

REGULAR PAPER

Using unmanned aerial vehicle (UAV) surveys and image analysis in the study of large surface-associated marine species: a case study on reef sharks *Carcharhinus melanopterus* shoaling behaviour

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A novel image analysis-based technique applied to unmanned aerial vehicle (UAV) survey data is described to detect and locate individual free-ranging sharks within aggregations. The method allows rapid collection of data and quantification of fine-scale swimming and collective patterns of sharks. We demonstrate the usefulness of this technique in a small-scale case study exploring the shoaling tendencies of blacktip reef sharks *Carcharhinus melanopterus* in a large lagoon within Moorea, French Polynesia. Using our approach, we found that *C. melanopterus* displayed increased alignment with shoal companions when distributed over a sandflat where they are regularly fed for ecotourism purposes as compared with when they shoaled in a deeper adjacent channel. Our case study highlights the potential of a relatively low-cost method that combines UAV survey data and image analysis to detect differences in shoaling patterns of free-ranging sharks in shallow habitats. This approach offers an alternative to current techniques commonly used in controlled settings that require time-consuming post-processing effort.

KEYWORDS

blacktip reef shark, *Carcharhinus melanopterus*, image analysis, shoaling behaviour, UAV

Significance Statement. The difficulty in observing and quantifying natural behaviours of wild marine organisms without disturbance limits our understanding of their behavioural responses to a changing environment. We developed an approach combining image analysis and unmanned aerial vehicle surveys to observe free-ranging large group-living epipelagic animals and rapidly quantify their movements and behaviour. We demonstrate the potential of this approach in a study exploring shoaling patterns and swimming dynamics of blacktip reef sharks in shallow lagoon microhabitats.

1 | INTRODUCTION

Collecting high quality data to examine the distribution, density or behaviour of free-ranging large marine organisms has challenged scientists for decades. This is particularly true for elasmobranchs and

large marine mammals for which measuring variation in densities over various spatial and temporal scales is necessary to gather the information necessary for developing sound conservation and management plans. Over the years, aerial surveys have been extensively used in studies of marine wildlife, particularly to assess their distribution and abundance (Bayliss, 1986; Hodgson *et al.*, 2016; Kajiura & Tellman, 2016; Marsh & Sinclair, 1989; Pollock *et al.*, 2006; Rowat *et al.*, 2009). Recent studies have demonstrated the potential of using unmanned aerial vehicles (UAV or drones) equipped with a high-resolution video camera to provide density estimates (or at least encounter rates) of marine fauna with no or limited disturbance (Hodgson *et al.*, 2013, 2016; Kiszka *et al.*, 2016). For example, Kiszka *et al.* (2016) showed that direct estimates of densities of reef-associated elasmobranchs can be obtained from UAV video surveys in shallow tropical lagoon habitats. Yet, UAV video surveys are often limited to assess the distribution and relative abundance of free-ranging surface aquatic

organisms (mostly air-breathing species such as marine mammals and sea turtles).

Currently, the techniques for quantifying the fine-scale behavioural patterns, such as swimming dynamics, aggregative tendencies and social interactions are limited. In a social context, the internal structure of an aggregation (e.g. the level of alignment between individuals or how far apart they are) has been identified as an important feature for understanding the formation, maintenance and the highly synchronized reactions observed in many fish shoals (Rieucau *et al.*, 2015). The recent development of quantitative approaches (e.g. multi-target computer tracking, post-processing analyses of acoustic or optic images and videos) to describe and analyse dynamic shoaling behaviour and how fish achieve coordinated movements has opened new avenues of research (Gerlotto *et al.*, 2006; Handegard *et al.*, 2012; Herbert-Read, 2016; Herbert-Read *et al.*, 2017; Rieucau *et al.*, 2016bb; Rosenthal *et al.*, 2015). However, the methods available currently require sophisticated and time-consuming post-processing procedures to extract data and are often restricted to be used in controlled-settings (e.g. tanks, sea cages). Here, we present a novel relatively low-cost quantification technique based on image analysis to detect and locate wild large epipelagic organisms in shallow systems and to rapidly quantify their fine-scale behaviours observed during UAV video surveys.

In many aquatic organisms, shoaling is a widespread phenomenon primarily considered as a strategy that provides important safety benefits through several mechanisms including predation risk dilution, predator detection, deterrence (for some species), confusion, collective responsiveness and synchronized evasive manoeuvres (Pitcher & Parrish, 1993; Rieucau *et al.*, 2015). Shoaling can also provide further important advantages such as enhanced food detection and acquisition (Pitcher *et al.*, 1982; Fernö *et al.*, 1998), migration facilitation (Makris *et al.*, 2009; Quinn & Fresh, 1984) and energetic and hydrodynamic efficiency (Domenici, 2001, 2010; Hemelrijk *et al.*, 2015). Variation in shoaling tendency in marine fish species is commonly observed in response to environmental variation, predation risk and anthropogenic disturbance (Boswell *et al.*, 2016; Fernö *et al.*, 1998; Makris *et al.*, 2009; Paramo *et al.*, 2010; Soria *et al.*, 2003), supporting the idea that fish shoals can display a high degree of behavioural and structural plasticity (Fernö *et al.*, 1998; Mackinson, 1999; Rieucau *et al.*, 2015). Shoal-level modifications are thought to reflect changes in the way fish in groups balance fitness trade-offs (e.g. feeding, survival or reproduction) (Ferno *et al.*, 1998; Freon *et al.*, 1992; Misund, 1993; Pitcher & Parrish, 1993). There is a growing body of evidence supporting the idea that collective responses yield a significant adaptive advantage, for instance, as they facilitate information transfer through the group (Handegard *et al.*, 2012; Katz *et al.*, 2011; Marras *et al.*, 2012; Rieucau *et al.*, 2014, 2016bb; Rosenthal *et al.*, 2015; Treherne & Foster, 1981). Recent research has also demonstrated that shoaling fish can make acute and rapid adjustments in their collective structure (e.g. swimming faster and being more aligned with their school mates) in response to changes in their local conditions (e.g. increased predation risk), in such a way that enhances collective information transfer among individuals and improves collective responsiveness (Rieucau *et al.*, 2016bb). Collective responses may also serve as an important process for structuring animal grouping patterns. Therefore, understanding the processes underlying information

transfer and how animals in groups organize themselves to ensure efficient information flow is important for the study of collective behaviour and sociality.

In group-living elasmobranchs, information transfer can play a pivotal role in various ecological contexts including predator avoidance, social foraging, agonistic interactions and mating (Ebert, 1991; Economakis & Lobel, 1998; Klimley, 1985; Sims *et al.*, 2000). While little is known about the collective behavioural patterns and shoaling dynamics of sharks, some species have been shown to perform following or parallel-swimming behaviour (Guttridge *et al.*, 2012; Mourier *et al.*, 2012). In light of declines in reef-shark populations worldwide (Graham *et al.*, 2010; Robbins *et al.*, 2006), it becomes important to describe and understand better their behavioural patterns, as well as determining the drivers of the formation of reef-shark aggregations. Several coastal shark species display aggregative behaviours and form preferred individual associations (Guttridge *et al.*, 2009; Loiseau *et al.*, 2016; Mourier *et al.*, 2012). However, it remains unknown whether reef sharks exhibit context-dependent adjustments of shoaling behaviour to changes in either biotic or abiotic factors. Such insights have remained elusive due to the difficulty in observing natural behaviour in the wild; therefore, there is a critical need for the development of a reliable technique to study gregarious sharks in their natural conditions.

In this paper, we illustrate the potential of our approach in a small-scale case study of shark shoaling behaviour. To date, most methods used to study shark behaviour, distribution and population dynamics include diver, fishery, or baited-camera dependent approaches (Bond *et al.*, 2012; Goetze & Fullwood, 2013; Papastamatiou *et al.*, 2009; Rizzari *et al.*, 2014). Yet, the intrusive nature of some of these methods may alter the natural behaviour of the species of interest. In this study, we employed our quantification approach to test whether free-ranging blacktip reef sharks *Carcharhinus melanopterus* (Quoy & Gaimard 1824) have the ability to display collective responses by modifying their collective tendency and shoal structural organization in response to changing environmental conditions or anthropogenic disturbances. We conducted constant-altitude UAV video surveys off the north coast of Moorea, French Polynesia. We measured *C. melanopterus* local densities and shoaling tendency (e.g. inter-individual distances and swimming alignment) in a shallow coral lagoon that contrasts in environmental conditions and anthropogenic activities: a deeper sandy bottom open water channel and a shallow sandflat area. In the sandflat, *C. melanopterus* are regularly baited for ecotourism purposes (Gaspar *et al.*, 2008).

2 | MATERIALS AND METHODS

2.1 | Study site and species

The study occurred off the north coast of Moorea, located in the Society Archipelago, French Polynesia (17° 32' S; 149° 52' W; Figure 1). We focussed our surveys in the shallow inner waters of the lagoon, where blacktip reef sharks aggregate on a sandflat area adjacent to a deeper channel. Shark and ray tourism, including provisioning (where animals are baited), occurs for pink whiprays *Pateobatis fai* (Jordan & Seale 1906) and *C. melanopterus* (Gaspar *et al.*, 2008). Reef and

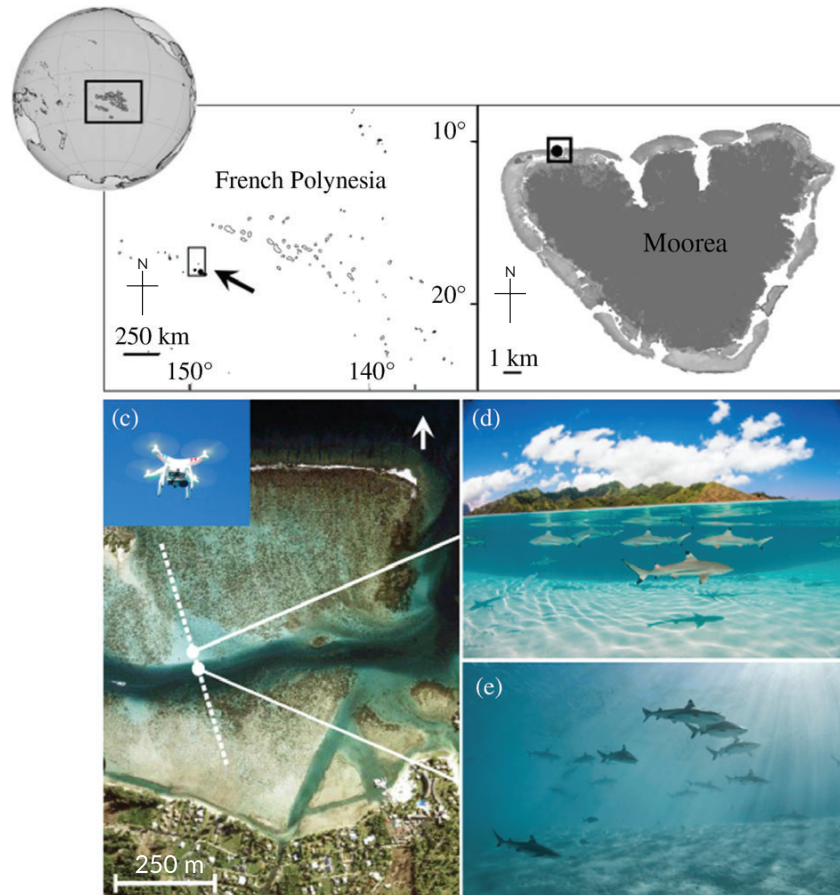


FIGURE 1 (a) Location of the Society Archipelago, French Polynesia and (b) the study site (●) off the north coast of island of Moorea. (c) The two adjacent microhabitats, sandflat and deep channel and the 400 m transect (—) flown by quadcopter drone to survey *Carcharhinus melanopterus* shoaling over (d) the sandflat and (e) in the deep channel (underwater photo credit: Lauric Thiault and Thomas Vignaud)

sandflats were 1.5 to 2 m depth while the channel was 2 to 7 m (tidal range 0.4 m; Figure 1). Adult *C. melanopterus* are 90–150 cm (total length, L_T) and primarily occur in intertidal reef flats, lagoons and seaward slopes of coral reefs. *Carcharhinus melanopterus* are the most abundant shark species in the waters of Moorea, including the lagoon and its surrounding outer reef waters (Mourier *et al.*, 2013). In Moorea, they form small spatial groups and seem to actively form preferred associations, which suggest some levels of sociality (Mourier *et al.*, 2012). The water clarity in the two microhabitats allowed us to easily detect sharks visually that swam close to the surface due to their contrast against the visual background.

2.1.1 | UAV surveys

Drone flights were conducted using a DJI Phantom II UAV quadcopter (30 × 30 × 18 cm) (www.dji.com) equipped with a GoPro Hero 3+ Silver edition camera (www.gopro.com) (with a 64 GB mini SD card) mounted underneath, as well as a set of six 5200 mAh Lithium Polymer batteries. The Phantom II included a Naza-M V2 multi-axis flight controller, GPS and compass that permitted stable flight conditions with consistent altitude and compensated for variable wind effects. During each flight, the camera recorded 1920 × 1080 pixels HD video at 30 frames/s in the wide field of view setting. The camera was

positioned to film straight down and a polarizing filter was used to minimize glare. A H3-3D 3-axis gimbal (DJI) was used to stabilize the GoPro. Originally, UAV surveys were designed to assess reef-shark and ray densities in the northern lagoon of Moorea (Kiszka *et al.*, 2016). For the purpose of this study, a 400 m transect was flown perpendicular to the fringing reef, a deeper channel and the back reef sandflat at a constant altitude of 12 m (Figure 1). Flights were undertaken on 10 different days between 2 and 25 July 2014 between 0800–1000 h and only when visibility conditions were good (absence of glare and wind, i.e. Beaufort < 1). On the sandflat, tourism and provisioning activities occur all day long (Gaspar *et al.*, 2008; Kiszka *et al.*, 2016).

A series of fixed images were selected from videos collected during aerial surveys. Owing to the orientation of the camera lens and our flight survey design with no hovering, we faced the logistical challenge that it was not possible to select multiple images of a particular *C. melanopterus* aggregation to be used as replicates because the whole visual scene moved from frame to frame affecting the accuracy of drone-to-shoal distance estimates. To overcome this challenge and to minimize image distortion (ultra-wide-angle or fisheye effect), we selected one representative frame by habitat per transect flight for which the position of the drone was as close to perpendicular as

possible relative to the *C. melanopterus* aggregation, with the shoal being c. central in the image. Only one frame per habitat was used to avoid possible pseudo replication that may result from the analysis of non-independent successive frames of the same aggregation.

2.1.2 | Quantification of *C. Melanopterus* collective behaviour

We developed a semi-automated tracking algorithm (Figure 2) that offers a graphical user interface in Matlab (Mathworks; www.mathworks.com) to detect and position individuals on aerial frames. Our algorithm was designed to quantify shoaling tendency of aggregated individuals (i.e. *C. Melanopterus* at our study site). This approach was employed to estimate the relative size of individuals (in pixels), inter-individual distances and swimming alignment of shoaling individuals across the two microhabitats sampled (sandflat and deeper channel). The procedure involved an initial point-and-click identification of all individual sharks on a given image followed by an automated analysis technique.

2.1.3 | Individual identification

Analysing still images collected from mobile devices (such as UAVs) implies that the whole scene moves from one image to another, making application of common image processing techniques, such as background removal or thresholding, unsuitable. Consequently, it was not possible to fully automate individual detections. Individual identification started by displaying a sample aerial image. In order to facilitate identifying of all individuals sighted in a single image, each image was cropped and adjusted to smaller areas of interest containing individuals. Further, an iterative process was initiated for which the cropped area [Figure 3(a)] was disaggregated into sub-images that were magnified using constant magnification.

2.1.4 | Post-processing analysis

For each sub-image, the observer located each individual by clicking on the most distant points of each individual, i.e. the anterior point of the head (H_x, H_y) and posterior point of the tail (T_x, T_y). This provided the central position (C_x, C_y), as the mean of those two points, the relative body length (L_B) as the Euclidean distance between head and tail (in pixels) and the swimming orientation (u, v) of each individual. Since

the analysis was performed on still images, there was no notion of speed. Consequently, our procedure provided the size of each individual and its orientation with respect to the origin of coordinates. In order to compare alignment between individuals, the orientation vector (u, v) was of importance. For this reason, we established a length (magnitude) for that vector that was equal to the labelled *C. melanopterus* length. This value did not affect further calculations as we were principally interested in comparing orientation of sharks (angles between nearest shoaling individuals), therefore this parameter could be set as a constant (e.g. a unitary vector). Once all individuals observed in a sub-image were identified, the identification process continued until the whole cropped area was scanned. Although we used sub-windows, the position of all sharks was expressed with respect to the origin of coordinates of the complete image, with (0,0) position corresponding to the upper left corner.

The L_B of each identified *C. melanopterus* was calculated as the Euclidean distance between the anterior point on the head and posterior point on the tail: $L_B = \sqrt{(T_x - H_x)^2 + (T_y - H_y)^2}$.

In order to quantify the distance between individuals, the nearest neighbour to each *C. melanopterus* was determined using the central position (C_x, C_y) as a reference. For each shark's central position, we identified the neighbour with the shortest Euclidean distance from a focal individual. Once all nearest neighbours were determined, we calculated alignment between an individual and its closest neighbour using their swimming orientation (u, v) and the magnitude of the vectors for comparison. Based on these values, the Dot Product can be used to calculate the swimming alignment: $ab = |a| \times |b| \times \cos(\theta)$, where a and b are the vectors defining the swimming orientation of two adjacent sharks, $|a|$ and $|b|$ represent the magnitude (i.e. lengths in pixels) of each vector a and b , respectively and θ is the angle (in degrees) between the vectors a and b . In our case, θ can be derived from the Dot Product equation as follows: $\theta = \cos^{-1} [(ab)/(|a||b|)^{-1}]$.

The distance between adjacent individuals and the alignment were compared with the median estimates for the shoal in a sampled image. We assumed that an individual was swimming in a coordinated manner with its nearest neighbour if the relative distance between them was smaller than $2 L_B$ (in pixels) and the angle towards the

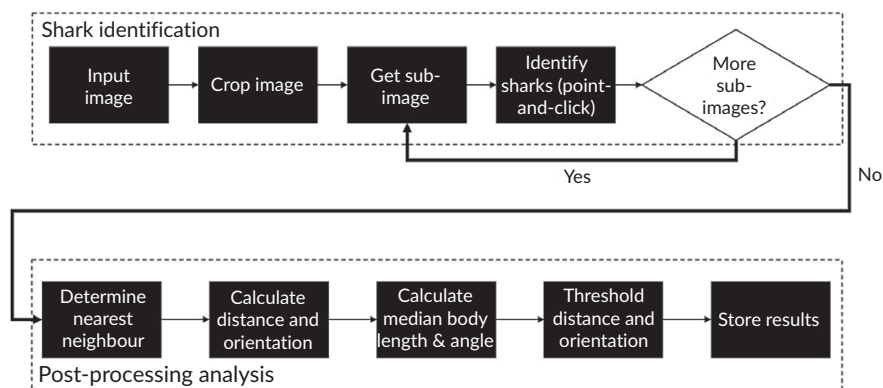


FIGURE 2 The algorithm operation flow showing the *Carcharhinus melanopterus* identification and post-processing analysis (behavioural metrics calculation) procedures

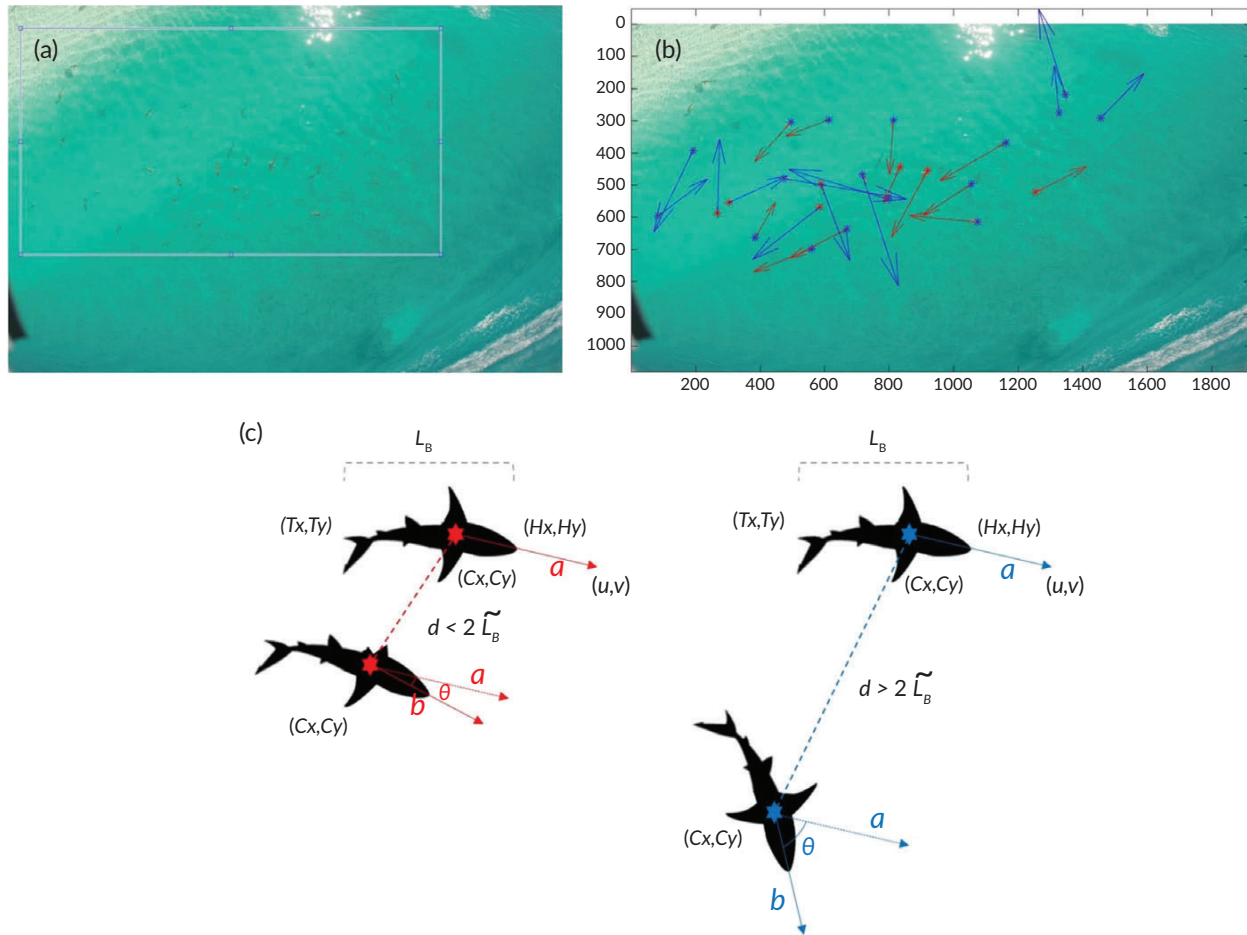


FIGURE 3 Sample image from unmanned aerial vehicle surveys. (a) The frame encompasses an aggregation of *Carcharhinus melanopterus* in the channel microhabitat and (b) the same aggregation after the post-processing analysis. (c) The quantification approach of collective tendencies and the behavioural proxies measured. ★, ★, the central position (Cx, Cy) of an individual in an image estimated from the position of its head (Hx, Hy) and its tail (Tx, Ty). The swimming orientation of each individual is given by (u,v); ★---★, distances between two closest sharks smaller than the threshold τ [i.e. twice the median body length (\tilde{L}_B) in pixels, estimated from L_B of all individuals in an image]; ★---★, distances between two closest individuals greater than τ ; θ , The angle between the swimming direction (u,v) of two closest *C. melanopterus* (a and b are the vectors defining the swimming orientation); \rightarrow , situations where $\theta < \bar{\theta}$ (where $\bar{\theta}$ is the median angle between all pairs of sharks in an analysed image, indicating that pairs of *C. melanopterus* are swimming in a well aligned manner); \rightarrow , cases where $\theta > \bar{\theta}$, indicating that the two closest *C. melanopterus* were less well aligned

closest neighbour was below the median angle, θ , between all pairs of sharks. The first criterion was based on the median distance of the set of L_B of all individuals measured within a sampled image and calculated as: $L_B = \bigcup_{i=1}^n \sqrt{(Tx_i - Hx_i)^2 + (Ty_i - Hy_i)^2}$, where n is the number of identified sharks. The median \tilde{L}_B , was calculated as the $\{(n + 1)0.5\}^{th}$ value of the sorted series, L_B . The conservative threshold, τ , was established from this value as being $\tau = 2\tilde{L}_B$. Distances between two closest individuals smaller than the established threshold (τ) were shown as red asterisks on the image [Figure 3(b,c)], where an asterisk represents the central position (Cx,Cy) of each shark within an image. Blue asterisks indicated between-individual distances greater than τ .

The second criterion to establish that two neighbouring *C. melanopterus* present in an image were shoaling was the relation between their angle, θ and the median angle between all pairs of sharks, $\bar{\theta}$. Cases where $\theta < \bar{\theta}$ between two closest individuals were

shown as red arrows (each arrow indicates the swimming direction of each individual). Conversely, cases where $\theta > \bar{\theta}$ indicated that the two closest sharks were swimming in a less well aligned manner and therefore represented by blue arrows [Figure 3(b,c)].

2.1.5 | Statistical analysis

A one-way ANOVA was used to test if the two microhabitats differed in *C. melanopterus* density. We examined whether *C. melanopterus* relative body size and shoaling tendencies (distance between nearest shoaling neighbour and alignment) changed between the sandflat and the channel habitats using a series of linear mixed effects models (LME). Habitat type was included as a fixed effect in the LMEs. It is possible that the selected images may not have been satisfactory independent units of replication; therefore, we included day of collection of each image as a random effect in each LME to control for pseudo replication and the likely non-independence of the series of

images analysed. We tested whether the number of boats and swimmers present on the sandflat during shark provisioning activities affected between-individual distances of *C. melanopterus* and alignment using LMEs with the same random effect structure. These analyses were conducted only on sandflat data because no boats or swimmers were observed in the channel habitat. All analyses were conducted in R 3.12 (The R Foundation for Statistical Computing; www.r-project.org) and LMEs were performed using the nlme package.

3 | RESULTS

Over the 10 survey days, 14 aerial images were analysed using our image analysis toolbox (6 of 20 images collected were discarded because no *C. melanopterus* were sighted) and a total of 136 individual *C. melanopterus* were measured ($n_{\text{sandflat}} = 78$; $n_{\text{channel}} = 58$). There was no difference in abundance of *C. melanopterus* between the sandflat and the channel habitats ($F_{1,16} = 0.20$, $p > 0.5$). The relative body size of *C. melanopterus* did not differ between the two microhabitats ($t = 0.93$, d.f. = 125, $p > 0.05$).

The distance between nearest neighbours did not differ in the two microhabitats ($t = -0.35$, d.f. = 125, $p > 0.5$; channel = 163.43 ± 15.7 pixels; sandflat = 126.90 ± 13.54 pixels; mean \pm S.D.) [Figure 4(a)]. However, there were habitat differences in alignment ($t = -2.03$, d.f. = 125, $p < 0.05$), with *C. melanopterus* displaying greater alignment over the sandflat ($37.01 \pm 5.01^\circ$; mean \pm S.D.) compared with the channel ($52.34 \pm 5.81^\circ$; mean \pm S.D.) [Figure 4(b)]. Nearest neighbour distance and alignment did not vary relative to the number of boats (between-individual distance: $t = -0.67$, d.f. = 6, $p > 0.5$; alignment: $t = -0.38$, d.f. = 6, $p > 0.5$) or swimmers in the sandflat habitat (between-shark distance: $t = 1.66$, d.f. = 6, $p > 0.1$; alignment: $t = 0.53$, d.f. = 6, $p > 0.5$).

4 | DISCUSSION

Our study demonstrates the potential of our method based on image analysis using UAV surveys to detect differences in shoaling patterns and swimming dynamics of surface-associated marine organisms. This approach provides the opportunity to observe free-ranging sharks in their natural environments and rapidly quantify their fine-scale movements and behaviour without lengthy post-processing procedures. The data collected using our approach can inform about swimming dynamics of epipelagic animals and their collective behaviour and it can be further used for other large subsurface marine vertebrates (e.g. marine mammals, large fishes) in shallow clear water. The next step in improving our approach will be directed at implementing automated video post-processing to track and quantify swimming dynamics.

Due to our small sample size, care must be taken when interpreting our results. We found that *C. melanopterus* swam with greater alignment with nearest neighbours in the shallow reef sandflat compared with when they were in the deeper channel. This may suggest that *C. melanopterus* have the ability to exhibit context-dependent adjustments of their shoaling tendencies. The two microhabitats

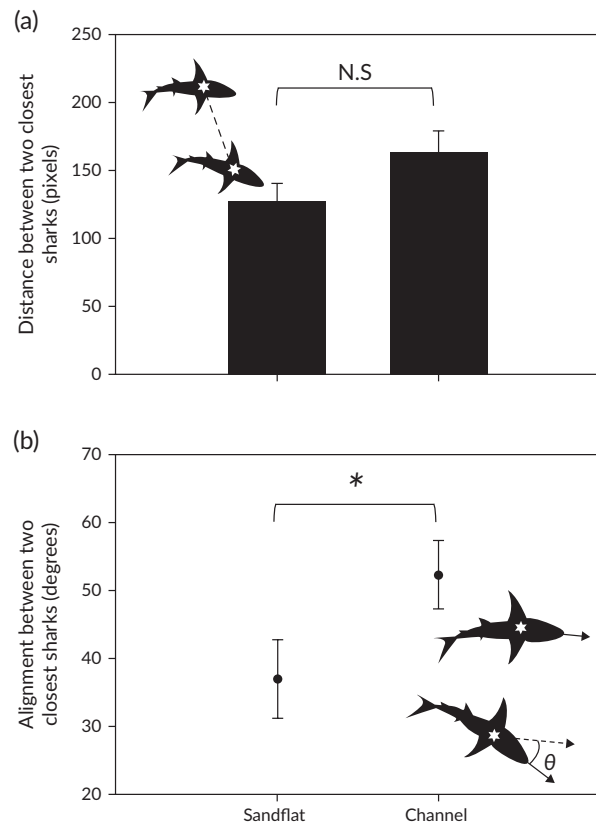


FIGURE 4 Mean \pm S.D (a) distance and (b) swimming alignment between two closest individual *Carcharhinus melanopterus* in the sandflat and channel microhabitats. N.S., No significant difference ($p > 0.05$); *, significant difference ($p < 0.05$)

sampled differed in abiotic (e.g. water depth, current strength) and anthropogenic (provisioning and ecotourism activities) factors. Although our small-scale study strengthens the general idea that shoaling in *C. melanopterus* is a dynamic process (Mourier *et al.*, 2012), we should now develop and conduct studies with greater sampling effort if we are to offer new insights about the mechanisms underlying aggregative behaviour of this facultative shoaling shark species.

Structural and behavioural changes at the shoal-level reflect how animals balance the benefits and costs of living in a group (Pitcher & Parrish, 1993; Rieucau *et al.*, 2015). Aggregated individuals face the ever-present challenge of making optimal decisions, within a collective context, to minimize their predation risk or similarly perceived threats such as human-induced disturbance (Frid & Dill, 2002), while optimizing other fitness-enhancing activities such as acquiring food, finding reproductive partners or suitable habitats (Krause & Ruxton, 2002). There is a growing body of evidence supporting that behavioural adjustments are aimed to promote efficient transfer of information within the shoal, collective responsiveness and evasion (Gerlotto *et al.*, 2006; Marras *et al.*, 2012; Rieucau *et al.*, 2016bb). By adopting a spatial organisation that facilitates the propagation of information among individuals, shoaling *C. melanopterus* may gain benefits through rapid and highly-coordinated collective manoeuvres when exposed to external stimuli (e.g. predators, sources of disturbance) or by having

access to food-related social information. It is now well-understood that a shoal's configuration and internal organisation (e.g. high levels of alignment between fish, reduced inter-fish distances) are important features to promote efficient information transfer among shoal members (Gerlotto *et al.*, 2006; Herbert-Read *et al.*, 2011; Marras *et al.*, 2012; Rieucau *et al.*, 2014, 2015). Shoal structural flexibility is considered as an adaptation improving information transfer among school members. The degree to which shoaling fish are aligned with others and how far apart they are, have been recognized as important factors in explaining how information can propagate rapidly in fish schools (Marras *et al.*, 2012; Rieucau *et al.*, 2014, 2016bb) and this regardless of how large the school is.

Although *C. melanopterus* can be preyed upon by large predators such as adult sicklefin lemon shark *Negaprion acutidens* (Rüppell 1837) or tiger sharks *Galeocerdo cuvier* (Péron & LeSueur 1822), these predators are generally absent inside the lagoon. It is, thus, unlikely that the observed changes in shoaling dynamics reflect response to a change in predation risk from larger shark species. Alternatively, it is possible that shoal-level adjustments can be induced by the presence of additional food resources in the sandflat habitat where provisioning by humans occurs often. In a social foraging context, a greater swimming alignment between individuals can enhance how efficiently foraging-related information propagates within the shoal. The formation of more polarized and cohesive shoals observed in the sandflat during foraging may provide individuals with higher feeding success due to the transmission of foraging information (i.e. location of food resource through local enhancement where individuals are being attracted to foraging companions; Galef and Giraldeau (2001)). No *C. melanopterus* were observed in the sandflat area in the absence of tourist boats and swimmers. Polarized collective swimming is also understood as a strategy that enables shoaling sharks to save energy, especially when swimming against strong currents (Klimley & Nelson, 1984). However, we found that *C. melanopterus* are less polarized in the channel habitat where they generally encounter stronger currents, a result that does not support the energy conservation hypothesis. It can also be argued that changes in swimming alignment can be mediated simply by water depth, with *C. melanopterus* swimming in deeper waters more likely to be further apart and less likely to be polarized with other shoaling individuals. Conversely, sharks may be forced to collectively swim in a more aligned manner to avoid collision with conspecifics in shallower waters, an effect that could be amplified in a habitat with food stimulation (provisioning). At this point, it is not possible to clearly tease apart the drivers (depth differences or the action of a social mechanism) of the observed differences of shoaling tendencies between the two habitats as no *C. melanopterus* were observed in the sandflat while no humans were present.

When employed in aquatic environments, UAV surveys are limited by the limit of detection of targeted objects in the water column. It is likely that this constraint has introduced some quantification errors as our observations were restricted to the horizontal plane making it challenging to ascertain the depth at which individual sharks were swimming. Thus, it is possible that an individual may have been miscategorised as being the closest-neighbour if it was located above or underneath a focal shark despite being far apart compared with the true closest companion on the same horizontal plane. It is important

to note, however, that the channel remains relatively shallow and we are confident that the uncertainty arising from the limited detectability in the vertical plane and the lack of depth information could have only marginally influenced our results.

Further efforts should be directed at implementing automated video post-processing to track and quantify swimming dynamics. Recent advances in automated tracking techniques such as the use of particle image velocimetry (PIV) allow researchers to measure swimming dynamics and collective reactions of pelagic fish with great precision, even in very dense shoals (Rieucau *et al.*, 2016aa,b). To overcome the important challenge of controlling for the drone movement, our tracking algorithm could be implemented with optic-flow based techniques. It would enable following and measuring of sharks' movements and behaviour even when the drone is in motion by estimating the drone motion as discrete image displacements to establish reference, isolating one or several moving objects (here individual sharks) and subtracting the background movement. Therefore, our method enhanced with automated tracking and video analysis will provide a tool for gaining further insights into social and collective behaviour of surface-associated large marine animals and ultimately can provide information of prime importance for the development of effective conservation and management plans of these long-lived species.

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