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Assessing the effects of coral reef habitat and marine protected areas on threatened megafauna using aerial surveys

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Abstract

1. Overfishing and habitat degradation are major threats to marine megafauna worldwide. Marine protected areas (MPAs) are effective spatial conservation tools for reducing anthropogenic pressures on threatened species but their benefits for megafauna are still debated. While the effects of MPAs on species abundances are widely reported, few studies have simultaneously investigated the confounding effect of habitat.
2. This study aimed at disentangling the effects of coral reef habitat and spatial protection on megafauna densities in a shallow lagoon partly covered by a no-take MPA in New Caledonia (South-west Pacific).
3. Twenty replicates of aerial-video surveys (representing 17 h of videos) were conducted during a 5-month period to estimate and map the densities of five megafauna taxa (dugongs, sea turtles, sharks, Dasyatidae rays and Myliobatidae rays). A permutational multivariate analysis of variance was then applied to assess and disentangle the effects of coral reef habitat obtained from high-resolution satellite imagery and spatial protection on megafauna taxa densities.
4. The analysis revealed a significant effect of protection for sharks and Myliobatidae, with observed densities respectively 9 and 3 times higher inside the MPA compared with outside. The results also highlighted a significant combined effect of habitat and protection for dugongs and Dasyatidae, as well as a significant effect of habitat alone for Dasyatidae. In contrast, no significant effect of habitat or protection was detected for sea turtles.
5. In conclusion, this study revealed positive effects of protection (alone or combined with habitat) for four of the five studied megafauna taxa, confirming the effectiveness of the current MPA. Future studies should be conducted over broader spatial and temporal scales to examine whether detected effects hold beyond the surveyed period and area.

KEYWORDS
aerial surveys, dugongs, endangered species, habitat, marine protected areas, rays, sea turtles, sharks

1 | INTRODUCTION

Marine megafauna, i.e. animals with maximum reported body mass > 45 kg, including marine mammals, sea turtles, sharks and rays (Estes et al., 2016), are among the most threatened species globally (McCauley et al., 2015; Pimiento et al., 2020). Rays and sharks are of highest concern, with 34% of the species assessed by the IUCN in 2021 classified as threatened (Dulvy et al., 2021). Worryingly, the global abundance of oceanic sharks and rays declined by 71% between 1970 and 2018 (Pacoureau et al., 2021), overfishing playing a major role in this decline (Dulvy et al., 2021). Even in remote regions of the Indo-Pacific such as New Caledonia or Chagos where commercial and recreational shark fishing are historically low or banned, the strong human footprint on shark populations is undeniable (Juhel et al., 2017; Ferretti et al., 2018). The ongoing loss of seagrass meadows across the globe is another major threat for endangered dugongs and sea turtles that critically depend on these habitats (Waycott et al., 2009; Turschwell et al., 2021). In combination, overfishing and habitat loss have extirpated sawfishes, the most vulnerable family of rays, from many nations (Yan et al., 2021).

Marine protected areas (MPAs) are certainly the most efficient spatial conservation tool for safeguarding marine biodiversity, now covering nearly 8% of the ocean (Grorud-Colvert et al., 2021). MPAs are geographically defined areas that are regulated and managed according to four different levels of protection ('minimally', 'lightly', 'highly' or 'fully' protected) based on allowed activities (Grorud-Colvert et al., 2021). Along with the ambitious goal of effectively protecting at least 30% of the ocean by 2030 (Jones et al., 2020) comes the immense challenge of strategically allocating this effort in relevant areas for conservation and the pitfalls of rapidly protecting large areas without any ecological considerations. Yet the adequate representation of key habitats fulfilling species ecological requirements is critical to the effectiveness of MPAs (Magris et al., 2021). Human-related factors such as local communities' engagement, allocated financial resources and protection enforcement, are also crucial to the effectiveness of MPAs (Edgar et al., 2014; Gill et al., 2017).

Various effects of MPAs on megafauna abundance, diversity and space use have been reported. Several studies found positive MPA effects on the abundance or diversity of sharks and rays in different parts of the world (Espinoza et al., 2020; Albano et al., 2021), even in relatively young MPAs (Jaiteh et al., 2016). Positive effects on space use were also identified for reef manta rays (*Mobula alfredi*), grey reef shark (*Carcharhinus amblyrhynchos*), bottlenose dolphin (*Tursiops truncatus*) and green sea turtle (*Chelonia mydas*) (Gilmour et al., 2022). Other studies reported mixed conservation outcomes of MPAs for megafauna. In New Caledonia, Juhel et al. (2017) found lower shark diversity and abundance in an old, large and restrictive MPA located close to the capital compared with MPAs in remote areas. Another study underlined the mismatch between MPAs and important habitats for dugongs (*Dugong dugon*) in New Caledonia (Cleguer et al., 2015). A global study showed that MPAs would need to be no-take and extend over 10 km of continuous reef habitat to protect most reef sharks such as the whitetip reef shark (*Triaenodon obesus*), while a 50 km extension would be necessary to protect more mobile species such as the nurse shark (*Ginglymostoma cirratum*) (Dwyer et al., 2020).

Until now, the majority of studies investigating the effects of MPAs on megafauna populations have relied on various telemetry techniques and underwater surveys. Satellite and acoustic telemetry have been widely employed to study animal ranges and movements in relation to MPAs (Dwyer et al., 2020; Bonnin et al., 2021; Hays et al., 2021; Roberts et al., 2021; Gilmour et al., 2022). Yet acoustic telemetry is constrained by the capacity to deploy large arrays of hydrophones, while satellite telemetry is limited by the frequency and precision of the GPS data and cost. Both techniques are invasive and provide information on a limited number of tagged individuals. Visual underwater censuses from scuba divers and baited remote underwater videos systems are commonly employed to count sharks and rays (and more rarely, sea turtles) inside and around MPAs (Jaiteh et al., 2016; MacNeil et al., 2020; Jabado et al., 2021; Flowers et al., 2022). However, some individuals or species remain unseen owing to natural rarity or elusiveness (Juhel et al., 2017; Boussarie et al., 2018). Aerial surveys provide a novel and alternative method for monitoring rare and elusive megafauna species such as dugongs (Mannocci et al., 2021). Their main advantage is the ability to provide abundance and distribution estimates across large spatial scales for a wide range of megafauna species (Mannocci et al., 2014; Martin et al., 2016; Laran et al., 2017). Video-surveys conducted from drones or light aircraft (Kiszka et al., 2016; Mannocci et al., 2021; Desgarnier et al., 2022) have the potential to outperform traditional observer-based aerial surveys in terms of accuracy and precision in the derived abundance estimates (Colefax, Butcher & Kelaher, 2018; Kelaher et al., 2020a).

While many studies have investigated the effect of MPAs on the abundance of megafauna species (Bond et al., 2012; Espinoza et al., 2014; Dwyer et al., 2020; Jabado et al., 2021; Flowers et al., 2022), few have simultaneously accounted for the effect of habitat, i.e. how the spatial heterogeneity of habitat influences species abundance (Osgood, McCord & Baum, 2019; Albano et al., 2021). Throughout this study, the word 'habitat' is used synonymously with 'benthic substrate habitat' (Diaz, Solan & Valente, 2004). Habitat is typically characterized and mapped through the use of underwater imagery (Zavalas et al., 2014; Fukunaga et al., 2019), satellite/airborne imagery (Muller-Karger et al., 2018; Bajjouk et al., 2019), and more rarely, acoustic techniques (Lillis et al., 2018; Costa, 2019). Accounting for the effect of habitat on the abundance of megafauna is crucial because differences in habitat type and quality between protected and unprotected sites can confound analyses of MPA effects (Miller & Russ, 2014) and overlooking habitat can lead to erroneous conclusions about the effectiveness and utility of MPAs (Claudet, García-Charton & Lenfant, 2010). Also, knowing whether the level of protection or the quality of habitat is most critical for marine megafauna is key to guide future conservation strategies (Albano et al., 2021).

In this study, 20 replicate aerial video-surveys were used to estimate the density of five megafauna taxa (dugongs, sea turtles, sharks and rays of the Dasyatidae and Myliobatidae families) in a shallow coral lagoon partly covered by a no-take MPA in New Caledonia. Densities were mapped inside and outside the MPA and the effects of habitat and protection level were assessed and compared for all studied taxa.

2 | METHODS

2.1 | Study area

The Poé study area is located on the western coast of New Caledonia in the South-west Pacific (Figure 1). It is characterized by a shallow (< 5 m) and relatively narrow (c. 2.5 km wide) lagoon, a barrier reef and two deeper channels reaching 25 m depth. The eastern part of this area was declared as a no-take MPA (IUCN category IV) in 2006 (Figure 1). The whole area is located within the broader South Province Park created in 2009 and the UNESCO World Heritage area established in 2008. The lagoons and shelf waters of New Caledonia were also recently identified as an Important Marine Mammal Area for its globally significant dugong population (IUCN-Marine Mammal Protected Areas Task Force, 2021).

The Poé area is popular as a vacation spot, with several campsites, hostels and hotels (including a 176 room beachfront resort) concentrated on the eastern side. Recreational activities include snorkelling, scuba diving and water sports (e.g. kayaking, kitesurfing) mostly on the eastern (protected) side of the area, as well as recreational rod and spear fishing on the western (unprotected) side of the area. To our knowledge, the impacts of these local infrastructures and activities on habitats and species have never been

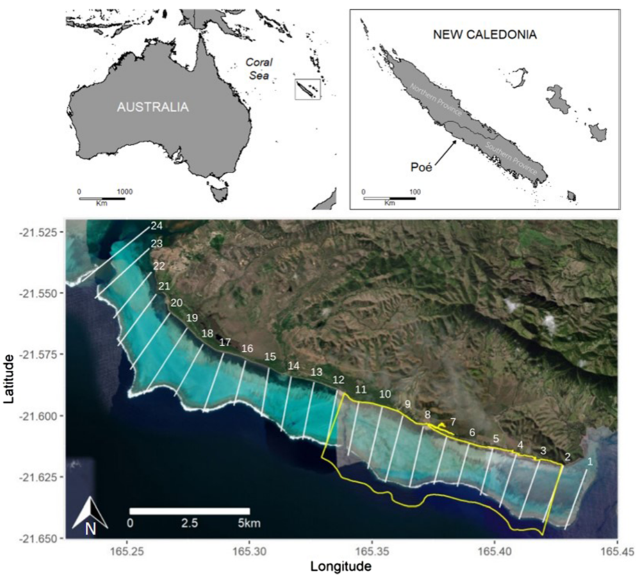

FIGURE 1 Location of the Poé study area on the western coast of New Caledonia (South-west Pacific). The 24 surveyed transects are shown by white lines and the marine protected area (MPA) is shown by a yellow line. The satellite image was obtained from OpenStreetMap (https://www.openstreetmap.org).

studied. Human frequentation was low throughout the course of the study (from 24 July to 29 November 2021) owing to the Covid-19 pandemic that led to international travel restrictions (from March 2020) and a local lockdown (announced on 7 September 2021).

2.2 | Aerial video-surveys

A GoPro Hero Black 7 camera was mounted under the right wing of an amphibious ultralight airplane (AirMax SeaMax), pointing downward (Figure 2a). The camera was configured to record videos at a rate of 24 frames per second in linear field of view mode at a resolution of 2.7 K (2704 × 1520 pixels) with integrated image stabilization. The camera was manually triggered before each flight. Telemetry data, including GPS coordinates and altitudes, were recorded by the GoPro along each flight (at a rate of 8–12 positions per second).

The plane followed 24 pre-defined transects (14 outside the MPA vs. 10 inside) oriented perpendicular to the coast (mean length 2.6 km) and spaced 1 km apart (Figure 1). Transects were flown at a target altitude of 47 m and a speed of 110 km h^{-1}. At this altitude, each image covered a surface area of 89 m width (the 'strip width') × 50 m length, corresponding to a ground sampling distance of 3 cm per pixel.

Weather conditions such as wind and sun glint are known to negatively impact megafauna detections (Colefax et al., 2019). To ensure optimal megafauna detection, transects were flown in minimal wind conditions (wind speed < 7 knots) and during morning hours (transects started between 7:30 and 10:30) to avoid midday sun glint. A polarizing filter was fitted to the GoPro to further reduce the sun glint. The area was surveyed on 20 different days from 24 July to 29 November 2021, representing a total surveyed area of 137.8 km^2 (6.8 km^2 per survey day) and 17.3 h of videos (on average 51 min per survey day, including 20 min inside the MPA).

2.3 | Video annotation

All videos were watched by a team of trained observers who recorded the times at which they spotted megafauna. Megafauna was detected from the surface to the bottom in the Poé lagoon and at, or immediately under, the surface (generally up to 2 m) on the barrier reef and in the two deeper channels present in the area. Spotted megafauna included dugongs (*D. dugong*), sea turtles, sharks and rays of the Dasyatidae and Myliobatidae families. Groupings of species were inevitable for sea turtles, sharks, Dasyatidae and Myliobatidae that could not be told apart from the air. The species composition of each taxon is detailed in Appendix S1.

Videos were imported into a custom application (https://megafauna-project.com/) for image extraction and annotation. Each video was extracted at a rate of 3 images per second. This extraction rate was selected because it allowed the same individual to be visible in consecutive images (with a 20% forward overlap) and to confirm its

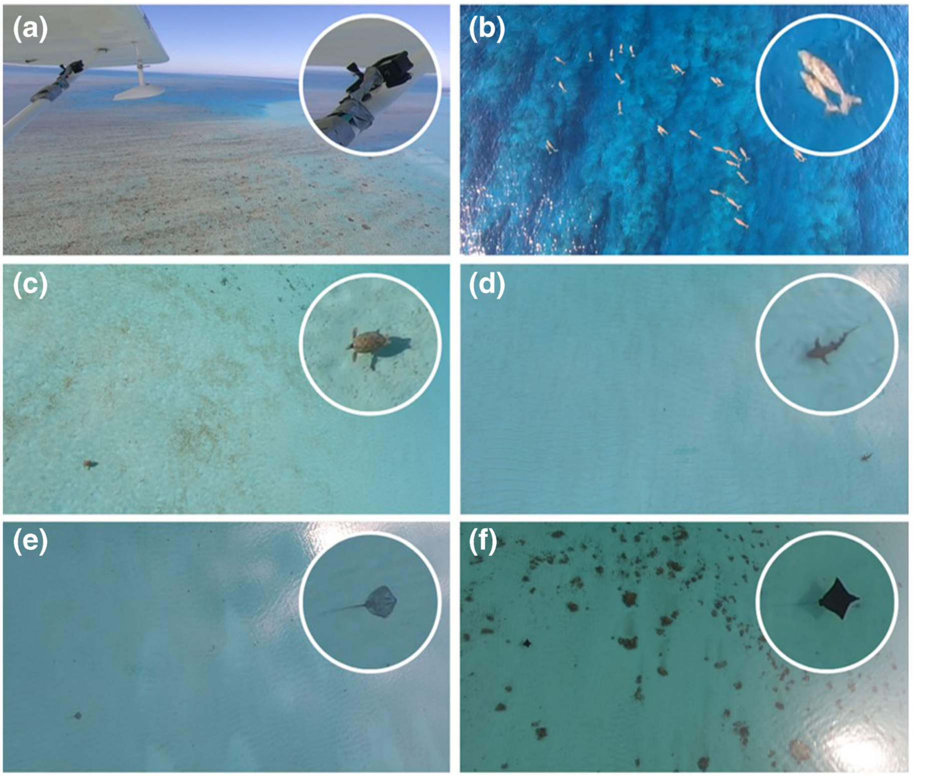

FIGURE 2 Images of (a) the GoPro Hero Black 7 camera fitted under the right wing of the plane; (b) a pair of dugongs; (c) a sea turtle; (d) a shark; (e) a Dasyatidae ray; and (f) a Myliobatidae ray collected from the aerial surveys. Additional images of each taxon are provided in Appendix S2.

identification. The annotation procedure consisted of manually drawing rectangular bounding boxes around individuals and ascribing to them the label of the relevant megafauna taxon (dugong, sea turtle, shark, Dasyatidae ray, Myliobatidae ray). Only individuals that could be identified with certainty as being part of a megafauna taxon were annotated. A double reading was done for all annotated images. Example images of all megafauna taxa are provided in Figures 2b–f. For each video, the custom application returned the GPS coordinates of all images extracted from this video along with their annotations (i.e. the pixel coordinates of the bounding box and the label of the megafauna taxon).

2.4 | Data cleaning

Off-effort portions of the video (i.e. transit from/to the airport) were removed, but between-transect portions (parallel to the coast) were kept in order to cover habitats in the nearshore and outer barrier reef portions of the study area. Duplicate observations of the same individual in consecutive images were removed if the centre of their annotation bounding boxes fell within the 20% forward overlap between images.

2.5 | Megafauna density calculation

Density was calculated for each megafauna taxon over a spatial grid of 0.0025° × 0.0025° cells (c. 250 × 250 m cells) following the strip transect methodology (assuming uniform detection within the strip width; Buckland et al., 2001; Buckland et al., 2012; Kiszka et al., 2016) as:

$$Di = \frac{ni}{w \times Li}$$

where *ni* is the total number of individuals for the grid cell *i*, *w* is the strip width (89 m) and *L* is the total length of transects in cell *i* (m). Taxa densities were expressed in numbers of individuals per hectare.

2.6 | Benthic habitat classification and mapping

The Allen Coral Atlas benthic habitat classification is the product of combining high-resolution (3.7 m) satellite imagery with machine learning to provide a global classification map of coral reefs in unprecedented detail (Kennedy et al., 2021). This classification has been extensively validated with ground-truth campaigns in coral reef ecosystems (including New Caledonia). Habitat is classified into six benthic habitat categories (coral/algae, microalgal mats, rock, rubble, sand and seagrass) for all shallow (up to 10 m deep) tropical reefs. Since the Allen Coral Atlas only provides habitat classification for waters shallower than 10 m, waters with depth greater than 10 m were lumped into an 'open sea' category. Densities per cell were intersected with these habitat categories and the location of the Poé MPA obtained from the world database on protected areas (IUCN, UNEP-WCMC, 2022).

2.7 | Habitat and protection effects on megafauna densities

A permutational multivariate analysis of variance (PERMANOVA) (Anderson, 2017) with 9999 permutations and dissimilarity matrices constructed with Euclidean distance was computed to assess the effects of habitat (six categories) and protection (inside/outside the no-take MPA) and their interaction on log-transformed megafauna densities. The PERMANOVA is a geometric partitioning of variation across a multivariate dataset. Statistical inferences are made in a distribution-free setting using a permutation-based algorithm. An *F*-statistic was used to compare variability within groups and among different groups and to test the null hypothesis that the centroids and dispersion of the groups are equivalent for all groups (Anderson, 2017). For all taxa with detected significant effects of habitat and/or protection, pairwise multilevel *t*-tests were further performed.

All analyses were performed in R (version 4.1.2). The package vegan (Oksanen et al., 2020) was used to run the PERMANOVA. All the data and code to reproduce the analyses are available from the following GitHub repository: https://github.com/MickaelHeudier/reserveffect.

3 | RESULTS

3.1 | Benthic habitat composition and distribution

The study area encompassed seven habitat classes (Figure 3a and b). Rubble and sand were the dominant habitat classes (each one encompassing 22% of the study area), followed by open sea (16%), microalgal mats (14%), coral/algae (13%), and rock and seagrass (6% each). Habitat compositions were rather similar inside and outside the MPA. The main differences were the proportions of microalgal mats (20% inside vs. 10% outside the MPA) and rock (3% inside vs. 8% outside the MPA). Rubble and sand were the dominant habitat classes in both protected and unprotected areas (22% and 20% vs. 22% and 23%, respectively).

3.2 | Spatial distribution of megafauna

A total of 845 dugongs, 950 sea turtles, 180 sharks, 569 Dasyatidae rays and 239 Myliobatidae rays were recorded during the 20 aerial surveys. Dugongs were aggregated on the external side of the fore reef by the mouth of the central channel inside the MPA (Figure 4a). This aggregation (over 40 individuals) persisted in eight of the 20 surveys (from July to September; Appendix S3A). Dugongs were also observed in the lagoon, mostly as single individuals. Sea turtles were distributed throughout the lagoon and the barrier reef, as well as in the deeper areas (Figure 4b). Sharks were distributed in the lagoon and on the barrier reef. A nearshore shark concentration in the MPA (Figure 4c) was observed during four of the surveys in November

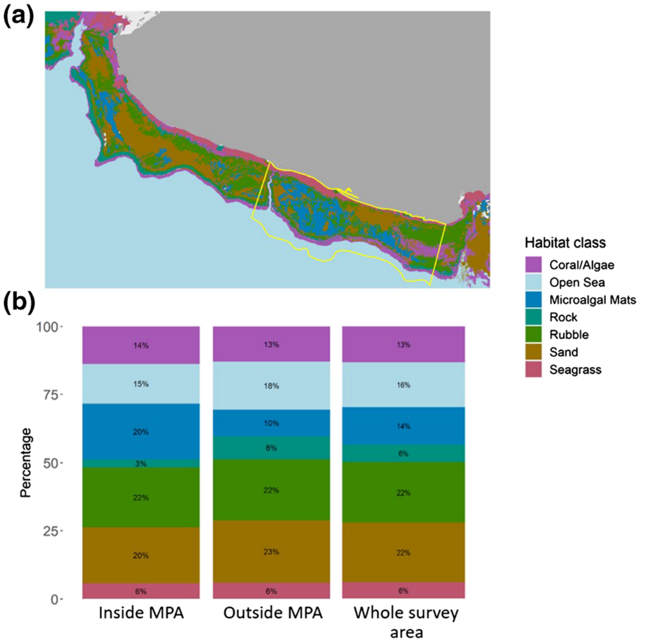

FIGURE 3 (a) Map of habitat classes with the MPA overlain in yellow. Habitat classes were derived from the Allen Coral Atlas for areas with depth shallower than 10 m. Areas with depth greater than 10 m were lumped into an 'open sea' category. (b) Percentages of habitat classes inside the MPA, outside the MPA and in the whole survey area. The colour legend is the same for panels (a) and (b).

(Appendix S3C). Dasyatidae were primarily observed in the central part of the lagoon (Figure 4d). Myliobatidae were distributed both in the lagoon and on the barrier reef, with a concentration inside the MPA (Figure 4e).

3.3 | Effects of habitat and protection on megafauna densities

No significant effect of habitat or protection was found on dugong density, but a combined effect of habitat and protection was detected (PERMANOVA: *F*-score = 1.75, *P*-value = 0.037; Figure 4f, Appendix S4), with significantly different dugong densities between rubble and open sea habitats intertwined with protection (pairwise *t*-test: *F*-score = 2.9082, *P*-value = 0.008; Figure 5a). Specifically, dugong densities were over 70 times higher in the open sea habitat inside the MPA compared with the rubble habitat outside the MPA. There was no significant effect of habitat or protection on sea turtle density (Figure 4f, Appendix S4). There was a significant effect of protection on shark density (PERMANOVA: *F*-score = 9.67, *P*-value = 0.001; Figure 4f, Appendix S4), with significantly higher values inside the MPA compared with outside (1:9 ratio; Figure 5b). A significant effect of habitat was found on Dasyatidae densities (PERMANOVA: *F*-score = 7.59, *P*-value = 0.001; Figure 4f; Appendix S4). Dasyatidae densities were significantly different between sand and coral/algae (1:13 ratio; pairwise *t*-tests:

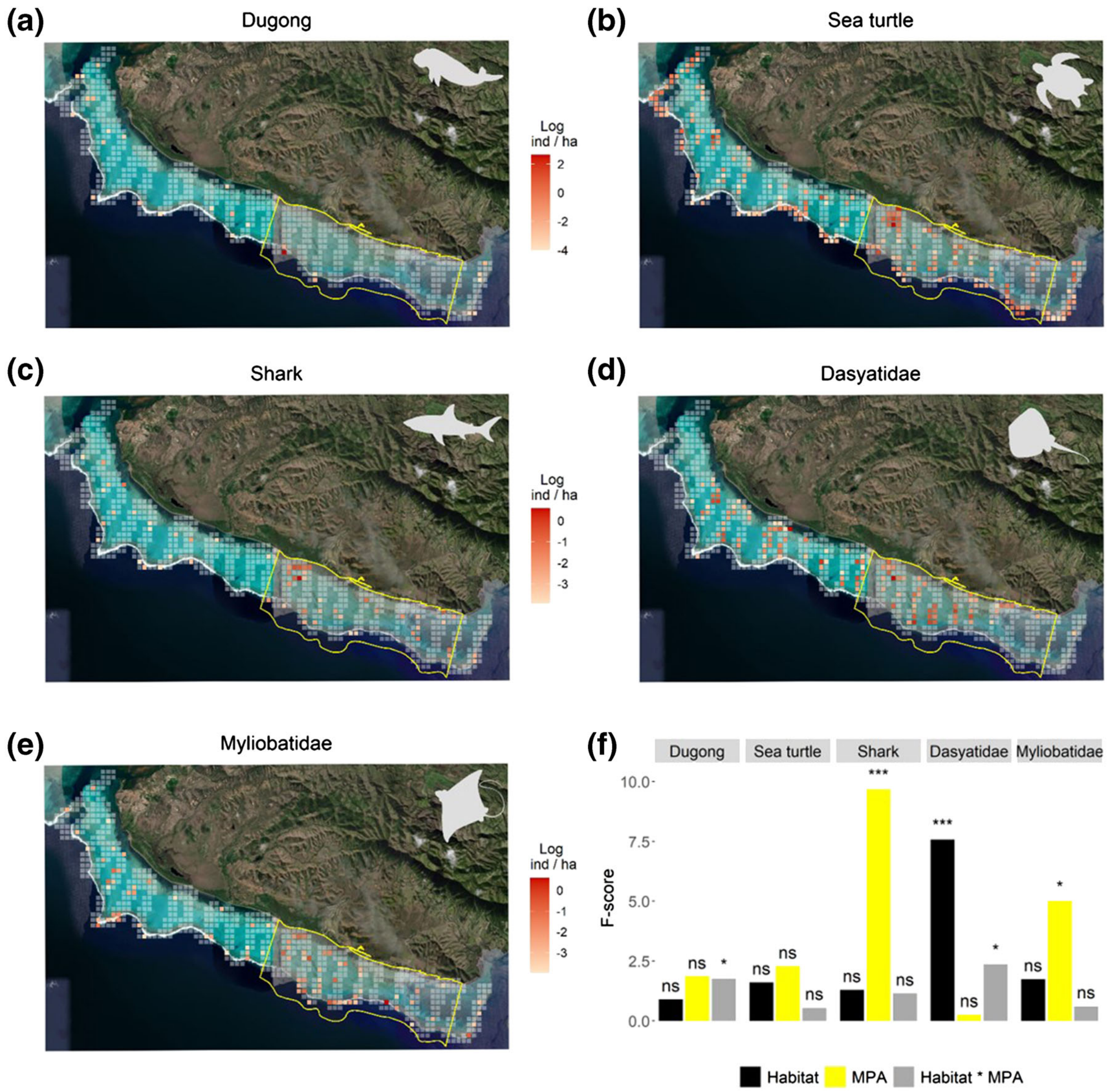

FIGURE 4 (a–e) Maps of log-transformed densities (individuals/ha) for each megafauna taxon derived from aerial video-surveys with the MPA overlain in yellow. (f) The results of the PERMANOVA to assess habitat, protection and habitat × protection effects on megafauna densities. Significance levels: ns, P-value > 0.05 non-significant; * 0.05 ≥ P-value > 0.01; ** 0.01 ≥ P-value > 0.001; *** P-value ≤ 0.001.

F-score = 13.7, P-value < 0.001), between sand and open sea (1:40 ratio; F-score = 20.1, P-value < 0.001), between microalgal mats and coral/algae (1:24 ratio; F-score = 16.2, P-value < 0.001) and between microalgal mats and open sea (1:82 ratio; F-score = 21.6, P-value < 0.001; Figure 5c). A combined effect of habitat and protection was also found for Dasyatidae (PERMANOVA: F-score = 2.36, P-value = 0.047; Figure 4f, Appendix S4) with significantly different densities between seagrass and open sea habitats intertwined with protection (pairwise t-test: F-score = 16.4, P-value < 0.001) (Figure 5d). Specifically, Dasyatidae densities were over 20 times higher in the seagrass habitat inside the MPA compared to the open sea habitat outside the MPA. A significant protection effect was found on Myliobatidae density (PERMANOVA: F-score = 5.01, P-value = 0.016; Figure 4f, Appendix S4), with significantly higher values inside the MPA compared with outside (1:3 ratio; Figure 5e).

4 | DISCUSSION

This study used a novel, aerial-based technique, to disentangle the effects of coral reef habitat and spatial protection on five megafauna taxa across a shallow lagoon in New Caledonia. A permutational multivariate analysis of variance applied to megafauna densities derived from 137.8 km^2 survey coverage over 5 months and high-resolution habitat information revealed contrasting results between taxa.

4.1 | Interpretation of taxon-specific results

A significant combined effect of habitat and protection was found for dugong, meaning that habitat and protection were not significant alone but became significant in concert. This effect was driven by the

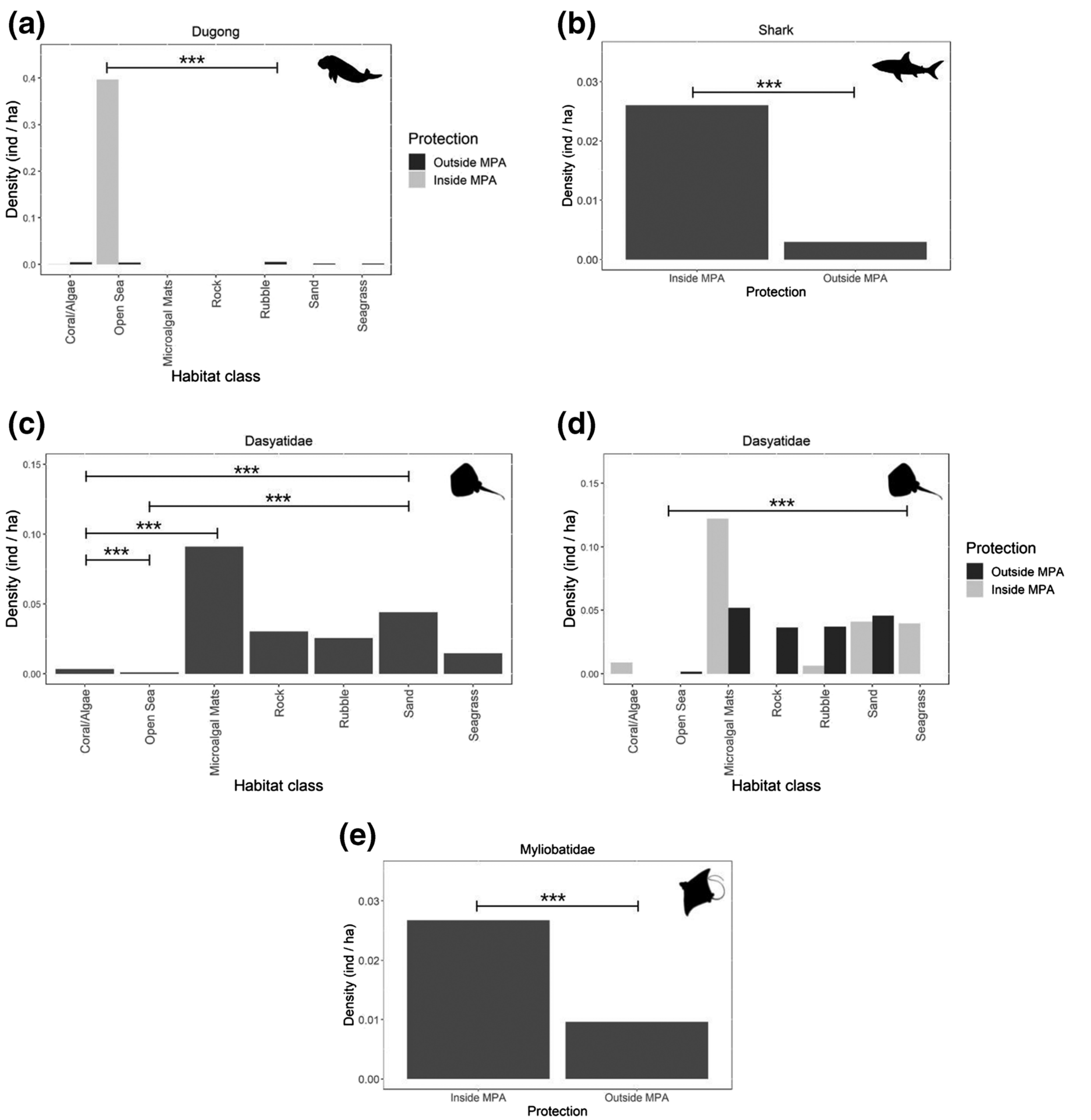

FIGURE 5 Results of significant pairwise *t*-tests (*P*-value ≤ 0.001) following the PERMANOVA. (a) Dugong for the effect of habitat × protection. (b) Sharks for the effect of protection. (c) Dasyatidae for the effect of habitat. (d) Dasyatidae for the effect of habitat × protection. (e) Myliobatidae for the effect of protection.

observed dugong aggregation in cooler months on the fore reef (within the open sea habitat class) inside the MPA. Such dugong aggregations were already reported from aerial surveys in the early 2000s (Garrigue, Patenaude & Marsh, 2008) and thermoregulation was recently hypothesized as their underlying reason, as the fore reef becomes warmer than the lagoon in the cool season (Derville, Cleguer & Garrigue, 2022). These results thus indicate that the Poé MPA encompasses important dugong habitat in cooler months, which seems to diverge from the results of Cleguer et al. (2015) that showed a spatial mismatch between important dugong habitat and MPAs at the scale of New Caledonia.

Significant effects of protection were found for sharks and Myliobatidae, with observed densities respectively 9 and 3 times higher inside the MPA compared with outside. These findings must be interpreted in the context of New Caledonia where elasmobranch populations are free from fishing pressures. Indeed, shark and ray catches are historically low in all New Caledonian waters (Juhel et al., 2017) while commercial and recreational fishing in coral lagoons are limited to finfish and invertebrates (Léopold et al., 2014). So, the positive statistical effect reported here cannot be due to the release of fishing pressure on elasmobranchs, as observed in no-take MPAs within heavily fished regions (Osgood, McCord & Baum, 2019;

Espinoza et al., 2020; Jabado et al., 2021; Flowers et al., 2022). A more plausible explanation is that the ban on fishing inside the Poé MPA may have led to locally enhanced availability of prey for sharks and Myliobatidae (i.e. finfish and invertebrates; Jacobsen & Bennett, 2013; Kleinertz et al., 2022), as hypothesized in other regions (Bond et al., 2012). Interestingly, no significant effects of benthic habitat were detected on sharks and Myliobatidae. Other habitat factors potentially explaining the observed densities of sharks and Myliobatidae in the Poé lagoon include reef structural complexity (Desbiens et al., 2021; Lester et al., 2022), tide (Schlaff, Heupel & Simpfendorfer, 2014; Ayres et al., 2021) and salinity (Schlaff et al., 2017). Temperature may also be an important factor given the demonstrated evidence of behavioural thermoregulation in both Myliobatidae (Matern, Cech & Hopkins, 2000) and reef sharks (Hight & Lowe, 2007; Speed et al., 2012). Although human presence can influence the movements and behaviour of elasmobranchs (Juhel et al., 2019; DeGroot et al., 2020), human frequentation is unlikely to have affected their densities in the present case, as the study took place in a period of tourism restrictions combined with a local lockdown owing to the Covid-19 pandemic. It is, however, possible that the lower human frequentation led these species to use some areas they would otherwise avoid owing to usually heavy human presence.

The results for Dasyatidae differed from those of other elasmobranchs, with a strongly significant effect of habitat on density. This finding is consistent with the association with soft bottoms of Dasyatidae, which are known for digging 'pits' in the sediment while looking for buried prey such as annelids and bivalves (O'Shea et al., 2011). Higher Dasyatidae densities were found in microalgal mats and sand habitats, in accordance with a study at Coral Bay (Western Australia) that recorded feeding pits in sand and in sand with algae (O'Shea et al., 2011) (corresponding to the definition of the microalgal mats class in the present study; Kennedy et al., 2021). The results further revealed a significant combined effect of habitat and protection for Dasyatidae (in particular between the open sea and seagrass habitats), meaning that protection became significant in combination with habitat. Other habitat factors with potential influence on Dasyatidae distribution may include tide (Gilliam & Sullivan, 1993) and light intensity (Cartamil et al., 2003).

No effect of habitat or protection was detected for sea turtles. These results appear to diverge from previous studies, including the study of Hays et al. (2021) who showed that even a small MPA can provide effective protection to hawksbill (*Eretmochelys imbricata*) and green sea turtles by encompassing their movements. Similarly, Nel, Punt & Hughes (2013) showed that coastal MPAs can protect loggerhead (*Caretta caretta*) and leatherback (*Dermochelys coriacea*) sea turtles in South Africa. Following the hypothesis of Roberts et al. (2021), the IUCN category IV of the Poé MPA may not allow sea turtles to fully benefit from the protected area since human activities are present, potentially impacting on sea turtle behaviour by reducing their time spent eating, foraging and breathing (Hayes et al., 2017). While seagrasses are the primary diet items of green sea turtles – one of the dominant species in New Caledonia (Read et al., 2015) – their distribution was unlikely to drive individuals inside the Poé MPA as their proportions in the protected vs. unprotected areas were almost equal.

4.2 | Limitations and perspectives

There are, however, several limitations inherent to the aerial-based approach for investigating habitat and protection effects on megafauna populations. First, the survey was conducted over a short 5 month period, representing a single season (the cool season) and a single year. The results should not be extrapolated beyond this study period, as they could significantly change owing to seasonal or interannual variability. Surveys should be replicated in the warm season and in other years to examine whether the observed effects of habitat and protection hold beyond the current study period. Surveys beyond the Poé area would also allow habitat and protection effects to be investigated more broadly. Second, while aerial surveys provide fast and accurate species density estimates over increasingly large areas, they are generally not appropriate for the re-identification of individuals over consecutive surveys (with the exception of whales or other large species characterized by distinctive patterns). Hence, the present approach can only compare density estimates between habitat and protection strata with no information on an individual's site fidelity. The latter information, typically obtained from telemetry studies (e.g. Derville, Cleguer & Garrigue, 2022), would provide complementary data to this study. Third, the detection of megafauna from aerial surveys is strongly affected by weather and environmental parameters, including wind, swell and water clarity (Fuentes et al., 2015; Hagihara et al., 2018; Colefax et al., 2019; Kelaher et al., 2020b). The calm, clear and shallow waters characterizing the Poé lagoon enabled megafauna detection from the surface to the bottom, alleviating the need to correct for species availability at the surface, the so-called 'availability bias' (Marsh & Sinclair, 1989). Aerial surveys would still be applicable in other places with different prevailing conditions (e.g. deeper, more turbid waters), but appropriate corrections for availability bias would be necessary (Fuentes et al., 2015; Hagihara et al., 2018). Spectral filtering offers a promising way forward for improving animal detection below the surface through the identification of optimal wavelengths maximizing the contrast between animals and their surroundings (Colefax et al., 2021). A fourth limitation of aerial surveys is their inability to identify animals at the species level, leading to species groupings (e.g. sea turtles or sharks). A lower altitude combined with a very high camera resolution would allow better species identification, ultimately yielding more informed conservation decisions based on species-specific data.

Another limitation of this study stems from the satellite-based characterization of habitats used in conjunction with aerial survey data to investigate the distributions of megafauna. Although the Allen Coral Atlas (Kennedy et al., 2021) provides a detailed classification of benthic habitat, the present study would benefit from up-to-date *in situ* information to describe other substrate characteristics with potential influence on megafauna distribution (e.g. the taxonomic composition of coral/seagrass communities) and better differentiation between substrates (particularly between corals and algae that are currently grouped under a single class). *In situ* habitat data would be particularly useful in areas deeper than 10 m out of reach of satellites that were lumped into a broad 'open sea' class in the present study. Beyond the sole characteristics of the benthic substrate, future studies should incorporate other determinants of megafauna distribution, such as water temperature, prey availability and human activities. Studies evaluating differences in fish assemblages between protected and unprotected areas at Poé would be particularly helpful to see whether higher prey availability could be driving the higher observed shark and Myliobatidae densities inside the MPA. Fine-scale studies quantifying recreational fishing and touristic activities would also be extremely useful in order to assess the impact of these activities on the distribution and densities of megafauna throughout the Poé area. Finally, repetitions of the survey in post-pandemic conditions may help to see if human frequentation can potentially alter species densities and distributions, in particular for elasmobranchs.

4.3 | Conservation implications

This study detected positive effects of protection (alone or combined with habitat) for four of the five studied megafauna taxa. Significantly higher densities of sharks and Myliobatidae were found inside the MPA compared with outside, although the underlying driver of this pattern has yet to be elucidated. The high densities of dugongs on the fore reef were effectively protected by the MPA, stressing the need to maintain its current outer boundary. The MPA also protected important soft bottom habitat (e.g. microalgal mats) for Dasyatidae, with densities observed in this habitat within the MPA twice as high as those outside. This finding underlines the need to protect soft bottom areas adjacent to coral reefs that provide important habitats for Dasyatidae as well as potentially other megafauna taxa.

In contrast, there was no positive effect of the Poé MPA for sea turtles. Sea turtles were the most abundant taxon in the study area, with a mean density of 0.5 individuals per hectare compared with 0.01 and 0.02 individuals per hectare for sharks and Myliobatidae, respectively. Because of their relatively high abundance in the area, sea turtles may exhibit weaker responses to spatial protection compared with other species characterized by lower abundances. The protection of rookeries may prove a more effective conservation measure for sea turtles. In New Caledonia, major sea turtle rookeries include the remote d'Entrecasteaux and Chesterfield atolls (Read et al., 2015). These atolls have been recently designated as MPAs (no-take and no-entry, respectively) and are likely to provide adequate protection of sea turtle rookeries.

In conclusion, the aerial methodology implemented in this study proved efficient for disentangling the effects of habitat and protection on megafauna densities in the Poé area. The findings underline the importance of the no-take MPA for reef-associated species like sharks, rays and dugongs, stressing the need to maintain and monitor it through time. Aerial surveys not only provide higher surface coverage than traditional underwater surveys (c. 7 km^2 in 1 h of flight as compared with 500 m^2 in 1 h of dive), but also allow the detection of elusive species that often go unnoticed in underwater surveys (Juhel et al., 2017). With appropriate corrections (e.g. for availability bias), this methodology can be extended to investigate habitat and protection effects on megafauna in other coral reef regions of New Caledonia and beyond.

AUTHOR CONTRIBUTIONS

Mickael Heudier: Conceptualization; formal analysis; visualization; writing—original draft. **David Mouillot:** Conceptualization; project administration; supervision; writing—review and editing. **Laura Mannocci:** Conceptualization; data curation; funding acquisition; methodology; project administration; supervision; visualization; writing—review and editing.

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CONFLICT OF INTEREST STATEMENT

All authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

The megafauna dataset is available at https://github.com/MickaelHeudier/reserveffect.

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SUPPORTING INFORMATION

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

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