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Seasonal aggregations of blacktip sharks *Carcharhinus limbatus* at a marine protected area in the Gulf of California, assessed by unoccupied aerial vehicle surveys

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ABSTRACT: No-take marine protected areas (MPAs) can provide spatial refuge for species throughout all or part of their life cycles. Cabo Pulmo National Park (CPNP) is a no-take MPA located on the south-east coast of the Baja California Peninsula, Mexico, where there has been an increase in the abundance and diversity of elasmobranch species since its closure to fishing. An unoccupied aerial vehicle was used to complete weekly aerial surveys over sandy habitat in CPNP to determine the relative abundance of blacktip sharks *Carcharhinus limbatus* over a 1 yr period in 2019. *C. limbatus* were only observed during winter months, and abundance per survey ranged between 7 and 1086 sharks (289 ± 59, mean ± SE), yielding a maximum density of 4827 ind. km^{-2}. A generalized additive model determined that sea surface temperature (SST), time of day, photoperiod and wind speed were significant influencers of *C. limbatus* abundance. According to this model, higher abundance is expected when SST is lower than 25°C, during the afternoon, at low wind speeds (<4 knots) and when photoperiod is between 12 and 13 h. The close proximity of *C. limbatus* to the shoreline is likely a result of a refuging behaviour, with sharks utilising the shallow sandy habitat to behaviourally thermoregulate and/or to avoid predators.

KEY WORDS: Aerial survey · Drone · Unoccupied aerial system · Generalized additive model · Elasmobranch · Cabo Pulmo National Park · Environmental factors · Refuging

1. INTRODUCTION

The blacktip shark *Carcharhinus limbatus* (Müller & Henle, 1839) is distributed throughout tropical and sub-tropical regions worldwide in waters associated with continental shelves, where it primarily feeds on teleost fish, crustaceans and cephalopods (Compagno 1984). It commonly reaches over 2 m in total length (TL) in the eastern Pacific (Bizzarro et al. 2007, Estupiñán-Montaño et al. 2018, Ketchum et al.

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2020), where it is distributed from the coasts of California (USA) to Peru (Compagno 1984). Large seasonal aggregations of this species are formed along the eastern coast of Florida (USA), which is a phenomenon evident from aerial surveys completed with occupied aircraft (Kajiura & Tellman 2016). It is currently assessed as 'Vulnerable' on the IUCN Red list (Rigby et al. 2021) due to its value to commercial and recreational fisheries worldwide, particularly in the Gulf of Mexico and south-east USA, where it is frequently captured (NMFS 2003, Morgan & Burgess 2007).

In Mexico, artisanal fisheries dominate the elasmobranch fishing industry, and sharks are targeted for meat, which is consumed locally, and for fins, which are exported (Sosa-Nishizaki et al. 2020). In the Gulf of California (GOC), *C. limbatus* shows signs of overfishing (Bizzarro et al. 2007), and little effort has been made to establish protective areas in nursery and aggregation sites, except for Cabo Pulmo National Park (CPNP), which has become a de facto no-take area for *C. limbatus* (Ketchum et al. 2020). CPNP is located on the south-east coast of the Baja California Peninsula and was designated as a no-take national marine park in 1995 (Reyes-Bonilla 1997). Within 10 yr of the park's creation, fish biomass was reported to have increased by 463% and biomass of top predators increased 11-fold (Aburto-Oropeza et al. 2011). The earliest record of *C. limbatus* in CPNP was in 1972 (Brusca & Thomson 1975), and observations of seasonal aggregations close to the shoreline have been reported by locals since 2008 (D. Castro pers. comm.) and by divers since 2011 (Ketchum et al. 2020) and confirmed from visual censuses carried out since 2013 (Asúnsolo-Rivera 2016, El-Saleh 2016).

Aggregating behaviour and group-living in sharks can be driven by biotic factors such as reproduction, prey availability, predator avoidance and social interaction (Jacoby et al. 2012). Aggregations can also be formed due to habitat selection, which is influenced by abiotic factors such as temperature, salinity, dissolved oxygen, tide and photoperiod, with fluctuations in these factors also acting as cues for movements and migrations (Schlaff et al. 2014). Juvenile *C. limbatus* along the coast of Texas show a preference for warm shallow waters, in close proximity to inlets and at salinities between 20 and 35 psu (Froeschke et al. 2010). In Florida, adult *C. limbatus* aggregate close to shore during winter, and their northerly migration occurs around the vernal equinox, when sea surface temperatures (SSTs) reach over 25°C (Kajiura & Tellman 2016). The occurrence of aggregations provides a unique opportunity to collect data that have proven difficult to obtain for elasmobranch species, as they are usually dispersed and wide-ranging (Musick et al. 2000).

Aerial surveys are commonly used to study large elasmobranch species, such as whale sharks *Rhincodon typus* owing to their detectability as surface-associated filter feeders (Cliff et al. 2007, Rowat et al. 2009, Ketchum et al. 2013). These surveys are traditionally carried out on board an aircraft by 2 observers who count animals from above (Pollock et al. 2006). Aerial surveys can be subject to perception bias, which occurs when animals are available for detection but are missed due to human error, and availability bias, which occurs when animals are within a survey area yet are not available for detection, i.e. they are cryptic at the time of the survey (Marsh & Sinclair 1989). In marine environments, availability bias can be caused by water visibility, water movement and sun glare, or by the depth of the animal in the water column (Colefax et al. 2018). These biases can be minimised with survey design, and in shallow areas where there is contrast between the target species and habitat substrate, it is possible to complete accurate abundance surveys (Kessel et al. 2013).

Unoccupied aerial vehicles (UAVs; 'drones') are emerging as invaluable tools for the aerial surveying of marine fauna, as they can be flown at lower altitudes than occupied aircraft and are relatively affordable, lightweight and user-friendly (Anderson & Gaston 2013). Multi-rotor UAVs are commonly used for surveying small areas such as bays, beaches and nearshore environments, owing to their small range and flight endurance, rapid vertical take-off capability and general guidelines that require UAVs to remain within line-of-sight (Raoult et al. 2020, Butcher et al. 2021). The need for surveillance at beaches has also driven the use of UAVs as a tool for detecting large apex shark species that could be a potential threat to swimmers (Butcher et al. 2019, Kelaher et al. 2019, Colefax et al. 2020). Their use to study smaller shark species is also increasing in the literature, which has included blacktip reef sharks *C. melanopterus* (Kiszka et al. 2016, Raoult et al. 2018, Rieucau et al. 2018), sickle-fin lemon sharks *Negaprion acutidens* (Raoult et al. 2018), lemon sharks *N. brevirostris* (Ayres et al. 2021), epaulette sharks *Hemiscyllium ocellatum* (Raoult et al. 2018), Pacific nurse sharks *Ginglymostoma unami* (Ayres et al. 2021) and *C. limbatus* (Doan & Kajiura 2020, Porter et al. 2020).

In the present study, a small quadcopter UAV was used to carry out aerial surveys over shallow sandy habitat in CPNP with the aim to (1) quantify the relative abundance of *C. limbatus* over a 1 yr period, (2) determine environmental factors that influence variations in abundance and (3) determine the effectiveness of the use of a UAV as a long-term monitoring tool at CPNP.

2. MATERIALS AND METHODS

2.1. Study area

CPNP is located at the entrance to the GOC, a semi-enclosed sea that joins with the Mexican Pacific (Fig. 1). This area is highly productive and biodiverse due to its transitional location, and it is the most northerly coral reef ecosystem in the Eastern Tropical Pacific (Alvarez-Filip et al. 2006). The marine park covers 71 km^2 and its establishment was advocated by the local community (Reyes-Bonilla 1997). Prior to its creation, local inhabitants relied heavily on fishing as a main source of income, but this switched to providing tourism services, and the park is now a popular destination for scuba-diving (Reyes-Bonilla & Alvarez-Filip 2008).

The area selected for the UAV surveys was a remote sandy beach located in the north of the park (Fig. 1), situated approximately 5 km north of Cabo Pulmo town, at a distance from frequent dive boat activity and not easily accessible to the public. This location was also chosen due to previous sightings of *Carcharhinus limbatus* established from local knowledge and the shallow water bathymetry (<5 m depths). Geographically, it is the longest stretch of uniform sand substrate within CPNP, which facilitates the detection of sharks from an aerial perspective.

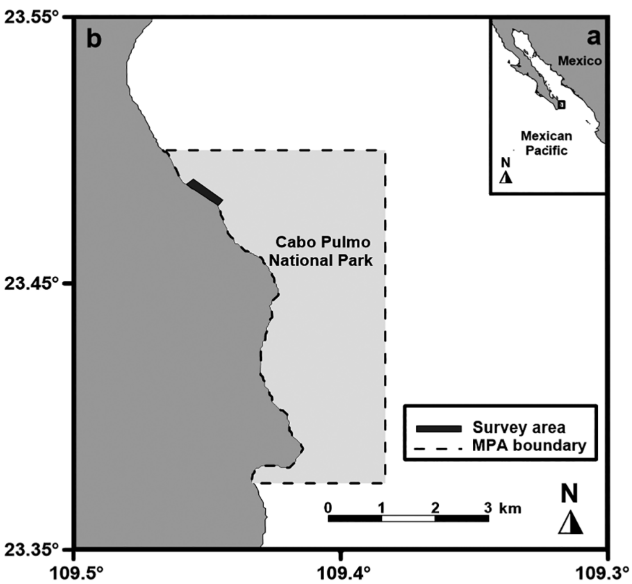

Fig. 1. (a) Location of study site in the Baja California Peninsula, Mexico; (b) no-take boundaries of Cabo Pulmo National Park and survey area covered by the unoccupied aerial vehicle flights. MPA: marine protected area

2.2. Aerial surveys

The aerial surveys were conducted using a small quadcopter (DJI Phantom 4™) with an inbuilt camera and stabilising gimbal. The flights were piloted through the application DJI Go 4 App™ on a tablet connected to a remote controller. All surveys were recorded in 4K (4096 × 2160) high-definition video at 25 frames s^{-1}. Surveys were completed approximately once a week between 11 January and 22 December 2019. For each survey, the UAV was flown along a 1.5 km transect parallel to the shoreline until the sandy habitat substrate became rocky-reef. During flights, the UAV camera was orientated facing straight down with a polarising lens to reduce sun glare. The edge of the shoreline remained in the field of view of the camera as a reference (Video S1 in the Supplement at www.int-res.com/articles/suppl/m678p095_supp/) and to allow for the surveys to be accurately repeated. The UAV was flown at an altitude of 100 m, which gave an offshore field of view of 150 m, resulting in a total area surveyed of 0.225 km^2. The field of view was calculated by taking physical measurements with a tape measure using reference points on the survey beach. The UAV was flown at a speed of 5.5 m s^{-1}, and the duration of each survey lasted up to 4.5 min, depending on the wind speed and direction at the time of flight. The pilot was positioned on the beach approximately halfway between the transect start and end point, and the UAV was kept within line of sight. Two survey flights were conducted on each sampling day, between 09:00 and 10:00 h and between 15:00 and 16:00 h. It was not possible to complete surveys outside of these timeframes, as sun glare reflecting off the surface of the water blocked out the view of the transect area. Surveys were only completed when wind speed was low to moderate (<15 knots) to allow for a relatively calm sea state (<3 on the Beaufort scale). This method takes a strip-transect approach, and all sharks were assumed to be available for detection if they were within the transect area during the survey. Once each transect was completed, the UAV was flown at a lower altitude (~20 m) over solitary or groups of sharks that appeared close to the surface or at the shallowest areas at the wave break to confirm the species. On one sampling day, a camera (GoPro) was lowered from a kayak to identify *C. limbatus* from an underwater perspective, and on days where the water visibility was clear enough, it was possible to identify the *C. limbatus* that were swimming adjacent to the shoreline.

For each flight, predictor variables were recorded, including cloud cover (on a scale of 0–8, where 0 is no cloud and 8 is 100% cloudy), tidal height (water level relative to mean lower low water), time of day, photoperiod (day length), moon phase, wind direction, wind speed and SST. Wind speed was taken manually on site with an anemometer prior to each flight. SST was taken with a field thermometer from just below the surface of the seawater in the middle of the transect area, within the first few meters of the shoreline. Tidal height was obtained from tide calendars (https://predmar.cicese.mx) from the nearest tide station in Cabo San Lucas (78 km south of CPNP), and time lag differences between the 2 locations were considered to be minor. Photoperiod and moon phase were determined for each survey day using the packages 'geosphere' (Hijmans 2019) and 'lunar' (Lazaridis 2014) in R version 4.0.2 (R Core Team 2020). Water visibility was also recorded using a rank between 1 (excellent), when sand ripples on the seabed were visible, and 5 (poor), when they were not.

2.3. Data analysis

For each survey, frames from the video were extracted and imported into ImageJ (v. 1.52) in sequence order. *C. limbatus* were counted manually from each frame using the 'multi-point' tool which tallies the number of times the user clicks the image and marks each point with a number. A second reviewer also counted from the frames, to ensure no individuals were missed in the initial count. The average of the 2 counts was used for the data analysis. All *C. limbatus* were assumed to be adults, based on estimations of a kayak measuring 4 m in length as a reference within the transect area on one of the sampling days.

All statistical analyses were completed using R version 4.0.2 (R Core Team 2020). A generalized additive model (GAM) was used to determine the effects of the predictor variables on *C. limbatus* abundance, as this type of regression model can evaluate non-linear relationships by using smoothing functions (Chambers & Hastie 1992). A negative binomial distribution with a log link function was used to account for over-dispersion (due to the large number of zero observations), as it independently models the mean and variance by including an additional parameter known as theta (Hilbe 2007). The degree of smoothing was restricted to avoid overfitting; thus, the number of basis functions was limited to 4. The GAMs were built using the package 'mgcv' (Wood 2017). Before models were built, Pearson's coefficient of correlation was used to investigate correlation between the predictor variables. SST and month were positively correlated, so these variables were not included together in the models. A backwards-stepwise approach was used to determine the final model by first creating a full model and then removing each predictor variable and assessing the score of Akaike's information criterion (AIC) and adjusted R^2 (Table 1). The best-fitted GAM with the lowest AIC score included 4 predictor variables: the smoothing functions for wind speed, photoperiod, SST and the categorical

Table 1. Selection of final generalized additive model using Akaike's information criterion (AIC) score and adjusted R^2 to predict blacktip shark *Carcharhinus limbatus* abundance in Cabo Pulmo National Park, Mexico, considering the following variables: sea surface temperature (SST, °C), wind speed (knots), time of day (morning 09:00–10:00 h, afternoon 15:00–16:00 h), tidal height (m), photoperiod (h), cloud cover (0–8), moon phase and wind direction. Model in **bold** represents final model selected and significant predictors: $^{***}p < 0.001$

Model	AIC	Adjusted R^2
SST + Time of day + Wind Speed + Photoperiod + Cloud Cover + Moon Phase + Tidal Height + Wind Direction	330.393	0.959
SST + Time of day + Wind Speed + Photoperiod + Cloud Cover + Moon Phase + Tidal Height	325.731	0.917
SST + Time of day + Wind Speed + Photoperiod + Cloud Cover + Moon Phase	322.789	0.920
SST + Time of day + Wind Speed + Photoperiod + Cloud Cover	318.763	0.917
SST* + Time of day*** + Wind Speed*** + Photoperiod*** **	**317.406**	**0.892**
SST + Time of day + Wind Speed	337.323	−0.063
SST + Time of day	357.754	0.573
SST	368.485	0.323

variable time of day. All remaining variables were not included and the final model can be expressed as follows:

$$\log(\eta) = \alpha + f_1\,(\text{SST}) + f_2\,(\text{Wind speed}) + f_3\,(\text{Photoperiod}) + \text{Time of day} \quad (1)$$

where η is *C. limbatus* abundance, α is the intercept, and f_x is the smoothing function (thin plate regression splines).

3. RESULTS

A total of 60 flights (n = 29 in the morning, 31 in the afternoon) were conducted over 34 sampling days. Results from 1 flight survey were excluded from the analysis due to water visibility being classified as 5 (seabed not visible); all remaining flights were classified as 1 or 2 (seabed visible). Seven flights (10.3%) were not completed at the survey site due to wind speeds increasing to over 15 knots, to ensure all *Carcharhinus limbatu*s were available for detection. For some days, it was not possible to travel to the field site due to weather conditions and the remoteness of the location; hence sampling did not occur every week in some months.

From reviewing the video footage, sharks were observed swimming alone or in small, dispersed groups that were distributed across the entire transect area. On other occasions they were found in large, dense aggregations (Fig. 2) that often extended outside of the field of view of the UAV. Sharks were frequently observed within the first few metres of the shoreline, just behind the wave break from both UAV footage and in the field. Within dense aggregations, some *C. limbatus* were near the surface of the water whilst others were underneath, closer to the seabed (Fig. 3). Sharks were often observed swimming somewhat in alignment with each other and on other occasions with a random orientation, that is, non-schooling.

The GAM explained 98% of the total deviance, and all 4 variables in the model, namely SST, time of day, wind speed and photoperiod, were influential and significant ($p < 0.001$) predictors of *C. limbatus* abundance (Table 1). According to this model, higher abundance is expected when SST is lower than 25°C, during the afternoon, in calm wind conditions (<4 knots) and when the photoperiod is between 12 and 13 h (Fig. 4). SST ranged between 22 and 31°C throughout the year at the survey site, and *C. limbatus* were absent in the warmest months between May and November, demonstrating strong seasonality (Fig. 5). In winter months, abundance ranged between 7 and 1086 individuals (289 ± 59, mean ± SE). The highest abundance recorded was on an afternoon survey on 29 January 2019, which yielded a density of 4827 sharks km^{-2}. Afternoon surveys had significantly higher abundances of *C. limbatus* (501 ± 90 individuals) than morning surveys (107 ± 30) and on each sampling day, SST was on average half a degree Celsius higher (0.52 ± 0.04°C) in the afternoon than in the morning. Wind speed ranged between 1 and 15 knots across all surveys, and a higher abundance of *C. limbatus* was predicted by the model at low wind speeds (Fig. 4).

Fig. 2. Dense aggregation of blacktip sharks *Carcharhinus limbatus* adjacent to the shoreline in Cabo Pulmo National Park, Mexico, during an unoccupied aerial vehicle survey

4. DISCUSSION

The aims of the present study were to quantify the relative abundance of *Carcharhinus limbatus*, to determine the factors that influence abundance and to evaluate the effectiveness of the UAV as a tool to survey the beach at CPNP long-term. The UAV successfully recorded and allowed the quantification of mass seasonal *C. limbatus* aggregations in CPNP previously unknown to the wider scientific community and determined SST, wind

Fig. 3. Close-up of a dense aggregation of blacktip sharks *Carcharhinus limbatus* with clear water visibility at Cabo Pulmo National Park, Mexico. Some sharks are near the surface of the water, whereas others are deeper in the water column, closer to the seabed

speed, time of day and photoperiod to be significant predictors of abundance. The UAV surveys have since been implemented as part of a long-term monitoring programme which was due to the repeatable nature of the surveys, the uniform shallow habitat and the fact that at this location, water clarity was rarely too low to prevent the detection of sharks from the air.

The higher abundance of *C. limbatus* during afternoon surveys corresponded with a peak in SST, with sharks moving into shallow warmer waters, potentially to behaviourally thermoregulate (Hight & Lowe 2007, DiGirolamo et al. 2012, Speed et al. 2012). Previous acoustically tagged *C. limbatus* were detected by an array of underwater receivers along the reef edge in CPNP between October and June (Ketchum et al. 2020). In winter, there is a steeper SST gradient between the shallow coastal waters and the reef further offshore, which could explain why *C. limbatus* were only present close to shore during the coldest months (December to April). Elevated water temperatures are thought to aid digestion in elasmobranchs (Di Santo & Bennett 2011, Papastamatiou et al. 2015) and can also facilitate gestation (Harris 1952, Economakis & Lobel 1998, Wallman & Bennett 2006, Hight & Lowe 2007, Mull et al. 2010, Jirik & Lowe 2012). The aggregations could therefore be formed by females using the warm water habitat to accelerate the growth of their embryos, before they migrate to give birth. A gravid female *C. limbatus* of 235 cm in TL was caught by poachers on the UAV survey beach in March 2013 (J. T. Ketchum pers. comm.). The shark contained 8 embryos, each measuring between 53 and 59 cm TL, which is below the birth size of *C. limbatus* in the upper and central GOC, where nursery areas have been described between May and August (Salomón-Aguilar et al. 2009), the timing of which corresponds with the absence of adult *C. limbatus* at CPNP. Alternatively, the aggregations of *C. limbatus* at CPNP could be of mixed-sex groups to facilitate mating, and although not observed from the UAV footage, this could occur offshore in deeper water or outside of the times of the aerial surveys.

Wind speed had a negative linear relationship with *C. limbatus* abundance, with the calm waters resulting from low wind speeds providing optimal conditions for reduced energy expenditure. *C. limbatus* exhibited minimal activity and were usually observed swimming slowly and leisurely nearshore; previous studies have indicated that this species is more active outside of daylight hours (Grace & Henwood 1997, Driggers et al. 2012, Legare et al. 2018, Lear et al. 2021). At moderate wind speeds (~10 knots), wave action against the beach was noticeably stronger. The lower abundance of *C. limbatus* predicted by the model could therefore be a result of sharks using deeper waters that are less impacted by wind disturbance at the surface. This was also demonstrated in North Carolina, USA, where low wind speeds resulted in higher densities of coastal shark species, including *C. limbatus,* in nearshore estuarine environments (DiGiacomo et al. 2020). The north end of the transect area in CPNP frequently displayed dense aggregations of *C. limbatus*. This area provides the highest level of protection from wind due to the presence of higher ground adjacent to the coast; hence, *C. limbatus* seem to select the most sheltered area of the beach to use as a refuge. Additionally, calmer water would likely incur less mixing and therefore be warmer for *C. limbatus* to utilise for thermoregulation. During high wind speeds (>15 knots), sampling did not take place to ensure that shark sightings were not distorted by high water movement and so that individuals were not missed in the counts (Colefax et al. 2019).

A refuge can refer to an area of safety, and in this regard, adult *C. limbatus* have been observed using shallow-water habitat in Florida to avoid predation

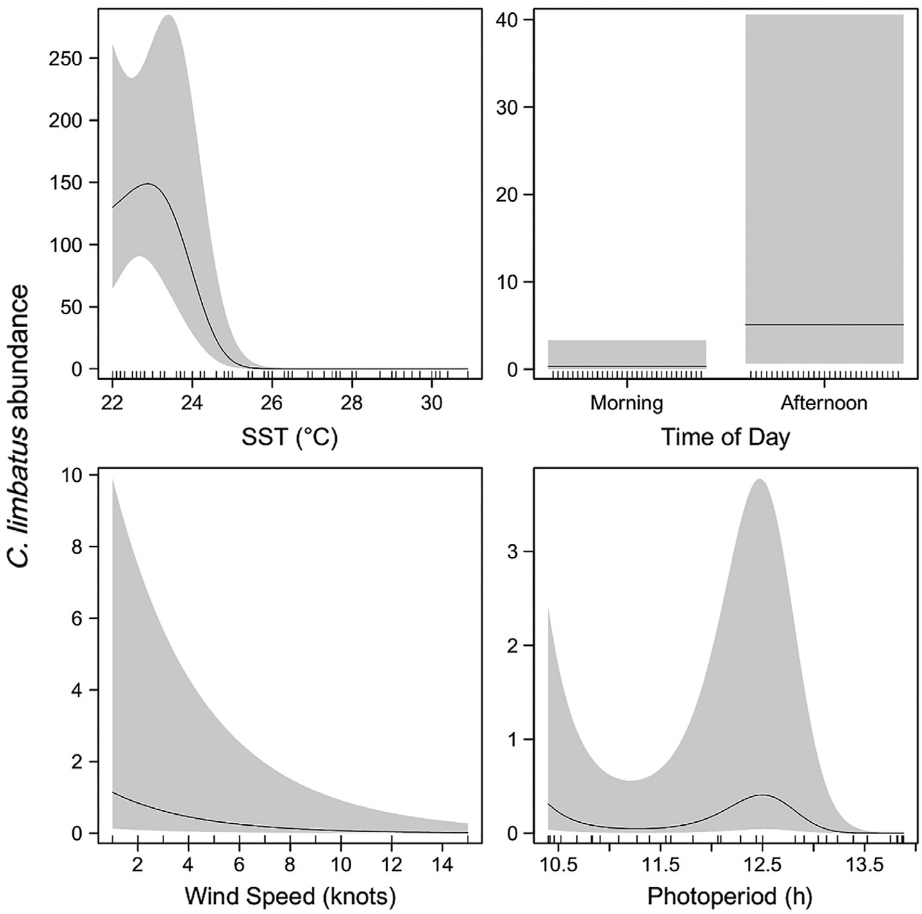

Fig. 4. Effect plots of the generalized additive model used to evaluate relationships between blacktip shark *Carcharhinus limbatus* abundance and sea surface temperature (SST), time of day, wind speed and photoperiod in Cabo Pulmo National Park, Mexico. Shaded area represents 2 SE, and rug plot (on the *x*-axis) shows observations of predictor variables

by great hammerhead sharks *Sphyrna mokarran* (Doan & Kajiura 2020). The last records of *S. mokarran* in the GOC were from the 1960s and they are now likely to have been extirpated from the region (Pérez-Jiménez 2014). However, other large shark species such as bull sharks *Carcharhinus leucas* and tiger sharks *Galeocerdo cuvier* inhabit the waters of CPNP (Reyes-Bonilla et al. 2016). The presence of these predators could drive the dense aggregations of *C. limbatus* adjacent to the shoreline. Similar behaviours are recorded in Shark Bay, Australia, where the presence of *G. cuvier* influences the habitat selection of herbivores and meso-predators (Heithaus et al. 2012). The aggregations could also be a result of sexual segregation with female *C. limbatus* refuging from males to avoid harassment (Sims et al. 2001, Wearmouth et al. 2012). Sexual segregation of this species on both spatial and temporal scales has been demonstrated along the coastline of Florida (Dodrill 1977) and South Africa (Dudley & Cliff 2010), but was not evident in the Gulf of Mexico (Bethea et al. 2015). The installation of stationary underwater cameras along the survey area would allow us to test this hypothesis, as we cannot determine the sex of the sharks present from the UAV alone.

The large aggregations of *C. limbatus* were only observed on surveys in CPNP during winter months, which corresponded to the presence of large schools of bait fish, such as Pacific sardines *Sardinops sagax*. Local fishermen refer to *C. limbatus* as 'Sardineros' as they are known to prey on sardines. *C. limbatus* were usually observed swimming slowly and unperturbed by the fish schools; however, there was an attempted predation on one occasion. The UAV filmed a shark chasing a small fish in the wave break, making sharp turns to prevent itself from beaching. It was not clear if the predation was successful as the UAV was returned to the pilot due to low battery. Locals in CPNP have also reported observations of sharks chasing fish adjacent to the shoreline, usually

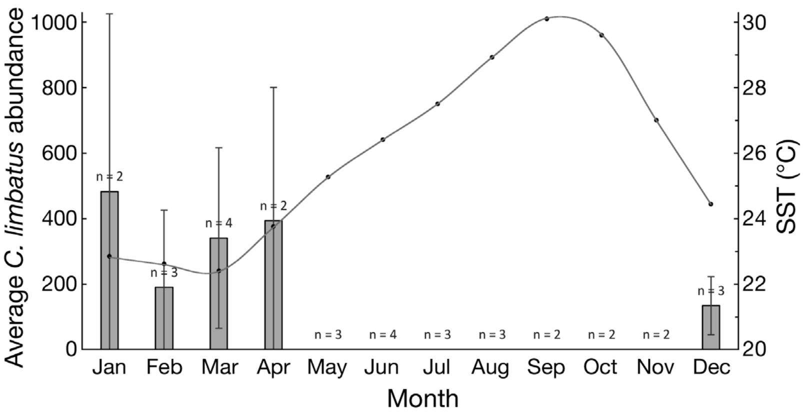

Fig. 5. Average sea surface temperature (SST) in relation to average monthly blacktip shark *Carcharhinus limbatus* abundance determined by unoccupied aerial vehicle surveys completed over a 1 yr period in 2019 in Cabo Pulmo National Park, Mexico (n = number of sampling days in each month). SST was taken in the field prior to survey flights

when water visibility is low enough for sharks to ambush them. *C. limbatus* could be opportunistically hunting the baitfish when conditions allow but are primarily of a crepuscular nature, resting in the shallows during the day before moving offshore to forage at night (Driggers et al. 2012). Similarly, juvenile *C. limbatus* only use shallow bays during daylight hours and disperse at night in Terra Ceia Bay, Florida, USA (Heupel & Simpfendorfer 2005), and in the United States Virgin Islands (Legare et al. 2015, 2018). *C. limbatus* in CPNP could also be feeding on species of higher trophic levels, such as yellowfin tuna *Thunnus albacares*, which was the most common prey item in the stomachs of *C. limbatus* caught off the Pacific coast of Ecuador (Estupiñán-Montaño et al. 2018).

The *C. limbatus* migration along the south-east coast of the USA has been well documented (Castro 1996), and aggregations have been quantified at the most southerly point of their migration route in Palm Beach, Florida (Kajiura & Tellman 2016). In late spring, abundance decreases as they embark on a northward migration, following cooler, more productive waters. A similar pattern was observed in CPNP as *C. limbatus* were absent from aerial surveys between May and November when SST was over 25°C. Acoustically tagged *C. limbatus* were also subsequently detected at seamounts north of CPNP in summer (Ketchum et al. 2020). Average SST decreases from the mouth to the upper island region of the GOC and increases slightly at the head (Soto-Mardones et al. 1999). *C. limbatus* overwinter in CPNP and start to migrate north when SST starts to increase in the lower GOC. Many marine predators perform seasonal north–south migrations to remain within their temperature niches and to follow shifts in prey distribution (Block et al. 2011). Along the south east coast of Florida, bait fish spawning is linked to SST and in turn the presence of *C. limbatus* (Kajiura & Tellman 2016). Ocean warming is already causing species to extend their home ranges as they migrate to higher latitudes (Robinson et al. 2015). This has implications in the GOC as it is a marginal sea that has already displayed signs of gradual warming, an overall trend of decreasing productivity and declines in predators such as the California sea lion *Zalophus californianus* (Adame et al. 2020). A satellite-tagged *C. limbatus* made an extensive 900 km migration from CPNP in April 2019 to the most northern region of the GOC by July (Ketchum et al. 2020). SST in the north of the GOC can be as high as 32°C in summer (Soto-Mardones et al. 1999), so the increase in SST above 25°C in CPNP could be acting as a cue for migration, rather than reflecting the temperature preference of *C. limbatus*. Results from acoustically tagged juvenile *C. limbatus* in Terra Ceia Bay, Florida, also suggest that migrations occur in response to sudden changes in temperature and not a threshold limit (Heupel 2007). The northern migration from CPNP could also be influenced by the increase in day length, as photoperiod was a significant predictor of *C. limbatus* in the GAM and has been linked to cue migrations in other elasmobranch species (Grubbs et al. 2007, Heupel 2007, Kneebone et al. 2012, Nosal et al. 2014).

The use of UAVs in marine environments is limited as surveys are affected by wind, rain, sun glare and water turbidity. Furthermore, surveys are constrained to daylight hours and are more applicable over shallow water for non-surface-associated species. Some of these limitations can be addressed, such as by the addition of advanced sensors on UAVs. Colefax et al. (2021) tested the use of a hyperspectral sensor for detecting submerged marine fauna and found wavelengths between 514 and 554 nm to be more effective than a standard camera. The use of a polarising filter and altering the direction of the UAV in relation to the sun can also reduce glare (Joyce et al. 2018). Additionally, aerial surveys can be combined alongside other methods to fill in data gaps (Kiszka & Heithaus 2018). For monitoring elasmobranchs in coastal areas, these can include terrestrial censuses (Hight & Lowe

2007, Speed et al. 2011), gill-net surveys (Froeschke et al. 2010), long-line surveys (Lear et al. 2021), baited-remote-underwater-video systems (Acuña-Marrero et al. 2018) and acoustic telemetry that can passively monitor elasmobranchs over long time periods (Heupel & Hueter 2001). In deeper-water environments, abundance estimates from aerial surveys can also be corrected for by incorporating movement data from tagged animals, such as the proportion of time sharks spend at the surface and would therefore be available for detection from the air (Westgate et al. 2014, Nykänen et al. 2018). Nevertheless, UAVs do overcome some of the disadvantages of traditional methods, as they are much less invasive and do not require the physical capture of the target species (Schofield et al. 2019).

Differentiating carcharhinid species from an aerial perspective can be challenging, and it is often not possible to identify sharks down to the species level, particularly if areas are inhabited by multiple species that share similar characteristics (Kelaher et al. 2019, DiGiacomo et al. 2020). Lemon sharks *Negaprion brevirostris* and bull sharks *C. leucas* are common carcharhinid species in the waters of CPNP. *C. leucas* can be distinguished from *C. limbatus* by a broader head shape and stout body and *N. brevirostris* by pectoral fin shape and the presence of a large second dorsal fin (Ayres et al. 2021). *N. brevirostris* were occasionally observed along the transect area, and counts of these sharks were excluded from the analysis. On most survey days, water visibility was sufficient to establish that the large aggregations were formed of a single species, *C. limbatus*, due to their homologous slender body shapes and long-pointed snouts (Fig. 3). The presence of *N. brevirostris* was more apparent when the UAV altitude was lowered; however, the limitation of the UAV battery life (~28 min) prevented the filming of all groups of sharks at lower altitudes. Further advances in battery technology will likely extend flight times and overcome this limitation in the near future.

The UAV altitude of 100 m was effective for detecting *C. limbatus* due to the sandy uniform habitat, the size of the sharks (~2 m TL) and the extent of the aggregations. A pilot study in the south of CPNP over sand and rocky-reef habitat demonstrated 100 m to be too high for reliably observing small *N. brevirostris* and for resting Pacific nurse sharks and although there have been previous sightings of *C. limbatus* at this location, they were not observed during the survey time frame (Ayres et al. 2021). The most suitable survey altitude is site- and species-specific, and pilot studies using replicas of target species can be tested to determine applicable altitudes (Butcher et al. 2019). When designing a UAV study, researchers need to consider the disturbance to wildlife, which correlates with altitude height. UAVs are known to disturb bird and pinniped species which can flee in response to their presence (Smith et al. 2016), and at low altitudes (<30 m) they can alter the behaviour of air-breathing marine species, such as dolphins (Ramos et al. 2018, Fettermann et al. 2019, Giles et al. 2021). There is little evidence to show that UAV noise disturbs elasmobranchs and other fully aquatic species (Mulero-Pázmány et al. 2017), as the underwater impact of UAV noise is minor (Christiansen et al. 2016). However, if sensitive non-target species are within survey areas, then they also need to be accounted for (Raoult et al. 2020). In terms of altitude limits, researchers must be aware of general regulations that prohibit UAVs to be flown above a 120 m altitude, to minimise the overlap with airspaces occupied by aircrafts (Raoult et al. 2020).

In some countries, like the USA, laws prohibit the use of UAVs in national parks, due to their disturbance to wildlife and visitors (Sandbrook 2015). As a general rule, UAVs are also prohibited from being flown over groups of people (Johnston 2019), and this needs to be considered for surveying in non-remote areas. Negative public perception and the misuse of UAVs has led to bans in several countries, which prevents important monitoring studies from being conducted (Linchant et al. 2015). In Mexico, and in the present study, UAV government registration and permission was required from the Comisión Nacional de Áreas Naturales Protegidas (CONANP) for the aerial surveys to be conducted for scientific investigation in the park. With ever-changing legislation, in this relatively new field, it is important that UAV regulations are followed so as to not impede the continuation of their use (Oleksyn et al. 2021). The UAV monitoring of vulnerable species and habitats will be particularly essential over the next few decades in the face of a changing climate and increasing anthropogenic impact.

Overall, the UAV was invaluable for monitoring the survey site, specifically due to the absence of a vantage point for visual censuses, a method previously used to monitor sharks in the south of CPNP (Ayres et al. 2021). Moreover, on a few occasions the UAV filmed people attempting to illegally fish within the park boundaries, and the authorities were notified. This highlights the potential use of UAVs as a tool for vigilance and surveillance of the park for poachers, which is very much needed (Anderson 2019), and particularly important for *C. limbatus* due to their proximity to the park boundaries. Furthermore, the current and future development of the surrounding area of CPNP and increases in tourism and boat activity within the park itself will likely negatively impact marine life, owing to factors such as pollution and noise disturbance (Calderon-Aguilera et al. 2021). The absence of *C. limbatus* during summer months, records of regular captures by fishers and evidence of a northward migration also highlight the vulnerability of this species to fishing pressures when outside the protection of CPNP. This study is the first to quantify in the scientific literature the large *C. limbatus* aggregations that are well known by the local community and adds to the growing body of knowledge that CPNP, a small no-take MPA, has shown increases of species abundance and diversity on an unprecedented scale.

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LITERATURE CITED

Aburto-Oropeza O, Erisman B, Galland GR, Mascareñas-Osorio I, Sala E, Ezcurra E (2011) Large recovery of fish biomass in a no-take marine reserve. PLOS ONE 6:e23601

Acuña-Marrero D, Smith ANH, Salinas-de-León P, Harvey ES, Pawley MDM, Anderson MJ (2018) Spatial patterns of distribution and relative abundance of coastal shark species in the Galapagos Marine Reserve. Mar Ecol Prog Ser 593:73–95

Adame K, Elorriaga-Verplancken FR, Beier E, Acevedo-Whitehouse K, Pardo MA (2020) The demographic decline of a sea lion population followed multi-decadal sea surface warming. Sci Rep 10:10499

Alvarez-Filip L, Reyes-Bonilla H, Calderon-Aguilera LE (2006) Community structure of fishes in Cabo Pulmo Reef, Gulf of California. Mar Ecol 27:253–262

Anderson K, Gaston KJ (2013) Lightweight unmanned aerial vehicles will revolutionize spatial ecology. Front Ecol Environ 11:138–146

Anderson RB (2019) Beyond 'success': community, governance, and the future of Cabo Pulmo National Park. Hum Organ 78:147–157

Asúnsolo-Rivera A (2016) Distribución, abundancia y riqueza de especies de tiburones en el arrecife de Pulmo. BSc dissertation, Universidad Autónoma de Baja California Sur, La Paz

Ayres KA, Ketchum JT, González-Armas R, Galván-Magaña F and others (2021) The use of an unoccupied aerial vehicle (UAV) to survey shark species over sand and rocky-reef habitats in a marine protected area. J Fish Biol, doi:10.1111/jfb.14838

Bethea DM, Ajemian MJ, Carlson JK, Hoffmayer ER and others (2015) Distribution and community structure of coastal sharks in the northeastern Gulf of Mexico. Environ Biol Fishes 98:1233–1254

Bizzarro JJ, Smith WD, Hueter RE, Tyminski JP and others (2007) The status of shark and ray fishery resources in the Gulf of California: applied research to improve management and conservation. Tech Rep 2009–01. Moss Landing Marine Laboratories, Moss Landing, CA

Block BA, Jonsen ID, Jorgensen SJ, Winship AJ and others (2011) Tracking apex marine predator movements in a dynamic ocean. Nature 475:86–90

Brusca RC, Thomson DA (1975) Pulmo Reef: the only 'coral reef' in the Gulf of California. Cienc Mar 2:37–53

Butcher PA, Piddocke TP, Colefax AP, Hoade B, Peddemors VM, Borg L, Cullis BR (2019) Beach safety: Can drones provide a platform for sighting sharks? Wildl Res 46: 701–712

Butcher PA, Colefax AP, Gorkin RA, Kajiura SM and others (2021) The drone revolution of shark science: a review. Drones 5:8

Calderon-Aguilera LE, Reyes-Bonilla H, Olán-González M, Castañeda-Rivero FR, Perusquía-Ardón JC (2021) Estimated flows and biomass in a no-take coral reef from the eastern tropical Pacific through network analysis. Ecol Indic 123:107359

Castro JI (1996) Biology of the blacktip shark, *Carcharhinus limbatus*, off the southeastern United States. Bull Mar Sci 59:508–522

Chambers JM, Hastie TJ (1992) Statistical models in S. Wadsworth & Brooks, Pacific Grove, CA

Christiansen F, Rojano-Doñate L, Madsen PT, Bejder L (2016) Noise levels of multi-rotor unmanned aerial vehicles with implications for potential underwater impacts on marine mammals. Front Mar Sci 3:277

Cliff G, Anderson-Reade MD, Aitken AP, Charter GE, Peddemors VM (2007) Aerial census of whale sharks (*Rhincodon typus*) on the northern KwaZulu-Natal coast, South Africa. Fish Res 84:41–46

Colefax AP, Butcher PA, Kelaher BP (2018) The potential for unmanned aerial vehicles (UAVs) to conduct marine fauna surveys in place of manned aircraft. ICES J Mar Sci 75:1–8

Colefax AP, Butcher PA, Pagendam DE, Kelaher BP (2019) Reliability of marine faunal detections in drone-based monitoring. Ocean Coast Manag 174:108–115

Colefax AP, Kelaher BP, Pagendam DE, Butcher PA (2020) Assessing white shark (*Carcharodon carcharias*) behavior along coastal beaches for conservation-focused shark mitigation. Front Mar Sci 7:268

Colefax AP, Kelaher BP, Walsh AJ, Purcell CR, Pagendam DE, Cagnazzi D, Butcher PA (2021) Identifying optimal wavelengths to maximise the detection rates of marine fauna from aerial surveys. Biol Conserv 257:109102

Compagno LJ (1984) FAO species catalogue, Vol 4, Part 1 and 2. Sharks of the world: an annotated and illustrated catalogue of shark species known to date. FAO Fish Synop 125. FAO, Rome

Di Santo V, Bennett WA (2011) Is post-feeding thermotaxis advantageous in elasmobranch fishes? J Fish Biol 78: 195–207

DiGiacomo AE, Harrison WE, Johnston DW, Ridge JT (2020) Elasmobranch use of nearshore estuarine habitats responds to fine-scale, intra-seasonal environmental variation: observing coastal shark density in a temperate estuary utilizing unoccupied aircraft systems (UAS). Drones 4:74

DiGirolamo AL, Gruber SH, Pomory C, Bennett WA (2012) Diel temperature patterns of juvenile lemon sharks *Negaprion brevirostris*, in a shallow-water nursery. J Fish Biol 80:1436–1448

Doan MD, Kajiura SM (2020) Adult blacktip sharks (*Carcharhinus limbatus*) use shallow water as a refuge from great hammerheads (*Sphyrna mokarran*). J Fish Biol 96: 1530–1533

Dodrill JW (1977) A hook and line survey of the sharks found within five hundred meters of shore along Melbourne Beach, Brevard County, Florida. PhD dissertation, Florida Institute of Technology, Melbourne, FL

Driggers WB III, Campbell MD, Hoffmayer ER, Ingram GW Jr (2012) Feeding chronology of six species of carcharhinid sharks in the western North Atlantic Ocean as inferred from longline capture data. Mar Ecol Prog Ser 465:185–192

Dudley SFJ, Cliff G (2010) Influence of the annual sardine run on catches of large sharks in the protective gillnets off KwaZulu-Natal, South Africa, and the occurrence of sardine in shark diet. Afr J Mar Sci 32:383–397

Economakis AE, Lobel PS (1998) Aggregation behavior of the grey reef shark, *Carcharhinus amblyrhynchos*, at Johnston Atoll, Central Pacific Ocean. Environ Biol Fishes 51:129–139

El-Saleh S (2016) The unforeseen recovery of a marine reserve. Abundance, residency and site fidelity of sharks in Cabo Pulmo National Park, Mexico. MSc dissertation, University of Lisboa

Estupiñán-Montaño C, Pacheco-Triviño F, Cedeño-Figueroa LG, Galván-Magaña F, Estupiñán-Ortiz JF (2018) Diet of three shark species in the Ecuadorian Pacific, *Carcharhinus falciformis, Carcharhinus limbatus* and *Nasolamia velox.* J Mar Biol Assoc UK 98:927–935

Fettermann T, Fiori L, Bader M, Doshi A, Breen D, Stockin KA, Bollard B (2019) Behaviour reactions of bottlenose dolphins (*Tursiops truncatus*) to multirotor unmanned aerial vehicles (UAVs). Sci Rep 9:8558

Froeschke J, Stunz GW, Wildhaber ML (2010) Environmental influences on the occurrence of coastal sharks in estuarine waters. Mar Ecol Prog Ser 407:279–292

Giles AB, Butcher PA, Colefax AP, Pagendam DE, Mayjor M, Kelaher BP (2021) Responses of bottlenose dolphins (*Tursiops* spp.) to small drones. Aquat Conserv 31: 677–684

Grace M, Henwood T (1997) Assessment of the distribution and abundance of coastal sharks in the US Gulf of Mexico and eastern seaboard, 1995 and 1996. Mar Fish Rev 59:23–32

Grubbs RD, Musick JA, Conrath CL, Romine JG (2007) Long-term movements, migration and temporal delineation of a summer nursery for juvenile sandbar sharks in the Chesapeake Bay region. Am Fish Soc Symp 50: 87–107

Harris JE (1952) A note on the breeding season, sex ratio and embryonic development of the dogfish *Scyliorhinus canicula* (L.). J Mar Biol Assoc UK 31:269–276

Heithaus MR, Wirsing AJ, Dill LM (2012) The ecological importance of intact top-predator populations: a synthesis of 15 years of research in a seagrass ecosystem. Mar Freshw Res 63:1039–1050

Heupel MR (2007) Exiting Terra Ceia Bay: an examination of cues stimulating migration from a summer nursery area. Am Fish Soc Symp 50:265

Heupel MR, Hueter RE (2001) Use of an automated acoustic telemetry system to passively track juvenile blacktip shark movements. In: Sibert JR, Nielsen JL (eds) Electronic tagging and tracking in marine fisheries. Springer, Dordrecht, p 217–236

Heupel MR, Simpfendorfer CA (2005) Quantitative analysis of aggregation behavior in juvenile blacktip sharks. Mar Biol 147:1239–1249

Hight BV, Lowe CG (2007) Elevated body temperatures of adult female leopard sharks, *Triakis semifasciata*, while aggregating in shallow nearshore embayments: evidence for behavioral thermoregulation? J Exp Mar Biol Ecol 352:114–128

Hijmans RJ (2019) geosphere: spherical trigonometry. R package version 1.5-10. https://CRAN.R-project.org/package=geosphere

Hilbe JM (2007) Negative binomial regression. Cambridge University Press, Cambridge

Jacoby DM, Croft DP, Sims DW (2012) Social behaviour in sharks and rays: analysis, patterns and implications for conservation. Fish Fish 13:399–417

Jirik KE, Lowe CG (2012) An elasmobranch maternity ward: Female round stingrays *Urobatis halleri* use warm, restored estuarine habitat during gestation. J Fish Biol 80:1227–1245

Johnston DW (2019) Unoccupied aircraft systems in marine science and conservation. Annu Rev Mar Sci 11: 439–463

Joyce KE, Duce S, Leahy SM, Leon J, Maier SW (2018) Principles and practice of acquiring drone-based image data in marine environments. Mar Freshw Res 70:952–963

Kajiura SM, Tellman SL (2016) Quantification of massive seasonal aggregations of blacktip sharks (*Carcharhinus limbatus*) in Southeast Florida. PLOS ONE 11: e0150911

Kelaher BP, Colefax AP, Tagliafico A, Bishop MJ, Giles A, Butcher PA (2019) Assessing variation in assemblages of large marine fauna off ocean beaches using drones. Mar Freshw Res 71:68–77

Kessel ST, Gruber SH, Gledhill KS, Bond ME, Perkins RG (2013) Aerial survey as a tool to estimate abundance and describe distribution of a carcharhinid species, the lemon shark, *Negaprion brevirostris.* J Mar Biol 2013:1–10

Ketchum JT, Galván-Magaña F, Klimley AP (2013) Segregation and foraging ecology of whale sharks, *Rhincodon typus*, in the southwestern Gulf of California. Environ Biol Fishes 96:779–795

Ketchum JT, Hoyos-Padilla M, Aldana-Moreno A, Ayres KA and others (2020) Shark movement patterns in the Mexican Pacific: a conservation and management perspective. Adv Mar Biol 85:1–37

Kiszka JJ, Heithaus MR (2018) Using aerial surveys to investigate the distribution, abundance, and behavior of sharks and rays. In: Carrier JC (ed) Shark research: emerging technologies and applications for the field and laboratory. CRC Press, Boca Raton, FL, p 71–82

Kiszka JJ, Mourier J, Gastrich K, Heithaus MR (2016) Using unmanned aerial vehicles (UAVs) to investigate shark and ray densities in a shallow coral lagoon. Mar Ecol Prog Ser 560:237–242

Kneebone J, Chisholm J, Skomal GB (2012) Seasonal residency, habitat use, and site fidelity of juvenile sand tiger sharks *Carcharias taurus* in a Massachusetts estuary. Mar Ecol Prog Ser 471:165–181

Lazaridis E (2014) lunar: lunar phase & distance, seasons and other environmental factors (Version 0.1-04). https://rdrr.io/cran/lunar/src/R/lunar-package.R

Lear KO, Whitney NM, Morris JJ, Gleiss AC (2021) Temporal niche partitioning as a novel mechanism promoting co-existence of sympatric predators in marine systems. Proc R Soc B 288:20210816

Legare B, Kneebone J, DeAngelis B, Skomal G (2015) The spatiotemporal dynamics of habitat use by blacktip (*Carcharhinus limbatus*) and lemon (*Negaprion brevirostris*) sharks in nurseries of St. John, United States Virgin Islands. Mar Biol 162:699–716

Legare B, Skomal G, DeAngelis B (2018) Diel movements of the blacktip shark (*Carcharhinus limbatus*) in a Caribbean nursery. Environ Biol Fishes 101:1011–1023

Linchant J, Lisein J, Semeki J, Lejeune P, Vermeulen C (2015) Are unmanned aircraft systems (UASs) the future of wildlife monitoring? A review of accomplishments and challenges. Mammal Rev 45:239–252

Marsh H, Sinclair DF (1989) An experimental evaluation of dugong and sea turtle aerial survey techniques. Wildl Res 16:639–650

Morgan A, Burgess GH (2007) At-vessel fishing mortality for six species of sharks caught in the Northwest Atlantic and Gulf of Mexico. Gulf Caribb Res 19:123–129

Mulero-Pázmány M, Jenni-Eiermann S, Strebel N, Sattler T, Negro JJ, Tablado Z (2017) Unmanned aircraft systems as a new source of disturbance for wildlife: a systematic review. PLOS ONE 12:e0178448

Mull CG, Lowe CG, Young KA (2010) Seasonal reproduction of female round stingrays (*Urobatis halleri*): steroid hormone profiles and assessing reproductive state. Gen Comp Endocrinol 166:379–387

Musick JA, Burgess G, Cailliet G, Camhi M, Fordham S (2000) Management of sharks and their relatives (Elasmobranchii). Fisheries 25:9–13

NMFS (2003) 2003 stock assessment and fishery evaluation for Atlantic highly migratory species. US Department of Commerce, NOAA/NMFS, Silver Spring, MD

Nosal AP, Caillat A, Kisfaludy EK, Royer MA, Wegner NC (2014) Aggregation behavior and seasonal philopatry in male and female leopard sharks *Triakis semifasciata* along the open coast of southern California, USA. Mar Ecol Prog Ser 499:157–175

Nykänen M, Jessopp M, Doyle TK, Harman LA and others (2018) Using tagging data and aerial surveys to incorporate availability bias in the abundance estimation of blue sharks (*Prionace glauca*). PLOS ONE 13:e0203122

Oleksyn S, Tosetto L, Raoult V, Joyce KE, Williamson JE (2021) Going batty: the challenges and opportunities of using drones to monitor the behaviour and habitat use of rays. Drones 5:12

Papastamatiou YP, Watanabe YY, Bradley D, Dee LE, Weng K, Lowe CG, Caselle JE (2015) Drivers of daily routines in an ectothermic marine predator: hunt warm, rest warmer? PLOS ONE 10:e0127807

Pérez-Jiménez JC (2014) Historical records reveal potential extirpation of four hammerhead sharks (*Sphyrna* spp.) in Mexican Pacific waters. Rev Fish Biol Fish 24:671–683

Pollock KH, Marsh HD, Lawler IR, Alldredge MW (2006) Estimating animal abundance in heterogeneous environments: an application to aerial surveys for dugongs. J Wildl Manag 70:255–262

Porter ME, Ruddy BT, Kajiura SM (2020) Volitional swimming kinematics of blacktip sharks, *Carcharhinus limbatus*, in the wild. Drones 4:78

R Core Team (2020) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna

Ramos EA, Maloney B, Magnasco MO, Reiss D (2018) Bottlenose dolphins and Antillean manatees respond to small multi-rotor unmanned aerial systems. Front Mar Sci 5:316

Raoult V, Tosetto L, Williamson JE (2018) Drone-based high-resolution tracking of aquatic vertebrates. Drones 2:37

Raoult V, Colefax AP, Allan BM, Cagnazzi D and others (2020) Operational protocols for the use of drones in marine animal research. Drones 4:64

Reyes-Bonilla H (1997) A new marine reserve in the Gulf of California. Conserv Biol 11:838

Reyes-Bonilla H, Alvarez-Filip L (2008) Long-term changes in taxonomic distinctness and trophic structure of reef fishes at Cabo Pulmo reef, Gulf of California. In: Proc 11th Int Coral Reef Symp, Fort Lauderdale, FL, p 790–794

Reyes-Bonilla H, Ayala-Bocos A, Melo FJFR, Zepeta-Vilchis R, Asúnsolo-Rivera A, Ketchum JT (2016) A bibliographic and field record chronology of sharks at Cabo Pulmo National Park, Gulf of California. Oceánides 31: 55–57

Rieucau G, Kiszka JJ, Castillo JC, Mourier J, Boswell KM, Heithaus MR (2018) 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. J Fish Biol 93:119–127

Rigby CL, Carlson J, Chin A, Derrick D, Dicken M, Pacoureau N (2021) Carcharhinus limbatus. The IUCN Red List of Threatened Species 2021: e.T3851A2870736. https://dx.doi.org/10.2305/IUCN.UK.2021-2.RLTS.T3851A2870736.en. Downloaded 5 November 2021

Robinson LM, Hobday AJ, Possingham HP, Richardson AJ (2015) Trailing edges projected to move faster than leading edges for large pelagic fish habitats under climate change. Deep Sea Res II 113:225–234

Rowat D, Gore M, Meekan MG, Lawler IR, Bradshaw CJA (2009) Aerial survey as a tool to estimate whale shark abundance trends. J Exp Mar Biol Ecol 368:1–8

Salomón-Aguilar CA, Villavicencio-Garayzar CJ, Reyes-Bonilla H (2009) Shark breeding grounds and seasons in the Gulf of California: fishery management and conservation strategy. Cienc Mar 35:369–388

Sandbrook C (2015) The social implications of using drones for biodiversity conservation. Ambio 44:636–647

Schlaff AM, Heupel MR, Simpfendorfer CA (2014) Influence of environmental factors on shark and ray movement, behaviour and habitat use: a review. Rev Fish Biol Fish 24:1089–1103

Schofield G, Esteban N, Katselidis KA, Hays GC (2019) Drones for research on sea turtles and other marine vertebrates — a review. Biol Conserv 238:108214

Sims D, Nash J, Morritt D (2001) Movements and activity of male and female dogfish in a tidal sea lough: alternative behavioural strategies and apparent sexual segregation. Mar Biol 139:1165−1175

Smith CE, Sykora-Bodie ST, Bloodworth B, Pack SM, Spradlin TR, LeBoeuf NR (2016) Assessment of known impacts of unmanned aerial systems (UAS) on marine mammals: data gaps and recommendations for researchers in the United States. J Unmanned Vehicle Syst 4:31−44

Sosa-Nishizaki O, García-Rodríguez E, Morales-Portillo CD, Pérez-Jiménez JC, del Carmen Rodríguez-Medrano M, Bizzarro JJ, Castillo-Géniz JL (2020) Fisheries interactions and the challenges for target and nontargeted take on shark conservation in the Mexican Pacific. Adv Mar Biol 85:39−69

Soto-Mardones L, Marinone SG, Parés-Sierra A (1999) Time and spatial variability of sea surface temperature in the Gulf of California. Cienc Mar 25:1−30

Speed CW, Meekan MG, Field IC, McMahon CR and others (2011) Spatial and temporal movement patterns of a multi-species coastal reef shark aggregation. Mar Ecol Prog Ser 429:261−275

Speed CW, Meekan MG, Field IC, McMahon CR, Bradshaw CJA (2012) Heat-seeking sharks: support for behavioural thermoregulation in reef sharks. Mar Ecol Prog Ser 463: 231−244

Wallman HL, Bennett WA (2006) Effects of parturition and feeding on thermal preference of Atlantic stingray, *Dasyatis sabina* (Lesueur). Environ Biol Fishes 75:259−267

Westgate AJ, Koopman HN, Siders ZA, Wong SNP, Ronconi RA (2014) Population density and abundance of basking sharks *Cetorhinus maximus* in the lower Bay of Fundy, Canada. Endang Species Res 23:177−185

Wood SN (2017) Generalized additive models: an introduction with R, 2nd edn. Chapman and Hall/CRC, Boca Raton, FL

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