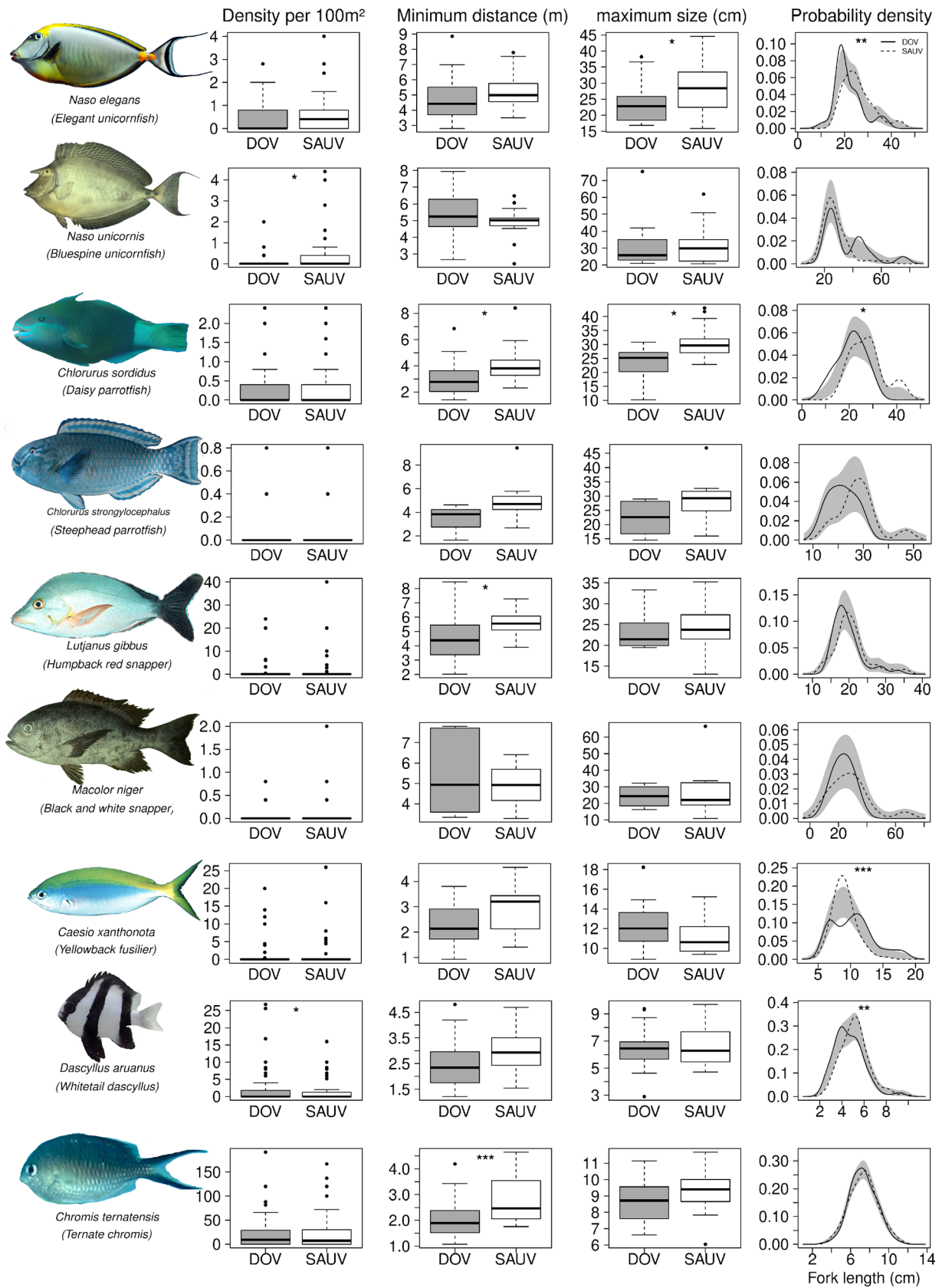


Figure 4. Difference between the diver operated video (DOV) and the semi-autonomous underwater vehicle (SAUV surveys on density, minimal distance to the camera and maximum size for nine fish species. Boxplots show interquartile (Q1–Q3) as box with median (Q2) as horizontal segment and minimal-maximal depicted by whiskers. Extreme measures, of 1.5 the interquartile range, are depicted as dots. Panels on the right illustrate Kernel Density Estimate analysis (KDE) on size frequencies between the DOV (solid line) and the SAUV (dashed lines). The grey area represents the combined uncertainty of both methods. Levels of significant difference between the DOV and the SAUV are represented by * ($P < 0.05$), ** ($P < 0.01$) and *** ($P < 0.001$).

$F_{12,95} = 4.72$, $P = 0.596$) and of their interaction ($n = 9999$, $F_{12,95} = 0.93$, $P = 0.589$).

Differences in fish composition (i.e. Jaccard dissimilarity) among sites estimated with SAUV were not

significantly correlated with differences estimated with DOV (Mantel test, perm: 9999, $r = 0.080$, $P = 0.329$). However, both differences in abundance and biomass dissimilarity (i.e. Bray-Curtis dissimilarities) were

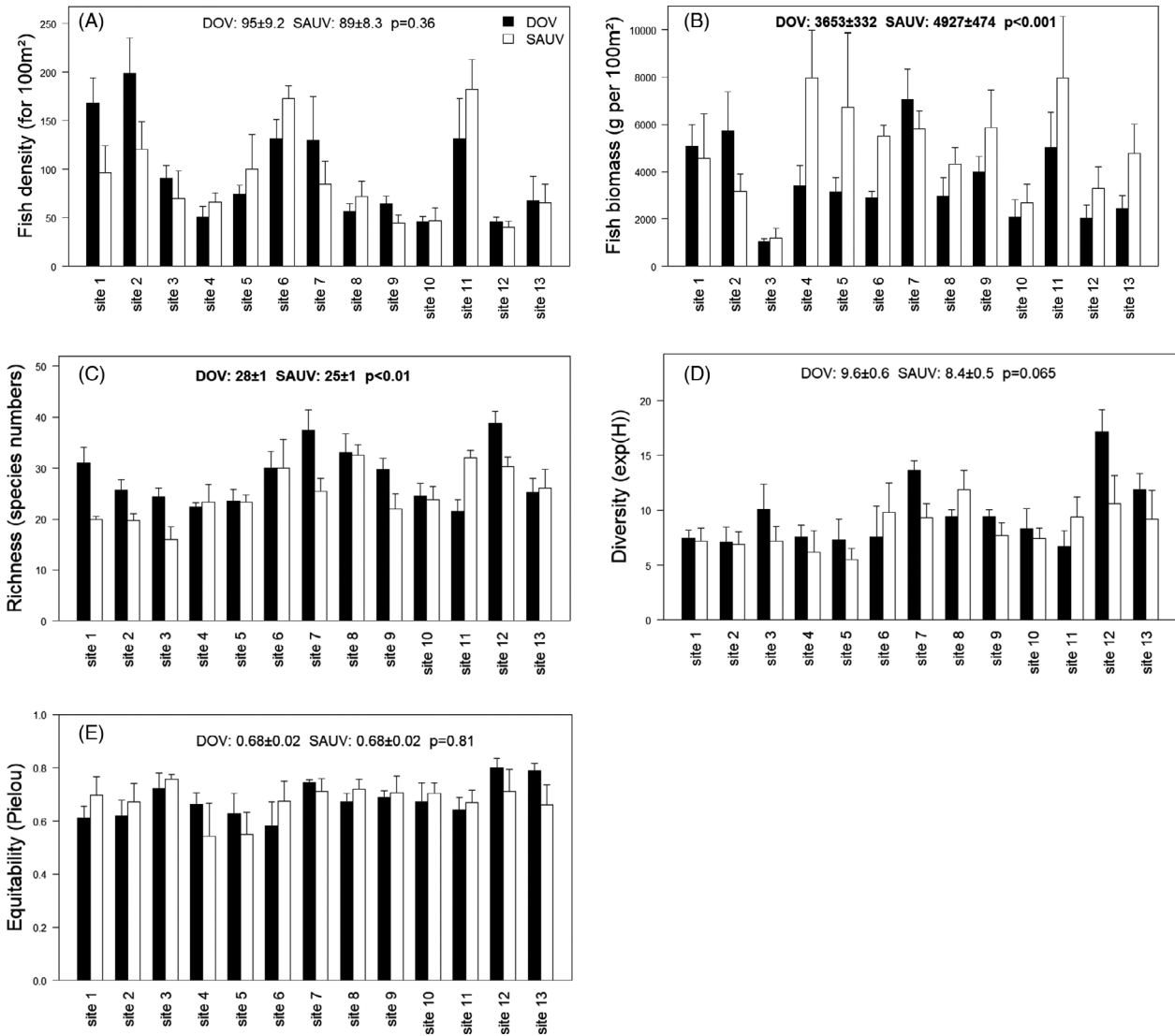


Figure 5. Fish density (A), total biomass (B), species richness (C) Shannon index (D) and Pielou’s evenness (E) averages per sites (\pm standard error) of assemblages estimated with the DOV (black) and the SAUV (white) for the 13 sites referenced in Figure 1. Average estimates for the DOV and the SAUV are displayed on top and in bold font if significant differences ($P < 0.05$) were revealed by a permutation test (see Data S2 for further details about the null model). DOV, diver operated stereo video; SAUV, semi-autonomous underwater vehicle.

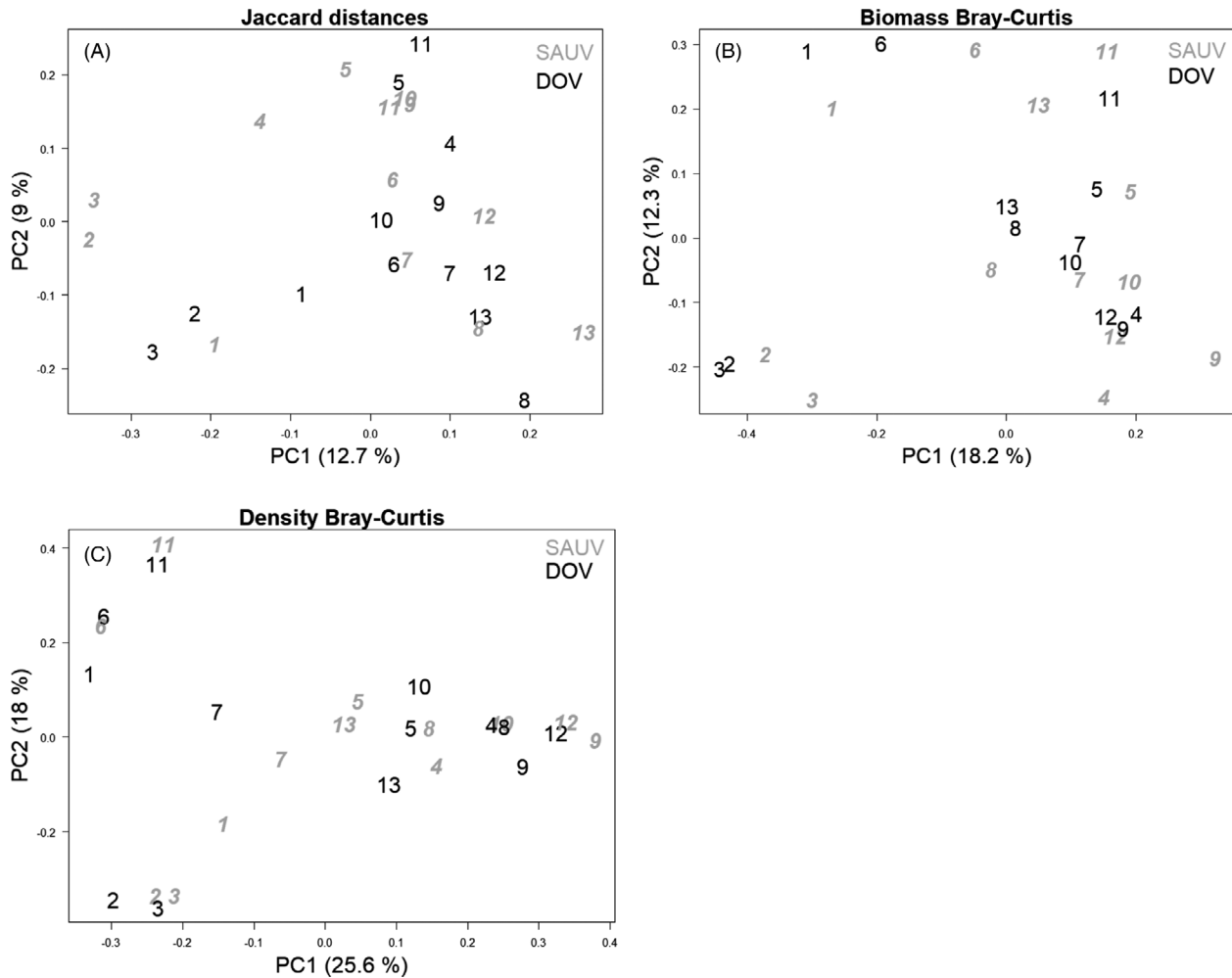


Figure 6. Principal coordinate analysis (PCoA) performed on the dissimilarity matrices computed with Jaccard distances (A), relative biomass Bray-Curtis (B) or species density Bray-Curtis (C) with the two survey methods (DOV in black and SAUV in grey). The first two axes represent, respectively, 21.7% (A), 30.5% (B) and 43.6% (C) of composition variances. Plot represents surveyed sites numbered as in Figure 1. DOV, diver operated video; SAUV, semi-autonomous underwater vehicle.

significantly correlated between survey methods (Mantel test on Bray-Curtis density, perm: 9999, $r = 0.649$, $P = 0.001$; Mantel test on Bray-Curtis biomass, perm: 9999, $r = 0.524$, $P = 0.002$). These differences are illustrated on PCoA biplots (Fig. 6).

The PCoA shows moderate explanation of the composition with, respectively, 21.7, 30.5 and 43.6% of the variance explained by the first two axes for the Jaccard dissimilarity, the biomass Bray-Curtis dissimilarity and the density Bray-Curtis dissimilarity analyses (Fig. 6).

Discussion

In this study, we compared differences in estimates of fish biodiversity between two stereo video transect-based approaches differing only by the carrier of the video

system: a diver or a SAUV. Our results demonstrated congruence among methods for most diversity metrics, but not for fish size and species richness.

SAUV recorded on average 35% higher fish biomass than DOV and the underestimation of biomass due to DOV was variable among sites (DOV recorded higher biomass than SAUV for only three sites out of 13). As similar density of fish were recorded by both methods, this discrepancy is driven by the larger-size individuals recorded with the SAUV at some sites. Indeed, SAUV recorded bigger specimens than DOV for two out of the 13 closely investigated species (Fig. 4) and a large predator species, *C. melampygus*, was only recorded with SAUV (a total of 14 individuals ranging from 22 to 52 cm length). Such differences could be related to fishing pressure and the recognition of human as a threat by large

fishes. Stankowich and Blumstein (2005) demonstrated that larger individuals are commonly showing anti-predator behaviours, meaning that they are more likely to run away from any source of disturbance. In Mayotte, marine resources' poaching is widespread over the lagoon and spearfishers are commonly spotted practising their activity on the fringing reef (PNMM, 2016; Wickel & Guillemot, 2012). Large individuals from families which are of commercial interest in the lagoon such as Scaridae, Lutjanidae, Acanthuridae and Serranidae are thus more likely to swim away from humans because they associate them with potential risk (Goetze et al., 2017). On the other hand, fishes may not have considered the robot as an immediate threat as it is smaller than a diver, has a cubic shape and has never been seen before. Furthermore, although the robot might emit a high-frequency sound due to the rotation of its thrusters, it appears to minimally disturb surrounding fishes (authors personal observation during preliminary tests of the robot on other Mayotte reefs). This lack of response could be related to the lack of perception of high frequency sounds for the majority of fish species (Ladich & Fay, 2013; Stimpert et al., 2019). Another difference was that SAUV operated on average 1 m higher than the DOV. Schramm et al. (2020) had a similar ROV-DOV height difference in their study and found higher densities for DOV which could be paired with higher biomass if average mass of fish were identical between surveys. In the present study, although some density differences can be noted among species (cf. Data S1), biomass variation was mainly related to large non-cryptic species whose detectability should not be affected by a 1 m altitude difference (see Data S3 for further discussion on altitude effect on measurements). One way larger fish would get more frequently recorded by SAUV would be if they swim up to 1 m higher above the recording field of view of DOV. This could be a possibility for long-range swimmers such as *C. melampygus* but unlikely for bottom associated species such as *C. argus* or *V. louti*, whose recorded individuals were consistently bigger when done via SAUV (cf. Data S1).

Minimal distance of fishes to cameras carried by the diver was on average 70 cm shorter distance to the camera carried by the SAUV, although such difference varied among species (Fig. 4). The larger and most significant differences were observed for the small and highly common reef species *D. aruanus* as well as for two large species *C. sordidus* and *L. gibbus*. As those species do not share ecological traits such as gregariousness or avoidance behaviour, it is unlikely that avoidance behaviour explains distance bias among species. Indeed, the SAUV performed transects on average 1.5 m above the coral substrate (minimal altitude for the used DVL sensor to work accurately). On the contrary, divers progressed mostly between

0.5 and 1 m from the coral, thus being generally closer to the seabed than the robot. Variation in minimal distance between fish and cameras from one carrying method to another could thus be influenced by the altitude difference during the recording. As demonstrated in Data S3, trigonometric calculations show that a fish measured close to the substrate at 1 m ahead of the camera, itself situated at 0.5 m from the substrate, would record a distance of 1.1 m, while the same setup with a camera altitude of 1.5 m would measure a distance of 1.8 m for the same fish position. This leads to a 0.7 m difference, which is in the range of measured differences in this study. Even if this distinction between methods cannot account for all variations, it could certainly explain differences in distances for sedentary species that would only get closer to the substrate as the robot or the diver pass above (i.e. *D. aruanus*).

DOV recorded on average three more species than SAUV, but as there were on average more than 25 species per transect, this difference is only 12%. In addition, multivariate analyses revealed that the SAUV survey yields different species composition and different structure of biomass than the DOV survey (Fig. 6). These differences in species richness and structure can be roughly summarized with the DOV survey more often recording Labridae such as *Thalassoma* and *Halichoeres*, genera renowned for their curiosity for divers, and Holocentridae such as *Myripristis* and Tetraodontidae such as *Canthigaster valentini*, often hidden in coral anfractuosity. The SAUV recorded species that were locally fished such as *Caranx melampigus*, *Lutjanus Bohar* and various *Naso* species, among which *N. unicornis*, which can reach more than 70 cm in length (cf. Data S1). Despite these differences, the two survey methods provided similar estimates of biomass-based Shannon diversity and Pielou's evenness (Fig. 5). Overall, SAUV survey appears equivalent to DOV surveys in assessing fish diversity and even seems to out-perform DOV in quantification of some large species. DOV tended to better survey small cryptic benthic species, likely due to smaller distances from the seafloor.

Among the few studies that evaluated the efficiency of using robot to survey fish assemblages, Schramm et al. (2020) is the most comparable to our work because they used scuba divers versus a tethered robot to perform DOV and ROV along transects, although this study was carried out on temperate fish assemblages. The study found comparable results with all transect methods, with higher species richness and higher density of individuals with the DOV approach than the ROV. Schramm et al. (2020) proposed that distance to the substrate and ROV sound production could be the source of such differences. In the present study, the SAUV did not really elicit more avoidance behaviour from fish since bigger individuals

were recorded with SAUV as also reported by Wetz et al. (2020) over an artificial habitat. Furthermore, in our work, – much like Schramm et al. (2020), – the SAUV surveyed further from the bottom than DOV but density did not change and species number was also higher for the DOV. Although we cannot exclude that both distance from the substrate, especially for small benthic species hidden in anfractuosity, and sound production generate such differences, other hypotheses related to behavioural bias due to motion or to the colour of the SAUV should be investigated (Stoner et al., 2008; Wetz et al., 2020).

Overall, although the SAUV recorded a slightly lower species richness than the DOV, the SAUV allowed to record larger individuals of the species targeted by fisheries and hence a higher biomass. SAUV of small size are thus a promising way to monitor fish assemblages at large spatial scale and/or high frequency, which is needed to track effects of global change (Holmes et al., 2013; Raoult et al., 2020; Samoilys & Carlos, 2000). The SAUV are not limited by depth and submersion time contrary with humans. For example, with a setup equivalent to the present work, assuming that a set of batteries allows 2 h of working time (i.e. present study), five sets of spare batteries would be sufficient for a SAUV to record nearly continuously transect videos all day long. In this case, if we account for site displacement and tool handling on the boat, it is feasible to record videos for 60 transects of 50 m long and 5 m wide that correspond to a total of 15 000 m² surveyed per day. This is nearly 10 times more than what two divers can do (assuming four replicates per site per dive). Furthermore, contrary with visual assessment, such a stereo video approach does not show significant inter and intra-observer variations during field data collection (Holmes et al., 2013). Therefore, this tool allows for the standardization of sampling protocols, which is required for meaningful comparison of biodiversity through space and time; a fact already recognized by initiatives proposing national and international standards (e.g. Ocean Best Practices System). Moreover, additional sensors [i.e. acoustic triangulation positioning system (Ultra Short Base Line) linked to GPS positioning, current meter, turbidity, conductivity, pH, photosynthetic active radiation, temperature...] can be carried by the SAUV to gather environmental data synchronously with faunal recordings. Finally, such apparatus allows up to 100 m-deep work (i.e. mesophotic ecosystems investigations remain hampered by lack of affordable deep-diving technology) along with the reaching of dangerous places where sending human operators is not feasible (i.e. collapsed caves, harmful algal blooms, sharks or crocodile habitats...). With such a small SAUV, deployment by hand from small boats becomes possible, making hazardous investigations promising. However, today, to be

really reliable, the SAUV must still be connected to the surface via a cable for necessary human monitoring. This tether is a drawback because the cable is prone to tangling in coral and increases drag while hampering robot movements. Nevertheless, progress in autonomous robotics will likely tackle the challenge of designing autonomous vehicles able to safely operate in complex environments (for example by means of real-time obstacle detection like in Dunbabin et al., 2019). Being able to optimize the height of the robot relative to the seabed, so that altitude bias relative to divers is minimized, remains an important consideration. Another key challenge is to reduce the time needed to analyse videos, which is now done by humans. However, recent advances in deep learning to automated fish counts on video are promising (Villon et al., 2018, 2020). In the context of the accelerating improvement of underwater robotics and computer vision, marine ecology is likely to soon enter into a new area of massive data collection and processing that will revolutionize the field as the next generation sequencing of DNA did for microbiology and genetics.

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References

- Andaloro, F., Ferraro, M., Mostarda, E., Romeo, T. & Consoli, P. (2013) Assessing the suitability of a remotely operated vehicle (ROV) to study the fish community associated with offshore gas platforms in the Ionian Sea: a comparative analysis with underwater visual censuses (UVCs). *Helgoland Marine Research*, **67**, 241–250. <https://doi.org/10.1007/s10152-012-0319-y>
- Bates, D., Mächler, M., Bolker, B. & Walker, S. (2015) Fitting linear mixed-effects models using lme4. *Journal of Statistical Software*, **67**, 1–48. <https://doi.org/10.18637/jss.v067.i01>
- Bowman, A.W. & Azzalini, A. (2010) R package 'sm': nonparametric smoothing methods (version 2.2–4). Available from: <http://www.stats.gla.ac.uk/~adrian/sm> [Accessed 07 December 2020].
- Burnham, K.P. & Anderson, D.R. (2002) *Model selection and multimodel inference*, 2nd edition, New York: Springer-Verlag. <https://doi.org/10.1007/b97636>

- Carpenter, B.M. & Shull, D.H. (2011) A comparison of two methods, paired-diver surveys and remotely operated vehicle surveys, for determining rockfish abundance.
- Cinner, J.E., Graham, N.A., Huchery, C. & Macneil, M.A. (2013) Global effects of local human population density and distance to markets on the condition of coral reef fisheries. *Conservation Biology*, **27**, 453–458.
- Dunbabin, M., Dayoub, F., Lamont, R. & Martin, S. (2019) Real-time vision-only perception for robotic coral reef monitoring and management. *IEEE ICRA Work. Underw. Robot. Percept.*
- Dunbabin, M., Roberts, J., Usher, K., Winstanley, G. & Corke, P. (2005) A hybrid AUV design for shallow water reef navigation. *Proceedings of the 2005 IEEE International Conference on Robotics and Automation*, 2105–2110. <https://doi.org/10.1109/ROBOT.2005.1570424>
- Edgar, G.J. & Stuart-Smith, R.D. (2014) Systematic global assessment of reef fish communities by the Reef Life Survey program. *Scientific Data*, **1**, 140007. <https://doi.org/10.1038/sdata.2014.7>
- Goetze, J.S., Januchowski-Hartley, F.A., Claudet, J., Langlois, T.J., Wilson, S.K. & Jupiter, S.D. (2017) Fish wariness is a more sensitive indicator to changes in fishing pressure than abundance, length or biomass. *Ecological Applications*, **27**(4), 1178–1189.
- Graham, N.A.J., McClanahan, T.R., MacNeil, M.A., Wilson, S.K., Cinner, J.E., Huchery, C. et al. (2017) Human disruption of coral reef trophic structure. *Current Biology*, **27**, 231–236. <https://doi.org/10.1016/j.cub.2016.10.062>
- Harmelin-Vivien, M.L., Harmelin, J.G., Chauvet, C., Duval, C., Galzin, R., Lejeune, P. et al. (1985) Evaluation visuelle des peuplements et populations de poissons: methodes et problemes. *Revue d'écologie*, **40**, 467–539.
- Helmohoz, P., Long, J., Munsie, T. & Belton, D. (2016) Accuracy assessment of Go Pro Hero 3 (Black) camera in underwater environment. *International Archives of the Photogrammetry, Remote Sensing and Spatial Information Sciences*. XXIII ISPRS Congress. **XLI-B5**, 477–483. <https://doi.org/10.5194/isprsarchives-XLI-B5-477-2016>
- Holmes, T.H., Wilson, S.K., Travers, M.J., Langlois, T.J., Evans, R.D., Moore, G.I. et al. (2013) A comparison of visual- and stereo-video based fish community assessment methods in tropical and temperate marine waters of Western Australia. *Limnology and Oceanography: Methods*, **11**, 337–350. <https://doi.org/10.4319/lom.2013.11.337>
- Jost, L. (2006) Entropy and diversity. *Opinion*, **2**, 363–375.
- Kulbicki, M., Guillemot, N. & Amand, M. (2005) A general approach to length-weight relationships for New Caledonian lagoon fishes. *Cybium*, **29**, 235–252.
- Ladich, F. & Fay, R.R. (2013) Auditory evoked potential audiometry in fish. *Reviews in Fish Biology and Fisheries*, **23** (3), 317–364. <https://doi.org/10.1007/s11160-012-9297-z>
- Langlois, T.J., Fitzpatrick, B.R., Fairclough, D.V., Wakefield, C.B., Hesp, S.A., McLean, D.L. et al. (2012) Similarities between line fishing and baited stereo video estimations of length-frequency: novel application of Kernel Density Estimates. *PLoS One*, **7**, e45973.
- Letessier, T.B., Juhel, J.B., Vigliola, L. & Meeuwig, J.J. (2015) Low-cost small action cameras in stereo generates accurate underwater measurements of fish. *Journal of Experimental Marine Biology and Ecology*, **466**, 120–126. <https://doi.org/10.1016/j.jembe.2015.02.013>
- Letourneur, Y. (1998) Length-weight relationship of some marine fish species in Réunion Island, Indian Ocean. *Naga*, **21**, 37–39.
- Lindfield, S.J., Harvey, E.S., Mcilwain, J.L. & Halford, A.R. (2014) Silent fish surveys: bubble-free diving highlights inaccuracies associated with SCUBA-based surveys in heavily fished areas. *Methods in Ecology and Evolution*, **5**, 1061–1069. <https://doi.org/10.1111/2041-210X.12262>
- Louis, S., Godary-Dejean, K., Lapierre, L., Claverie, T. & Villéger, S. (2017a) Formal method for mission controller generation of a mobile robot. https://doi.org/10.1007/978-3-319-64107-2_48
- Louis, S., Lapierre, L., Onmek, Y., Dejean, K.G., Claverie, T. & Villeger, S. (2017b) Quaternion based control for robotic observation of marine diversity. *Ocean. 2017 - Aberdeen 2017-October*, 1–7. <https://doi.org/10.1109/OCEANSE.2017.8085006>
- Mallet, D. & Pelletier, D. (2014) Underwater video techniques for observing coastal marine biodiversity: a review of sixty years of publications (1952–2012). *Fisheries Research*, **154**, 44–62. <https://doi.org/10.1016/j.fishres.2014.01.019>
- Munday, P.L., Jones, G.P., Pratchett, M.S. & Williams, A.J. (2008) Climate change and the future for coral reef fishes. *Fish and Fisheries*, **9**, 261–285. <https://doi.org/10.1111/j.1467-2979.2008.00281.x>
- Neuswanger, J.R., Wipfli, M.S., Rosenberger, A.E. & Hughes, N.F. (2016) Measuring fish and their physical habitats: versatile 2D and 3D video techniques with user-friendly software. *Canadian Journal of Fisheries and Aquatic Science*, **73**, 1861–1873. <https://doi.org/10.1139/cjfas-2016-0010>
- Obura, D.O., Aeby, G., Amorntthamarong, N., Appeltans, W., Bax, N., Bishop, J. et al. (2019) Coral reef monitoring, reef assessment technologies, and ecosystem-based management. *Frontiers in Marine Science*, **6**, 1–21. <https://doi.org/10.3389/fmars.2019.00580>
- Pielou, E.C. (1966) The measurement of diversity in different types of biological collections. *Journal of Theoretical Biology*, **13**, 131–144.
- PNMM (2016) Rapport d'activités. Available from: <https://en.calameo.com/read/0035029487634d949b1ee> [Accessed 26 April 2021].
- Raoult, V., Tosoletto, L., Harvey, C., Nelson, T.M., Reed, J., Parikh, A. et al. (2020) Remotely operated vehicles as alternatives to snorkellers for video-based marine research. *Journal of Experimental Marine Biology and Ecology*, **522**, 151253. <https://doi.org/10.1016/j.jembe.2019.151253>

- R Core Team (2020) *R: A language and environment for statistical computing*. Vienna: R Foundation for Statistical Computing. Available from: <https://www.R-project.org/> [Accessed 30 January 2021].
- Robinson, J.P.W., Wilson, S.K., Robinson, J., Gerry, C., Lucas, J., Assan, C. et al. (2019) Productive instability of coral reef fisheries after climate-driven regime shifts. *Nature Ecology & Evolution*, **3**, 183–190.
- Samoilys, M.A. & Carlos, G. (2000) Determining methods of underwater visual census for estimating the abundance of coral reef fishes. *Environmental Biology of Fishes*, **57**, 289–304. <https://doi.org/10.1023/A:1007679109359>
- Schramm, K.D., Harvey, E.S., Goetze, J.S., Travers, M.J., Warnock, B. & Saunders, B.J. (2020) A comparison of stereo-BRUV, diver operated and remote stereo-video transects for assessing reef fish assemblages. *Journal of Experimental Marine Biology and Ecology*, **524**, 151273. <https://doi.org/10.1016/j.jembe.2019.151273>
- Somerton, D.A., Williams, K. & Campbell, M.D. (2017) Quantifying the behavior of fish in response to a moving camera vehicle by using benthic stereo cameras and target tracking. *Fishery Bulletin*, **115**, 343–354. <https://doi.org/10.7755/FB.115.3.5>
- Stankowich, T. & Blumstein, D.T. (2005) Fear in animals: A meta-analysis and review of risk assessment. *Proceedings of the Royal Society B-Biological Sciences*, **272**, 2627–2634. <https://doi.org/10.1098/rspb.2005.3251>
- Stimpert, A.K., Madrigal, B.C., Wakefield, W.W. & Yoklavich, M.M. (2019) Acoustic influence of underwater mobile survey vehicles on the soundscape of Pacific rockfish habitat. *Journal of the Acoustical Society of America*, **146**, EL45–EL51. <https://doi.org/10.1121/1.5109914>
- Stoner, A.W., Ryer, C.H., Parker, S.J., Auster, P.J. & Wakefield, W.W. (2008) Evaluating the role of fish behavior in surveys conducted with underwater vehicles. *Canadian Journal of Fisheries and Aquatic Science*, **65**, 1230–1243. <https://doi.org/10.1139/F08-032>
- Stuart-Smith, R.D., Brown, C.J., Ceccarelli, D.M. & Edgar, G.J. (2018) Ecosystem restructuring along the Great Barrier Reef following mass coral bleaching. *Nature*, **560**, 92–96.
- Sward, D., Monk, J. & Barrett, N. (2019) A systematic review of remotely operated vehicle surveys for visually assessing fish assemblages. *Frontiers in Marine Science*, **6**, 1–19. <https://doi.org/10.3389/fmars.2019.00134>
- Villon, S., Mouillot, D., Chaumont, M., Darling, E.S., Subsol, G., Claverie, T. et al. (2018) A deep learning method for accurate and fast identification of coral reef fishes in underwater images. *Ecological Informatics*, **48**, 238–244. <https://doi.org/10.1016/j.ecoinf.2018.09.007>
- Villon, S., Mouillot, D., Chaumont, M., Subsol, G., Claverie, T. & Villéger, S. (2020) A new method to control error rates in automated species identification with deep learning algorithms. *Scientific Reports*, **10**, 10972.
- Wand, M. (2011) KernSmooth: functions for kernel smoothing for Wand & Jones (1995). R package version 223-7. Available from: <http://CRAN.R-project.org/package=KernSmooth>. Accessed 07 December 2020.
- Wartenberg, R. & Booth, A.J. (2014) Video transects are the most appropriate underwater visual census method for surveying high-latitude coral reef fishes in the southwestern Indian Ocean. *Marine Biodiversity*, **45**, 633–646. <https://doi.org/10.1007/s12526-014-0262-z>
- Wetz, J.J., Ajemian, M.J., Shipley, B. & Stunz, G.W. (2020) An assessment of two visual survey methods for documenting fish community structure on artificial platform reefs in the Gulf of Mexico. *Fisheries Research*, **225**, 105492. <https://doi.org/10.1016/j.fishres.2020.105492>
- Wickel, J. & Guillemot, N. (2012) Les peuplements ichtyologiques de Mayotte - synthèse des connaissances, caractérisation et recherche d'indicateurs d'impacts de la pêche.
- Woodhead, A.J., Hicks, C.C., Norström, A.V., Williams, G.J. & Graham, N.A.J. (2019) Coral reef ecosystem services in the Anthropocene. *Functional Ecology*, **33**, 1023–1034.

Supporting Information

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Data S1. List of species with corresponding family measured in that study.

Data S2. Comparison of five diversity indices computed based on fishes recorded using DOV (diver operated video) or SAUV (semi-autonomous underwater vehicle).

Data S3. How altitude could have affected measurements?