Who lives in the open sea? Distribution and densities of surfacing marine megafauna in three subregions of the South Pacific (New Caledonia, Wallis and Futuna, and French Polynesia)

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ABSTRACT

Context. Assessing the distribution and abundance of marine fauna and the ecological status of coastal and pelagic ecosystems is key to biodiversity conservation, but the monitoring of mobile marine species raises multiple logistical and financial challenges. **Aims.** The project describes the distribution, abundance and taxonomic assemblage of several marine megafauna taxa in three subregions of the western and central South Pacific Ocean (New Caledonia, Wallis and Futuna, and French Polynesia). **Methods.** Large-scale aerial surveys were conducted using a standardised multi-taxon protocol, to characterise the occurrence and abundance of marine megafauna over 2.5 million km^2. Analysing more than 122 000 km of transects, the densities of 22 different taxa were estimated: seven taxonomic groups of marine mammals (Physeteridae, Kogiidae, Ziphiidae, Globicephalinae, Small Delphininae, Large Delphininae, and Dugongidae), a single group for hard-shelled sea turtles, three groups of elasmobranchs (including whale sharks), and 11 groups of seabirds (including Phaethontidae, Hydrobatidae, Fregatidae and Sulidae). **Key results.** Contrasting patterns of species distribution were found. Marine mammal diversity increases north and west, with a distinct species assemblage in New Caledonia, compared to other subregions. A strong latitudinal gradient was observed across French Polynesia, independent of taxa. **Conclusions.** This study provides the first comparison of marine species assemblages across the three oceanic subregions and sets a regional baseline for the biogeography of marine megafauna in the region. **Implications.** The taxonomic and spatial extension of the results opens up new perspectives for the development of local conservation measures, especially for taxa with already documented population declines.

Keywords: aerial survey, cetacean, dugong, elasmobranch, marine mammal, marine megafauna, seabird, sea turtle, Southwest Pacific Ocean.

Introduction

Marine megafauna (defined here as marine mammals, seabirds, sea turtles, and large elasmobranchs) face major conservation challenges worldwide (Dulvy *et al.* 2014). These include overfishing, illegal captures, bycatch, reduced resource availability, plastic and chemical pollution, habitat loss or degradation, and global warming and its effect on ecosystems (Worm *et al.* 2006; Lefort *et al.* 2015; Senko *et al.* 2020; Finlayson and van de Merwe 2021; van Weelden *et al.* 2021; Nelms *et al.* 2023). Addressing these threats requires the development of appropriate management and mitigation strategies, which in turn require reliable estimates of the abundance and distribution of marine megafauna (Williams *et al.* 2002). However, effective offshore monitoring poses several challenges due to the high financial and logistical costs of marine survey campaigns. As a result, population trends of most marine megafauna species, their ecological functions, and species interactions within marine communities are poorly studied, despite the fact that they are expected to play a major role in marine ecosystem processes (Estes *et al.* 2016).

Collection: Marine Mammals in the Pacific

Used for many decades, aerial surveys are an efficient platform for collecting wildlife data over large spatial extents (Caughley *et al.* 1976), and in short time frames (Davis *et al.* 2022). Aircraft facilitate large-scale monitoring, and relatively rapid inter-regional comparisons of the abundance and density of target species. Comparable boat-based surveys can take weeks to monitor the same area that an aerial survey can cover in a matter of days. Thus, systematic aerial surveys can be less expensive than large-boat surveys to monitor a given area despite being significantly more expensive per unit of time (Davis *et al.* 2022). These advantages have led to the increasing use of aerial transects for monitoring and estimating the relative abundance of marine mammals and seabirds (e.g. Pollock *et al.* 2006; Henkel *et al.* 2007; Certain and Bretagnolle 2008; Hammond *et al.* 2013; Laran *et al.* 2017*a*, 2017*b*; Pettex *et al.* 2017), while less developed for sea turtles (Lauriano *et al.* 2011; Fuentes *et al.* 2015) or elasmobranchs (Westgate *et al.* 2014; Notarbartolo di Sciara *et al.* 2015). To further reduce costs, simultaneous observations of multiple species groups can be conducted within a single aerial survey (Lauriano *et al.* 2011; Mannocci *et al.* 2013*a*; Laran *et al.* 2017*a*), providing the opportunity to describe marine megafaunal assemblages with minimal bias on data collection (Lambert *et al.* 2019; Stephenson *et al.* 2023).

A compilation of published geospatial databases of marine mammals transect surveys between 1975 and 2005 shows very poor representation of the Pacific, Indian and South Atlantic Oceans (Kaschner *et al.* 2012). On average, only 10% of the predicted range of cetacean species was covered by at least one study, and offshore waters have the greatest lack of data on species composition and abundance estimates. Furthermore, most research on marine mammal species in remote areas such as French Polynesia, New Caledonia or Wallis and Futuna is focused on nearshore waters. For example, most of the studies in those three subregions are primarily dedicated on seasonal humpback whales (*Megaptera novaeangliae*) (Gannier 2004; Garrigue *et al.* 2015, 2020; Derville *et al.* 2019, 2020), or dugongs (*Dugong dugon*), for the lagoons of New Caledonia (Cleguer *et al.* 2020; Derville *et al.* 2022; Garrigue *et al.* 2022). A few studies exist for other species such as the rough-toothed dolphin (*Steno bredanensis*) (Gannier and West 2005; Oremus *et al.* 2012; Albertson *et al.* 2017), the spinner dolphin (*Stenella longirostris*) (Gannier and Petiau 2006; Oremus *et al.* 2007), or the Indo-Pacific bottlenose dolphin (*Tursiops aduncus*) (Bonneville *et al.* 2021). However, they do not provide estimates of local population sizes and offer limited prospects for conservation. Similarly, knowledge on marine megafaunal species such as seabirds or sea turtles in these three subregions of the south-west and central Pacific is still scarce and/or based on old observational records. Consequently, this lack of data is a major handicap in the implementation of conservation measures such as the designation of marine protected areas (MPAs) or the effective management of anthropogenic activities.

The first objective of this study was to establish a baseline map of the diversity and densities of marine mammals, seabirds, elasmobranchs, and sea turtles in three subregions of the western and central South Pacific Ocean (New Caledonia, Wallis and Futuna, and French Polynesia), using a standardised aerial survey methodology in order to compare megafaunal assemblages along longitudinal gradients and biogeographic provinces. This survey was part of a larger initiative, the REMMOA (Recensement des Mammifères marins et autre Mégafaune pélagique par Observation Aérienne) surveys launched in 2008 by the French Agency for Marine Protected Areas (now the Office Français de la Biodiversité, OFB) to conduct an aerial census of marine mammals and other pelagic megafauna throughout the tropical waters of the French Exclusive Economic Zone (EEZ) to provide marine conservation agencies with baseline information on the marine megafaunal distribution. This large-scale project was conducted in the Caribbean-Guiana (Mannocci *et al.* 2013*a*), south-western Indian Ocean (Mannocci *et al.* 2013*b*; Laran *et al.* 2017*a*), French Polynesia (Lambert *et al.* 2014; Mannocci *et al.* 2014) and southwestern Pacific within New Caledonia (Receveur *et al.* 2022) and Wallis and Futuna waters.

In addition to greatly improved cost-effectiveness, the rationale for developing such multi-taxa surveys using a standardised methodology is to address ecological questions at the community level by collecting information on a wide range of taxa that are visible from the air.

Materials and methods

Study area and survey designs

The geographical extent of the sampling design was chosen to cover a latitudinal and longitudinal gradient and a diversity of marine habitats, but also with regard to the availability of suitable airfields and aircraft maintenance facilities (Fig. 1). Surveys were conducted during the southern tropical wet season (from mid-October to early May), in order to maximise good weather conditions for aerial detection (especially wind speed). The total survey area covers 2.5 million km^2 throughout the tropical western and central South Pacific Ocean (Fig. 1). It overlaps with three biogeographic provinces in the Longhurst system (Longhurst 2010), which aims to represent the broad-scale processes that drive ocean productivity. First, the Archipelagic Deep Basin has a very large latitudinal extent from 22°N to 35°S, a complex topography including deep basins and shelves, and includes New Caledonia and the Coral Sea at its eastern boundary. The second province is the Western Pacific Warm Pool, a 'typical' tropical system, with an oligotrophic mixed layer and known to be at the heart of the El Niño Southern Oscillation (ENSO) mechanism (Longhurst 2010) and including Wallis and Futuna on its south-eastern border. Finally, the South Pacific Subtropical Gyre, characterised by nutrient depleted waters and often described as the most uniform and stable region of the open ocean (Longhurst 2010) which includes French Polynesia.
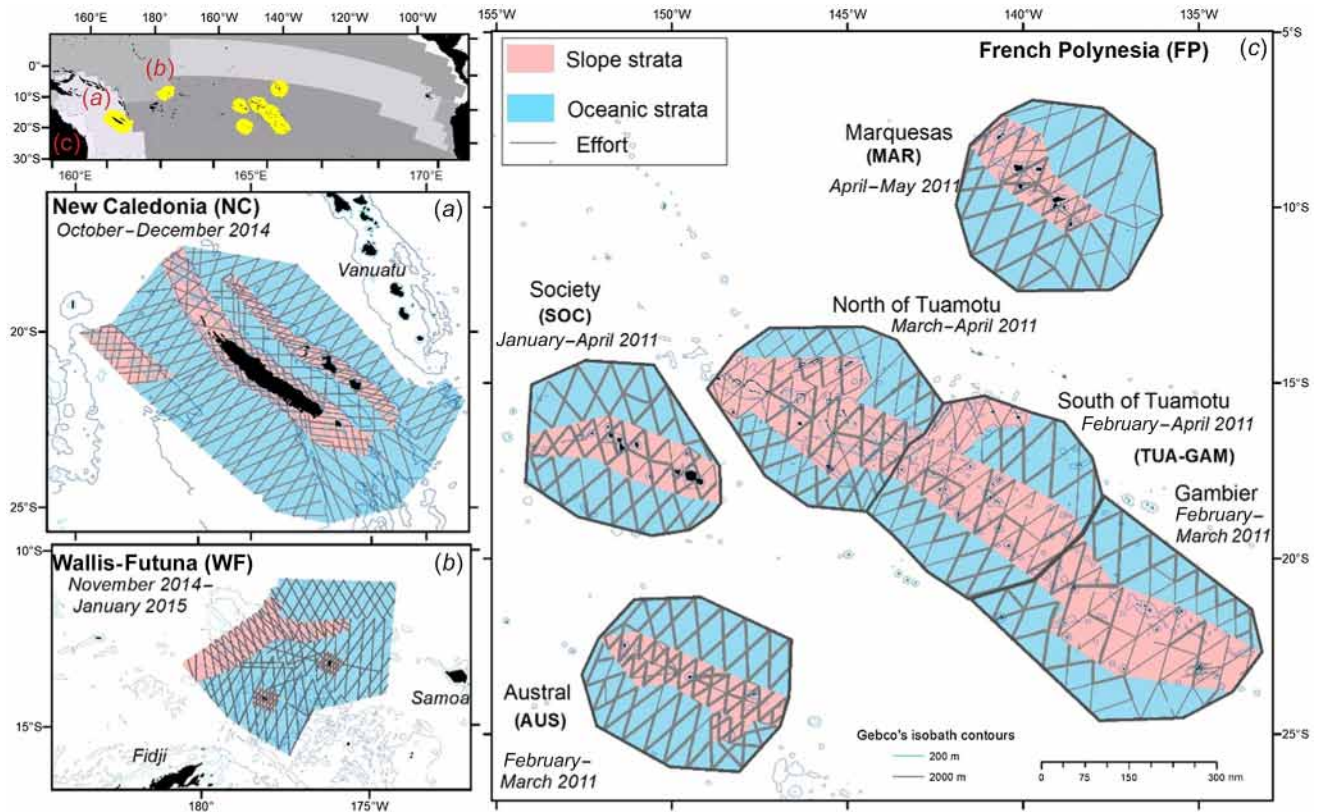
Fig. 1. Study area and track of effort for REMMOA aerial surveys in the Tropical Pacific Ocean. (*a*) New Caledonia in 2014, (*b*) Wallis and Futuna EEZ in 2015, and (*c*) French Polynesia in 2010, with bold line corresponding to effort covered two times. Top left: the Longhurst Biogeographical Provinces (from http://www.marineregions.org) with (*a*) in the Archipelagic deep basins, (*b*) in the Western Pacific warm pool, and (*c*) in the South Pacific gyre. *a–c* maps are at the same scale.

The New Caledonia subregion (25–17°S, 160–171°E) is part of the south-west Pacific, which is considered as the centre of major water pathways from the subtropics to the equator and to southern latitudes (Ganachaud *et al.* 2007). New Caledonia's EEZ is included in the Natural Park of the Coral Sea, the fifth largest MPA in the world (1.3 million km²). The study area includes oceanic waters located outside of the barrier reef of the main island up to 250 km to the west, including the shallow banks of Landsdowne and Fairway, and the Loyalty and Walpole Islands to the east, Bélep and d'Entrecasteaux Reefs to the north, and the Isle of Pines in to the south (Fig. 1). This subregion encompasses a variety of habitats including slope, shallow banks, seamounts, and abyssal plains. It was surveyed from October to December 2014. The Chesterfield-Bampton and Bellona submarine plateaus were not surveyed due to their distance from the nearest airfield (Table 1).

The second subregion comprises most of the EEZ of Wallis and Futuna (WF, 15–10°S, 4–9°W). It includes the volcanic islands of Wallis and Futuna and the uninhabited Alofi, as well as some seamounts to the north of Rothuma, Cook's Dome and Waterwhich Sandbank, and deep offshore waters to the south (Fig. 1). This subregion was surveyed between late November 2014 and mid-January 2015.

Finally, the third subregion which makes up the second largest maritime domain in the South Pacific, is French Polynesia (26–6°S, 154–133°W). Five main archipelagos, all oriented northwest–southeast, create major obstacles to ocean currents in this area. Due to the size of the EEZ, the subregion has been divided into four distinct survey blocks (an isolated group of strata, Fig. 1). The central Tuamotu Archipelago is the largest and includes numerous islands and atolls. Adjacent to it and at its southeastern border is the more dispersed Gambier Archipelago, both of which are included in the Tuamotu-Gambier survey block (TUA-GAM). To the west and south are two major island groups separated by wide deep passages: the Society and Austral archipelagos (Martinez *et al.* 2009). The French Polynesia subregion exhibits a strong latitudinal gradient in primary production, from the depleted south, to the northern Marquesas Archipelago (Table 1). The western part of the latter benefits from contrasting strong primary production compared to the surrounding oceanic waters, due to a remarkable island mass effect (Martinez and Maamaatuaiahutapu 2004). In addition, the complex geomorphology of the Marquesas archipelago creates a diversity of marine habitats (Galzin *et al.* 2016). This subregion was surveyed from January to early April 2011.

Survey design in each subregion was pre-determined by airfield locations on islands and aircraft endurance, then the

Table 1.   Extents of the surveyed areas during REMMOA project, effort and period by subregion.

Subregions	Blocks	Area (km²)	Total effort (km)	Effort selected for analyses	Period
Wallis and Futuna		230 722	22 840	21 824	November 2014–January 2015
New Caledonia		542 216	43 301	38 675	October–December 2014
French Polynesia		1 761 472	101 280	62 165	
Austral	(AUS)	261 557	23 500	15 212	February–March 2011
Gambier	(GAM)	336 802	13 648	12 103	February–March 2011
Society	(SOC)	271 881	17 854	12 127	January–April 2011
South of Tuamotu	(TUAM)	297 924	14 139	7188	February–April 2011
North of Tuamotu		286 174	15 571	9708	March–April 2011
Marquesas	(MAR)	307 133	16 569	5826	April–May 2011
Total		2 534 410	167 422	122 664	

accessible spatial extent was divided into smaller blocks, which were in turn stratified into bathymetric strata: slope (<2000 m) and oceanic (>2000 m). Survey design was optimised with a zigzag track layout, performed with Distance 6.2 software (Thomas *et al.* 2010) using Equal space zigzag for the New Caledonia and Wallis and Futuna subregions. In French Polynesia tracks were designed manually using a geospatial software (ArcMap from Esri), the survey plan was carried out and some transects were flown a second time on the same axes (56% of the effort in this subregion; Fig. 1) to minimise logistical constraints for the pilots of the three aircraft, with a time lag between crossings of 1 day to 3 months (average 16 days). For the three subregions, the effort/area ratio was not homogeneous between strata, in order to collect enough sightings for specific habitats for distribution modelling. Details are available in the field reports (Van Canneyt *et al.* 2011, 2015).

Aerial survey protocol

Surveys were conducted using a standard line-transect methodology (Buckland *et al.* 2001), as previously used for marine mammals (Hammond *et al.* 2013), but adapted for a multi-target protocol (Laran *et al.* 2017*a*; Lambert *et al.* 2019). To achieve the planned effort in a relatively short period of time, we simultaneously used three twin-engine Britten Norman Islander (BN-2 high-winged aircrafts with fixed landing gear). Transects were flown at 90 knots (167 km.h^{-1}) with a target altitude of 600 feet (183 m). The survey team consisted of 12 to 19 different observers per subregion (with the same team in New Caledonia and Wallis and Futuna), including five observers consistent across the three subregions. Observers attended a 1-week training course before participating in the surveys, which included a few training flights. Each flight typically consisted of two observers scanning the sea surface on either side of the aircraft with the naked eye in order to survey close to the track line through both bubble windows. Both were connected by intercom to the data recorder and the pilot.

To minimise bias due to observer fatigue, crew members rotated approximately every hour, with an off-duty observer on board. Data were collected using the SAMMOA software (SAMMOA 2014), which provides an audio recording that can be used for post-validation. Observers recorded all environmental conditions impacting the detection of animals: sea state (Beaufort scale), turbidity (from 0 for clear water to 2 for turbid water, where animals are only visible very close to the surface), cloud cover (0–8 octas), glare angle (0–360°) and severity (from 0 with no glare to 3 a strong glare that affects the ability to detect sightings), and a subjective ranking of sighting conditions (excellent, good, medium, poor). These covariates were recorded for each transect and whenever any of them changed. Observers scanned the sea surface and subsurface as well as the air column searching for all targeted taxa. Maximum collection distance from the transect was 200 m for seabirds, jellyfish, plankton (as *Trichodesmium* mats) and marine debris using a strip transect methodology, assuming that all available individuals were seen within the 200 m on either side of the transect, while for boat sightings two 500 m strip were considered. Both distances were marked on the landing gear. In addition, surfacing flying fish species, from *Exocoetidae* family, were counted using two manual counters and aggregated by section of transect. For marine mammals, sea turtles, and elasmobranchs, perpendicular distance was measured with clinometers when the animal was abeam. Number of individuals in each sighting, and presence of juvenile were also recorded. All taxa were identified to the lowest taxonomic level possible. Several taxa that could not be distinguished from the air, such as small sized delphinids, hard-shelled turtles or 'grey' terns, were grouped together for analyses (see Supplementary Table S1–S4 for the list of taxa). In this study, only sightings of marine mammals, seabirds, sea turtles and large fish were considered.

The aircraft stayed on the track line except when circle-back manoeuvres were engaged in order to check identification, group size or to collect digital images for some specific marine mammal sightings. The effort was stopped for a few

minutes and resumed when the aircraft rejoined the track at the stopping point. Flights were scheduled only in good weather condition (Beaufort scale <4) with the Zygrib interface (www.zygrib.org) for visualisation of NOAA-GFS standard weather forecast grib files.

Data analysis

A total of 167 422 km of transects were flown across the three subregions. To visualise the spatial distribution of identified taxa, the number of individuals encountered per kilometre was mapped on a 60 km × 60 km grid (to optimise effort homogeneity among cells).

For density estimates, only effort and sightings collected under good conditions (sea state <4 Beaufort and subjective condition equal to, or better than, 'Medium' on both sides of the aircraft) were retained thereby limiting variation in perception bias.

The strip transect methodology for seabirds assumes perfect detection within 2 m × 200 m bands (each side of the aircraft). For other taxa, sightings with larger perpendicular distances were truncated (≈5% of sightings) and excluded (Buckland *et al.* 2001), and detection functions were fitted. The effective strip widths (ESW) were estimated for all species or groups of species using Distance sampling methodology (Thomas *et al.* 2010), with the R package PelaCDS (ver. 0.1.0.9002) from *Pelaverse* package environment[1]. Data from all three subregions were pooled, as these surveys share the same protocol, training procedures and partially the same observers across subregions.

Hazard rate and half normal models were fitted to perpendicular distances, and for each taxa the model that minimised the Akaike Information Criterion (AIC) was selected as the detection function (see Supplementary Fig. S1). Multiple Covariate Distance Sampling analysis (MCDS, Marques and Buckland 2004) was tested using sea state, turbidity, cloud cover and glare severity as covariates. Mean group size and encounter rate were estimated for each bathymetric strata for seven marine mammal taxa, eleven seabird groups, three elasmobranch groups and the hard-shelled sea turtles. And then densities were re-estimated (weighted according to strata area), as the coefficient of variation, following Buckland *et al.* (2001).

The detection probability on the track line is typically composed of the perception and the availability bias. No specific protocol was implemented to estimate the perception bias and it was kept as constant as possible (standardised protocol, same aircraft types, partly same observers). Regarding the availability bias, information on diving behaviour and the proportion of time spent visible at surface of the different species was collected from the literature and used as the correction (Thomson *et al.* 2012). Correction factors applied to density estimates were assumed to be equal to 1 for seabird taxa and summarised on Table 2 for other groups. The same

Table 2. Correction bias factor estimated for availability of taxonomic groups, from average proportion of time spent at surface collected in the literature (see Laran *et al.* 2017*a*, Table S1).

Taxa	Family	Group	% time spent at surface
Marine mammals	Deep diver	Physeteridae	20
		Kogiidae	10
		Ziphiidae	9
	Globicephalinae	Large Globicephalinae	70
		Risso's dolphins	
		Small Globicephalinae	
	Delphininae	Large Delphininae	75
		Small Delphininae	
	Dugongidae		83.4[A]
Sea turtles	Hard-shelled turtles		35
Elasmobranchs		Whale sharks	25[B]
		Sharks	10
		Rays	50

Additional references from:
[A]Hagihara *et al.* (2016, 2018).
[B]Andrzejaczek *et al.* (2022).

proportions were used as in the previous study in the south-west Indian Ocean (see Laran *et al.* (2017*a*), Table S1); supplemented by an availability correction factor of 0.834 for dugongs estimated in New Caledonia, using a global value for all water depths (Hagihara *et al.* 2016, 2018) and 0.25 as the mean percentage of time spent in the top 5 m for more than 60 individuals of whale sharks (*Rhincodon typus*) (Andrzejaczek *et al.* 2022).

To examine regional patterns in the marine megafaunal community, we compared relative densities of 22 different taxa, corrected (for availability bias only) in six survey areas considered as sample sites: New Caledonia, Wallis and Futuna, and French Polynesia divided among Austral, Society, Tuamotu-Gambier (TUA-GAM) and Marquesas. For each, the community assemblage was investigated with Principal Component Analysis (PCA) using the multivariate analysis R package FactoMineR of R 2.7 (Lê *et al.* 2008).

Results

A total of 122 664 km of transect were retained for analyses from the three subregions, including 38 675 km for New Caledonia, 21 824 km for Wallis and Futuna and 62 165 km for the French Polynesia conducted in good sighting conditions (Table 1). Sighting conditions filters resulted in

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[1]https://gitlab.univ-lr.fr/pelaverse/pelacds.

a significant reduction in effort for the TUA-GAM and Marquesas survey blocks in French Polynesia (Table 1).

Detection functions for marine mammals, sea turtles and elasmobranchs were presented by group (Fig. S1). MCDS analysis obtained minimum AIC for Globicephalinae and sea state, same for Kogiidae and sea turtles with glare severity, but none had a logical trend (Fig. S2), excepted for Ziphiidae which was the only group where MCDS was included to estimate abundance, the others were estimated through CDS without any covariates.

Marine mammals

A total of 19 species of marine mammals were identified at the species level (or genus level for *Kogia* spp) from 602 sightings (5169 individuals) across the three subregions (see Table S1 for details by species and subregion). Results were pooled into taxonomic groups, with the exception of the dugong, because of the general difficulty of identifying species from the air. Selected taxa were: Balaenopteridae, Ziphiidae, Kogiidae, Physeteridae, small Delphininae (*S. longirostris, Stenella attenuata, Delphinus* spp) large Delphininae (*Tursiops truncatus, Lagenodelphis hosei, Steno bredanensis, T. aduncus*), small Globicephalinae (*Peponocephala electrea, Feresa attenuata*), large Globicephalinae (*Globicephala macrorhynchus, Pseudorca crassidens, Orcinus orca* or the well distinctive *Grampus griseus*). The minimum diversity was encountered in Austral, with only five distinct taxonomic groups, increasing north-ward and west-ward to 18 groups in New Caledonia, including four species of baleen whales and the dugong. Delphininae account for a quarter of the sightings, except in Wallis and Futuna (41%). Deep divers, such as Physeteridae, Kogiidae and Ziphiidae accounted for one quarter of sightings in Wallis and Futuna to one-third in the other two subregions (Fig. 2). Occurrences of Globicephalinae were about the same in all subregions. Balaenopteridae were seen from October to January in New Caledonia and Wallis and Futuna, but not at all in French Polynesia, which was surveyed later, between January and early May.

Marine mammals, in terms of individuals per kilometre of effort, exhibited a patchy distribution in French Polynesia, favouring nearshore waters, with the exception of the western part of Marquesas, where cells with the maximum index of individuals per kilometre were found even offshore (Fig. 3). In New Caledonia and Wallis and Futuna, their distribution is more homogeneous. Among taxonomic groups, deep divers were the most evenly distributed with juveniles (about 1/3 to 1/2 the size of adults) encountered in all subregions (Fig. S3). Higher densities of Ziphiidae and Kogiidae were estimated in the Marquesas survey block, with 0.08 and 0.06 individuals/km^2, respectively (corrected density, Table 3). Large and small Delphininae preferred waters around islands, except in Wallis and Futuna and west of the Marquesas (French Polynesia) where they were also encountered offshore. Juveniles were encountered in all three subregions (Fig. S3). Wallis and Futuna had the highest corrected density of small Delphininae with 0.05 individuals/km^2 (CV = 31%), twice that of New Caledonia, while the density of large Delphininae peaked in New Caledonia (0.03 individuals/km^2, CV = 38%). The encounter rate of Globicephalinae peaked west of New Caledonia, in the Coral Sea (west of Grande Terre Island, where several sightings included juveniles), and west of the Marquesas, but the higher densities were estimated in Wallis and Futuna (0.07 individuals/km^2, CV = 55%) and New Caledonia (0.06 individuals/km^2, CV = 55%), with values at least three times higher than in central and northern French Polynesia (Table 3).

Cumulative density (corrected for availability) of marine mammals was minimal in the oligotrophic waters of Austral (Fig. 4). It increased towards the north of French Polynesia, culminating in the Marquesas, where it was similar to that of New Caledonia and, to a lesser extent, Wallis and Futuna. New Caledonia had the more diverse composition with similar estimates for Delphininae, Globicephalinae, and deep divers
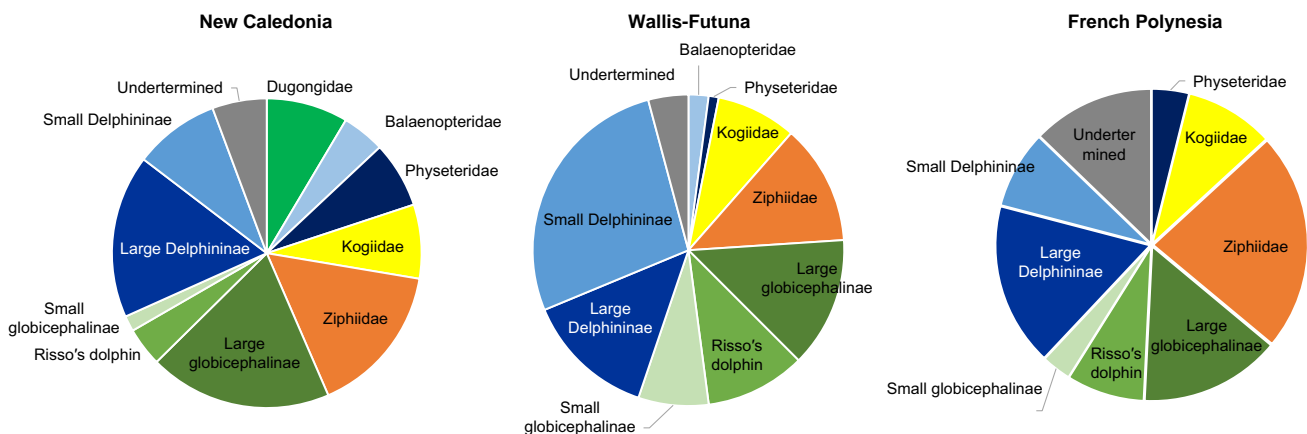

Fig. 2. Taxonomic composition of sightings of marine mammals (on transect of effort) collected over the three subregions.
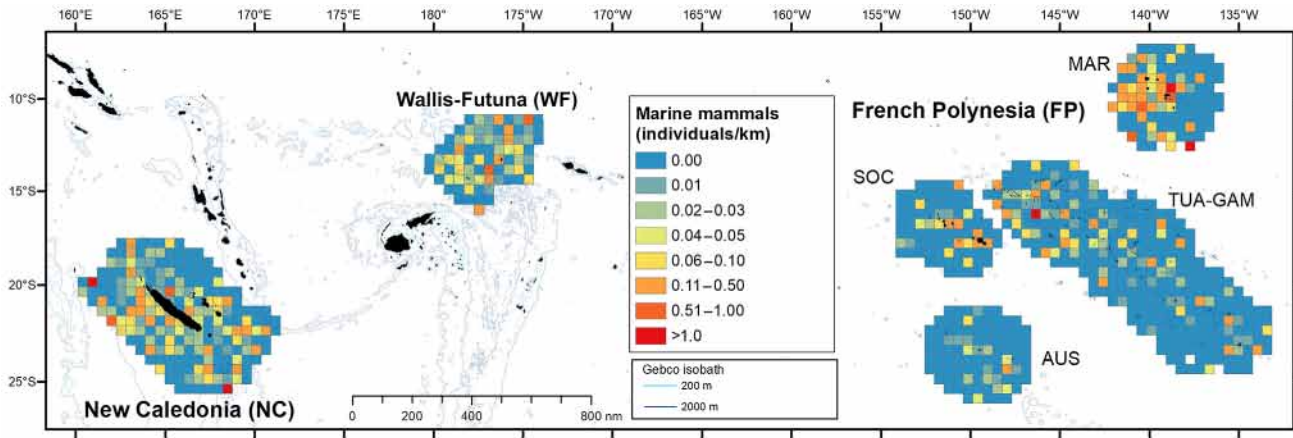
Fig. 3. Spatial distribution of individuals visually detected per kilometre for marine mammals in the three Pacific's subregions: New Caledonia, Wallis and Futuna and French Polynesia during REMMOA surveys. Each pooled on a 60 km × 60 km grid cell and given in individuals per kilometre. Cells accounting for a minimum effort of 50 km.

(Ziphiidae, Physeteridae and Kogiidae). Wallis and Futuna was dominated by small Delphininae and Globicephalinae (mainly Risso's dolphin, melon-headed whales and pygmy killer whales). And among the deep divers, Longman's beaked whales (*Indopacetus pacificus*) were particularly abundant, while in the Marquesas Ziphiidae and Kogiidae were dominant.

Seabirds

Of the 25 842 seabird sightings (73 310 individuals), 4094 could be assigned to single species and 16 011 were identified at the genus level (eight genera). The remaining sightings (5737) could only be identified at higher taxonomic levels (Table S2). Species with only one sighting record were considered to be rare and were excluded from tables and analyses. For consistency, sightings were pooled into 11 different taxonomic groups: 'Brown' terns, 'Grey' terns, White terns, Noddies, Hydrobatidae, 'Grey' petrels, 'Brown' petrels, Shearwaters, Sulidae, Phaethontidae, Fregatidae and silver gull (*Larus novaehollandiae*) for New Caledonia only (see Tables 4 and S3 for detail on species).

Taxonomic diversity appeared to be roughly similar across subregions, with most categories found in all three subregions (Table 4). Encounter rate of seabirds (in individuals/km) showed contrasting patterns, with high values in the north of the TUA-GAM survey block (French Polynesia) and the south-west coast of New Caledonia (Fig. 5). Similarly, the cumulative density of seabirds peaked in TUA-GAM, followed by Marquesas, New Caledonia and Society survey blocks (Fig. 4). New Caledonia hosts the highest densities of shearwaters and 'Grey' petrels, with densities decreasing along a west-east longitudinal gradient, decreasing by one or two orders of magnitude in Wallis and Futuna and French Polynesia (Table 4; Fig. S4). This presence seems to be rather coastal and coincides with the breeding of petrels

(Tahiti petrel, *Pseudobulweria rostrata*; black-winged petrel, *Pterodroma nigripennis* and Gould's petrel, *P. leucoptera*) or shearwaters (wedgetailed, *Ardenna pacifica*; short-tailed shearwaters, *Ardenna tenuirostris*) breeding or migrating during the beginning of the monitoring in December. Conversely, noddies, white terns, Sulidae and Fregatidae were most abundant in French Polynesia compared to western subregions. Phaethontidae stood out as the only group with homogeneous densities in all three subregions.

Elasmobranchs

A total of 702 sightings (905 individuals) of elasmobranchs were collected during line transect efforts (Table S4). The highest occurrence (individuals/km) was observed along the west coast of New Caledonia and west of Marquesas (Fig. 6), while only a few encounters were observed in the south of French Polynesia. Both Marquesas and New Caledonia have similar densities of rays (Table 3), while shark density peaked in New Caledonia, then in TUA-GAM (Fig. 4).

Only a few conspicuous taxa could be identified at the species level from the air, notably the whale shark, only encountered as single individuals. Although encountered in all three subregions, whale sharks were particularly abundant along the west coast of Grande Terre (New Caledonia) and in the waters of Wallis and Futuna (surveyed from October to January; Fig. 6), where the density was highest (Table 3).

Sea turtles

A total of the 260 sea turtle sightings (equivalent to 287 individuals) were collected during the transect effort. Only three were identified as leatherback turtles (*Dermochelys coriacea*) (Table S4), one in each of the three subregions, indicating the scarcity of this relatively distinctive species, at least during the survey period.

Table 3. Results obtained for taxonomic groups of marine mammals and other megafauna, with uncorrected and corrected estimates (using Table 2 correction factors) of relative densities (individuals/km^2) with corresponding coefficient of variation (CV in %) and relative abundance with 95% confidence interval (CI), estimated over the three subregions New Caledonia (NC), Wallis and Futuna (WF) and blocks of French Polynesia (FP-AUS, Austral; SOC, Society; TUA-GAM, Tuamotu-Gambier; MAR, Marquesas).

| Taxa | Subregion -blocks | Uncorrected for availability | | | | | Corrected for availability | | | |
| | | Density | CV (%) | Abundance | CI 95% | | Density | Abundance | CI 95% | |
					Min	Max			Min	Max
Dugongidae	NC	0.0010	32	554	301	1022	0.001	664	361	1225
Small Delphininae	NC	0.0211	35	11 424	4058	33 790	0.028	15 232	5411	45 053
	WF	0.0366	31	8453	3394	21 674	0.049	11 271	4525	28 899
	FP-AUS	–		–	–	–	–	–	–	–
	FP-SOC	0.0114	86	3475	804	15 029	0.015	3604	829	15 651
	FP-TUA-GAM	0.0062	51	5716	1199	27 854	0.008	7621	1599	37 139
	FP-MAR	0.0087	68	2473	617	10 029	0.012	3297	823	13 372
Large Delphininae	NC	0.0229	38	12 416	4188	38 304	0.031	16 555	5584	51 072
	WF	0.0109	38	2517	827	7887	0.015	3356	1103	10 516
	FP-AUS	–		–	–	–	–	–	–	–
	FP-SOC	0.0030	88	734	143	3786	0.004	943	183	4864
	FP-TUA-GAM	0.0022	55	2030	513	8139	0.003	2707	684	10 852
	FP-MAR	0.0075	78	2111	431	10 366	0.010	2815	575	13 821
Globicephalinae	NC	0.0423	42	22 932	7121	86 048	0.060	32 760	10 173	122 926
	WF	0.0477	55	11 012	2856	43 710	0.068	15 731	4080	62 443
	FP-AUS	0.0006	79	170	43	669	0.001	243	61	956
	FP-SOC	0.0149	52	3682	1192	11 399	0.021	5017	1630	15 477
	FP-TUA-GAM	0.0154	61	14 164	3447	60 481	0.022	20 234	4924	86 401
	FP-MAR	0.0163	67	4631	1398	15 337	0.023	6616	1997	21 910
Kogiidae	NC	0.0011	29	621	231	1806	0.011	6210	2310	18 060
	WF	0.0013	38	291	101	876	0.013	2910	1010	8760
	FP-AUS	0.0005	60	119	29	504	0.005	1190	290	5040
	FP-SOC	–	–	–	–	–	–	–	–	–
	FP-TUA-GAM	0.0003	62	240	60	987	0.003	2400	600	9870
	FP-MAR	0.0065	43	1834	818	4108	0.065	18 340	8180	41 080
Physteridae	NC	0.0010	40	544	136	2352	0.005	2720	680	11 760
	WF	0.0002	101	38	7	197	0.001	190	35	985
	FP-AUS	0.0012	93	313	67	1469	0.006	1565	335	7345
	FP-SOC	–		–	–	–	–	–	–	–
	FP-TUA-GAM	0.0001	102	A	A	A	A	A	A	A
	FP-MAR	–	–	–	–	–	–	–	–	–
Ziphiidae	NC	0.0047	24	2554	1025	6629	0.052	28 378	11 389	73 656
	WF	0.0014	4	334	101	1143	0.016	3711	1122	12 700
	FP-AUS	0.0011	53	293	83	1041	0.012	3256	922	11 567
	FP-SOC	0.0014	69	367	108	1242	0.016	4078	1200	13 800
	FP-TUA-GAM	0.0022	27	2063	741	6175	0.025	22 922	8233	68 611
	FP-MAR	0.0076	41	2145	935	4982	0.084	23 833	10 389	55 356
Hard-shelled turtles	NC	0.0094	13	5104	3712	7427	0.027	14 583	10 606	21 220
	WF	0.0024	37	561	196	1678	0.007	1603	560	4794

(Continued on next page)

Table 3. (*Continued*).

| Taxa	Subregion -blocks	Uncorrected for availability					Corrected for availability			
		Density	CV (%)	Abundance	CI 95%		Density	Abundance	CI 95%	
					Min	Max			Min	Max
	FP-AUS	0.0005	59	129	31	544	0.001	369	89	1554
	FP-SOC	0.0011	85	342	80	1459	0.003	760	177	3257
	FP-TUA-GAM	0.0022	25	2069	952	4767	0.006	5911	2720	13 620
	FP-MAR	0.0007	100	195	38	1002	0.002	557	109	2863
Rays	NC	0.0158	13	8556	6173	12 333	0.032	17 112	12 346	24 666
	WF	0.0021	33	473	160	1496	0.004	946	320	2992
	FP-AUS	0.0009	51	228	65	797	0.002	456	130	1594
	FP-SOC	0.0027	51	789	266	2425	0.005	1266	420	3982
	FP-TUA-GAM	0.0041	25	3731	1532	10 474	0.008	7462	3064	20 948
	FP-MAR	0.0182	24	5165	2700	9975	0.036	10 330	5400	19 950
Sharks	NC	0.0094	17	5107	2884	9277	0.094	51 070	28 840	92 770
	WF	0.0019	29	438	142	1430	0.019	4380	1420	14 300
	FP-AUS	0.0001	102	A	7	177	0.001	340	70	1770
	FP-SOC	0.0055	74	1620	402	6541	0.055	12 910	3200	52 130
	FP-TUA-GAM	0.0082	19	7512	4172	14 441	0.082	75 120	41 720	144 410
	FP-MAR	0.0031	44	892	337	2399	0.031	8920	3370	23 990
Whale sharks	NC	0.0004	34	233	85	694	0.002	932	340	2776
	WF	0.0016	27	360	145	916	0.006	1440	580	3664
	FP-AUS	0.0004	60	105	27	415	0.002	420	108	1660
	FP-SOC	0.0005	60	130	32	544	0.002	519	129	2178
	FP-TUA-GAM	0.0002	60	199	48	845	0.001	796	192	3380
	FP-MAR	–	–	–	–	–	–	–	–	–

ALow density for abundance estimate.
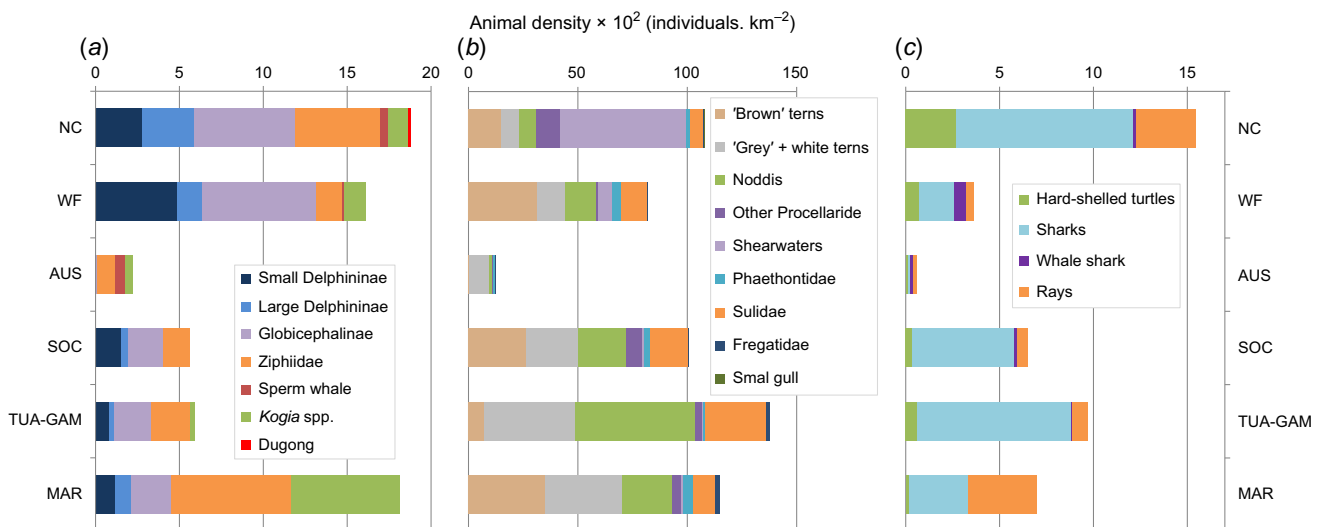
Fig. 4. Cumulative densities ($\times 10^2$ individuals/km²) across the six distinctive survey blocks of the tropical Pacific Ocean, corrected for availability bias considering averaged proportion of time spend at surface for (*a*) cetaceans, (*c*), turtles, sharks and rays; while (*b*) seabird densities were not corrected. (NC, New Caledonia; WF, Wallis-Futuna; and for French Polynesia AUS, Austral, SOC, Society; TUA-GAM, Tuamotu-Gambier and MAR, Marquesas).

Table 4. Results obtained for seabirds: relative densities (in individuals/km²) with corresponding coefficient of variation (CV in %) and relative abundance with its 95% confidence interval (CI), estimated per taxonomic group and survey blocks over the three subregions New Caledonia (NC), Wallis and Futuna (WF) and blocks of French Polynesia (FP-AUS, Austral; SOC, Society; TUA-GAM, Tuamotu-Gambier; MAR, Marquesas), with no correction for availability.

Taxa	Subregion – blocks	Density	CV (%)	Abundance	CI 95%	
					Min	**Max**
Silver gull (small gull)	NC	0.0172	100	1378	308	6161
'Brown' terns	NC	0.1491	18	80 841	42 833	159 837
	WF	0.3151	15	72 709	44 335	119 500
	FP-AUS	0.0019	51	492	140	1714
	FP-SOC	0.2634	27	65 030	35 622	118 722
	FP-TUA-GAM	0.0715	23	65 807	35 527	123 289
	FP-MAR	0.3481	20	98 640	59 951	164 957
'Grey' terns	NC	0.0653	18	35 405	23 726	53 285
	WF	0.0021	49	487	155	1560
	FP-AUS	0.0001	99	A	A	A
	FP-SOC	0.0022	48	567	197	1703
	FP-TUA-GAM	0.0103	25	9463	4723	19 765
	FP-MAR	0.0115	64	3252	989	12 090
White terns	NC	0.0152	12	8249	5070	13 607
	WF	0.1241	11	28 632	20 248	40 758
	FP-AUS	0.0934	12	24 417	17 528	34 046
	FP-SOC	0.2375	25	60 099	37 079	100 945
	FP-TUA-GAM	0.4073	5	375 119	297 613	474 522
	FP-MAR	0.3447	12	97 671	71 193	135 341
Noddies	NC	0.0802	22	43 463	25 711	73 770
	WF	0.1413	39	32 612	13 477	80 079
	FP-AUS	0.0144	40	3772	1437	9946
	FP-SOC	0.2160	26	56 604	29 382	109 693
	FP-TUA-GAM	0.5487	12	505 280	320 103	807 827
	FP-MAR	0.2243	17	63 550	41 397	97 648
Hydrobatidae	NC	0.0009	31	465	151	1516
	WF	0.0001	101	A	A	A
	FP-AUS	–		–	–	–
	FP-SOC	0.0004	73	113	22	586
	FP-TUA-GAM	–		–	–	–
	FP-MAR	0.0095	26	2696	1370	5311
'Grey' petrels	NC	0.0589	9	31 910	23 924	43 339
	WF	0.0040	22	912	469	1826
	FP-AUS	0.0011	39	291	108	808
	FP-SOC	0.0049	24	1208	683	2187
	FP-TUA-GAM	0.0019	26	1768	667	4934
	FP-MAR	0.0036	41	1030	477	2224
'Brown' petrels	NC	0.0503	12	27 279	17 342	43 541
	WF	0.0069	56	1584	520	5674
	FP-AUS	0.0040	27	1040	504	2158

Table 4. (*Continued*).

Taxa	Subregion – blocks	Density	CV (%)	Abundance	CI 95%	
					Min	**Max**
	FP-SOC	0.0436	14	11 729	7998	17 212
	FP-TUA-GAM	0.0260	10	23 942	15 734	37 444
	FP-MAR	0.0395	14	11 179	7613	16 650
Shearwaters	NC	0.5767	11	312 692	210 308	469 006
	WF	0.0634	16	14 618	8890	24 134
	FP-AUS	–		–	–	–
	FP-SOC	0.0065	34	1648	710	3886
	FP-TUA-GAM	0.0056	15	5138	2839	9795
	FP-MAR	0.0081	27	2288	1127	4652
Sulidae	NC	0.0567	17	30 751	17 790	57 506
	WF	0.1180	14	27 223	16 383	45 478
	FP-AUS	–		–	–	–
	FP-SOC	0.1746	22	49 058	27 655	87 120
	FP-TUA-GAM	0.2779	14	255 939	149 057	448 567
	FP-MAR	0.1011	31	28 640	13 312	62 083
Phaethontidae	NC	0.0192	8	10 392	7480	14 677
	WF	0.0417	7	9618	7458	12 513
	FP-AUS	0.0101	15	2634	1752	3964
	FP-SOC	0.0300	11	8193	6038	11 119
	FP-TUA-GAM	0.0096	13	8879	5145	15 495
	FP-MAR	0.0480	12	13 605	10 179	18 204
Fregatidae	NC	0.0042	22	2263	1124	4653
	WF	0.0015	28	352	121	1067
	FP-AUS	0.0003	72	82	16	421
	FP-SOC	0.0008	58	189	66	544
	FP-TUA-GAM	0.0155	29	14 286	6212	33 707
	FP-MAR	0.0190	19	5375	3203	9033

See Tables S2 and S3 for details by species.
[A]Low density for abundance estimate.

Hard-shelled sea turtles were encountered in all subregions, mostly in coastal waters, where the index of individuals per km peaked (Fig. 7). Global density of hard-shelled sea turtles was highest in New Caledonia, followed by Wallis and Futuna and TUAM-GAM, although densities were almost four times lower (Table 3, Fig. 4).

Megafauna assemblages

When considering cumulative corrected densities for all taxa (Fig. 4), consistent general patterns emerged, with the western-most subregion (New Caledonia) peaking for marine mammals, turtles, and elasmobranchs, the Marquesas for marine mammals and the TUA-GAM for seabirds only.

From the PCA conducted over the six survey blocks representing the three subregions and including densities of 22 different vertebrate taxa (seven marine mammal groups, hard-shelled sea turtles, three groups of elasmobranchs and 11 seabird groups), biogeographical provinces were well isolated and the latitudinal gradient was highlighted. PCA axis 1 explained 40% of the variance and discriminated New Caledonia with the dugong, large Delphininae, silver gull, 'grey' petrels, shearwaters, 'grey' terns and hard-shelled turtles, apart from other subregions (Fig. 8), as visible on the species correlations for the first dimensions of the PCA (Fig. S5). PCA axis 2, discriminated the northern of French Polynesia (Marquesas) from the southern (Austral), accounting for 26% of the variance with higher contribution of Ziphiidae, Kogiidae, Fregatidae, Hydrobatidae and rays associated with Marquesas. The next two following axes explained 17% and 13% of the variance respectively, with association of Wallis and Futuna with small Delphininae, Globicephalinae, whale
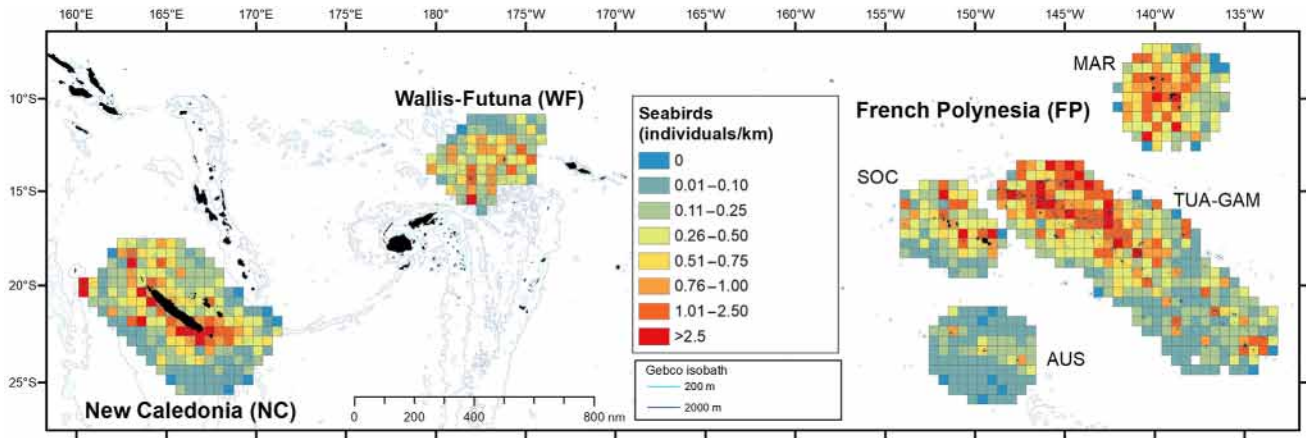
Fig. 5. Spatial distribution of individuals visually detected per kilometre for seabirds in the three Pacific's subregions: New Caledonia, Wallis and Futuna and French Polynesia during REMMOA surveys. Each pooled on a 60 km × 60 km grid cell and given in individuals/km. Cells accounting for a minimum effort of 50 km.
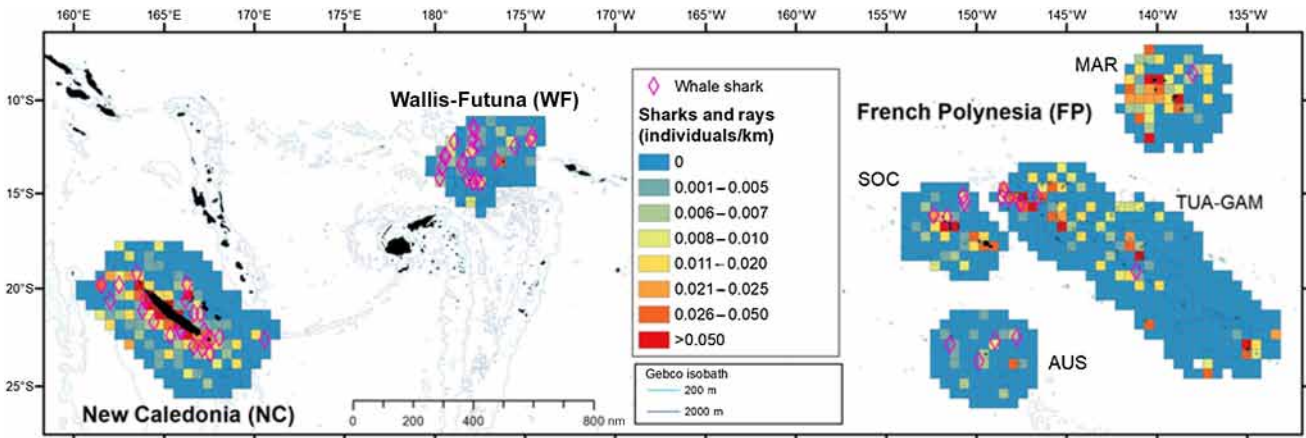

Fig. 6. Spatial distribution of individuals visually detected per kilometre for elasmobranchs (sharks including whale shark and rays), in the three Pacific's subregions: New Caledonia, Wallis and Futuna and French Polynesia during REMMOA surveys. Each pooled on 60 km × 60 km grid cell and given in individuals per kilometre. Cells accounting for a minimum effort of 50 km. Sightings of whale sharks were plotted (pink diamond).

shark, 'brown' tern and Phaethontidae while TUA-GAM were associated with Sulidae, noddies and sharks, contrary to the Austral archipelago associated with Physeteridae.

Discussion

We analysed a series of comprehensive and methodologically homogeneous visual surveys to establish a regional baseline for the distribution and density of marine megafauna across the western and central South Pacific Ocean. The marine mammal diversity increased north-ward and west-ward, while their densities and those of seabirds rose following a south–north gradient through French Polynesia. This study provides the first comparison of marine species assemblages among the three oceanic subregions studied. It discriminates

New Caledonia from other subregions that have shown a latitudinal gradient. Multi-taxa data collected during aerial surveys allows the monitoring of marine megafauna, and provides a comprehensive baseline for the conservation of coastal and oceanic waters.

However, the timing of the surveys (aiming to maximise the low-wind period to optimise sighting conditions) had a substantial effect on the observed distribution of migratory species such as baleen whales, which were almost absent in this study, several species of seabirds, sea turtles, or possibly the whale shark. In particular, the latter appears to move between the three major ocean basins (Sequeira *et al.* 2013). Therefore, our results should be interpreted with caution.

Given the methodological limitations of aerial sampling and correction bias, the main improvement would be to estimate the availability bias from local and species-specific
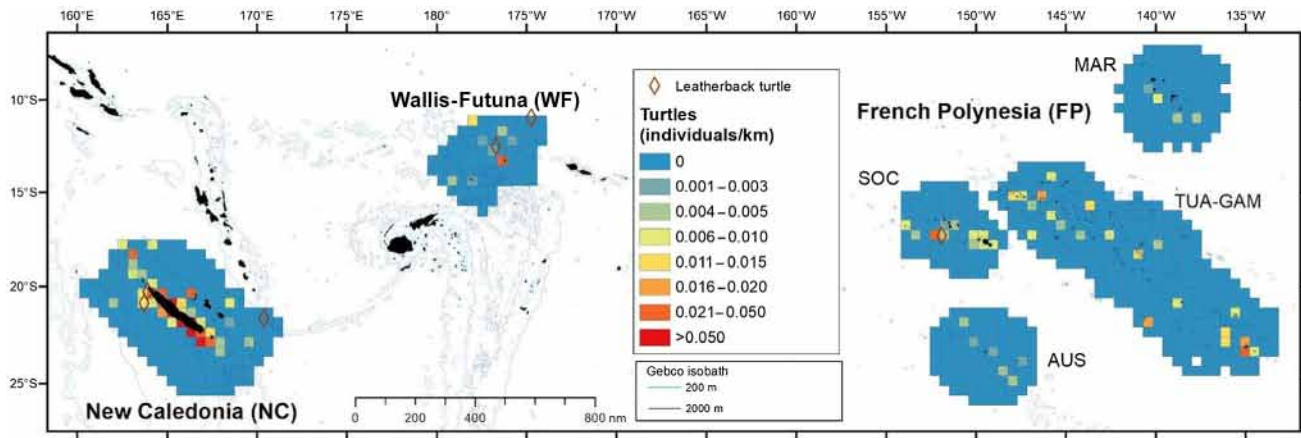
Fig. 7. Spatial distribution of individuals visually detected per kilometre for hard-shelled sea turtles (with sightings of leatherback turtles) in the three Pacific's subregions: New Caledonia, Wallis and Futuna and French Polynesia during REMMOA surveys. Each pooled on a 60 km × 60 km grid cell and given in individuals per kilometre. Cells accounting for a minimum effort of 50 km. Sightings of leatherback turtles were plotted (brown diamond).

diving patterns and to consider spatial heterogeneity of sighting conditions to account for the perception bias, but this was not possible during our study. General limitations have been discussed previously in the south-western Indian Ocean study (Laran *et al.* 2017a).

Marine mammals

Interestingly, the corrected abundance estimate (for availability bias only) for dugongs in our study is 660 individuals (CV: 32%), which is consistent with previous estimates from dedicated aerial surveys ranging from 649 to 898 (CV: 30% and 25%, respectively) in November 2011 and 2012 (Cleguer *et al.* 2017). Given that the sampling design of the REMMOA survey was not dedicated to lagoon habitats and that we applied a coarse availability bias correction, it is likely that using a more refined bias correction, with sighting location and specificity of each protocol could reduce the difference between these results.

Prior to our REMMOA survey, only four marine mammal species were known to occur in the waters around Wallis and Futuna (Doremus *et al.* 2010; Miller 2023). The present study allowed 13 new species or genera to be added to this list (Table S1). The distribution of this remarkable diversity denotes a widespread use of the EEZ by marine mammals.

Of the 15 odontocete species already reported in the French Polynesia subregion (Reeves *et al.* 1999; Gannier 2000, 2002, 2004, 2009; Gannier and West 2005; Gannier and Petiau 2006; Oremus *et al.* 2012), 14 were recorded during the REMMOA aerial surveys in 2011. We recorded some species in archipelagos where they had not been observed before, especially around the Austral and Gambier Archipalago, which were poorly documented before (cf. Table S1). Our standardised survey effort allows for the first time to clearly visualise the strong latitudinal gradient for

Delphininae and Globicephalinae, confirming the previously mentioned high diversity of the Marquesas (Gannier 2009). The waters of the Society Archipelago show a high number of individuals per kilometre for marine mammals, and is confirmed by coastal transects carried out around some islands during the REMMOA survey (but not included in the present analyses as overlapping spatially (see Laran *et al.* 2012) are consistent with previous results (Gannier 2000). Our study emphasises the importance of the Society Archipelago for cetacean conservation, particularly for spinner dolphins or rough-toothed dolphins which show site fidelity between groups and little movement between archipelagos (Oremus *et al.* 2007, 2012). When considering densities, corrected for availability bias, Kogiidae and Ziphiidae are almost as abundant as Delphininae and Globicephalinae combined in the Marquesas. In addition, juveniles were observed in half of the 13 sperm whale encounters, suggesting the Marquesas Archipelago is a nursing ground.

Seabirds

All three subregions studied in this study include important seabird colonies. However, comparing published figures for breeding populations with the abundances estimated at sea is not straightforward. Indeed, many open-ocean seabird populations include abundant non-breeding segments (immatures and sabbatical adults) that are not bound to colonies and can therefore wander over large stretches of the ocean. As a consequence, seabirds observed at sea in any of the three subregions considered here can be composed of a combination of local breeders foraging at sea, a fraction of local non-breeders foraging in the area surrounding their colony of origin, and a number of non-breeders from other regions of the Pacific and Indian Oceans, keeping in mind that the latter may outnumber the former. Therefore, an
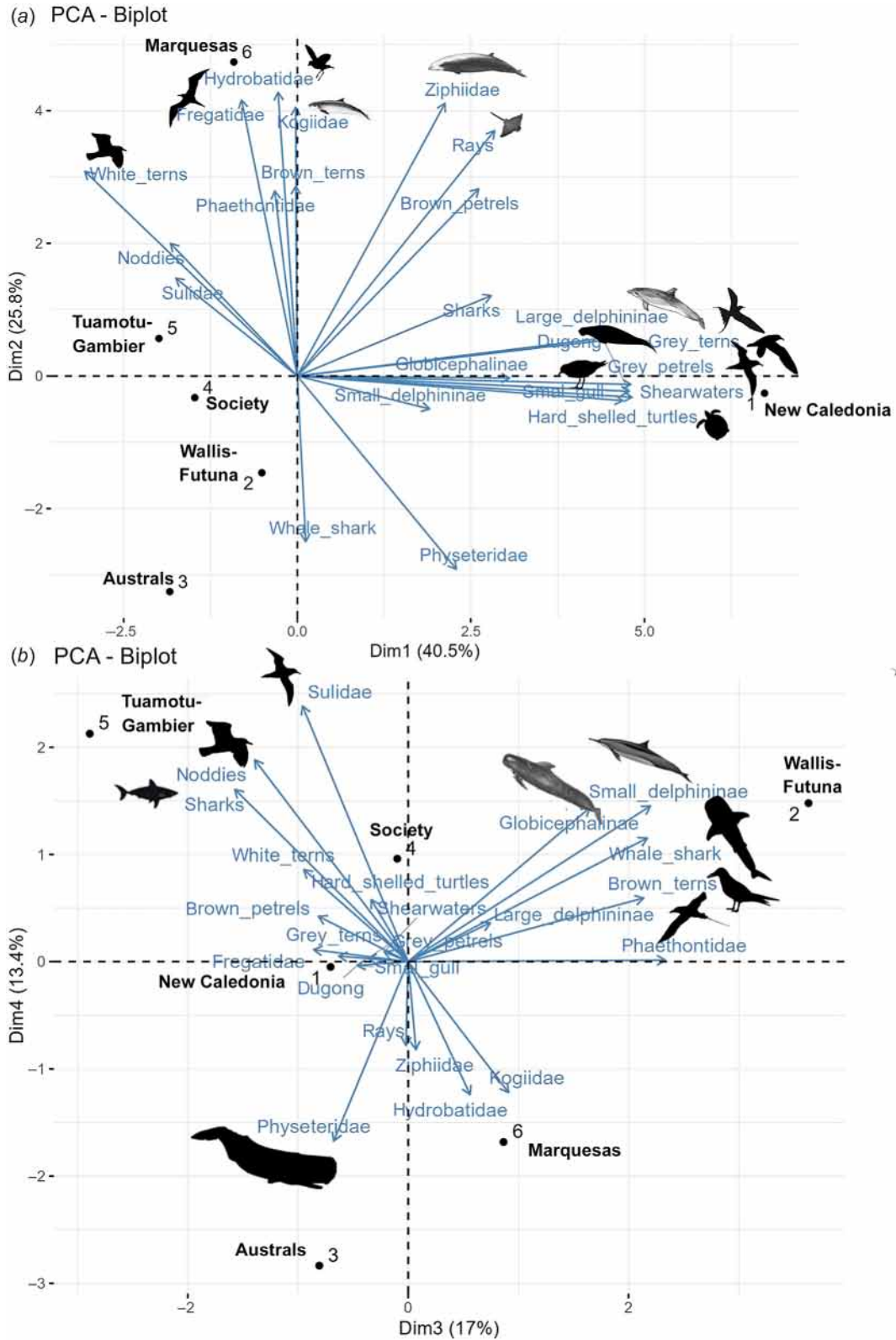
Fig. 8. Result of the first two axes (*a*) and the third and fourth axes (*b*) of the Principal Component Analysis obtained with the corrected densities of 22 groups of megafauna over six distinct survey blocks of the three Pacific subregions. Survey blocks discriminate by axes are underlined and associated species (contribution to the PCA dimension greater than 9) are represented by silhouette (from https://www.phylopic.org/).

exact match between abundance at sea and the size of local colonies cannot be expected. In contrast, past land-based seabird monitoring has been heterogeneous in the three subregions studied, both spatially (uneven geographic coverage) and temporally (intermittent survey efforts). Available data are generally scarce, leaving considerable uncertainty about the distribution, abundance and phenology of breeding seabird species, and limiting the comparability of census data. Therefore, this information on seabirds at sea is less accurate than direct counts at colonies, but is still important because it provides information on major foraging areas and may make it possible to identify areas of increased presence that may correspond to unknown colonies or resting sites.

There are two main limitations in this study. First, the phenology of the species encountered and the short timeframe of the survey. Tropical seabird communities generally host species with both seasonal and aseasonal breeding activity (e.g. Baudat-Franceschi 2011, 2012), therefore observations collected over short periods of time (here 2–4 months) may not reflect the full diversity and/or abundance of breeding species in a given region. Second, in relation to their specific foraging behaviour, with some having both parents travelling short distances multiple times per day (e.g. brown noddy, *Anous stolidus*; roseate tern, *Sterna dougallii*) (Maxwell *et al.* 2016; Pratte *et al.* 2021), while others have parents that alternately travel away from the colony over several days (e.g. wedge-tailed shearwater, Tahiti petrel; Ravache *et al.* 2020; Weimerskirch *et al.* 2020).

The REMMOA surveys covered approximately one-third of the New Caledonian EEZ. Due to practical and logistical constraints, the survey tracks did not include the Chesterfield-Bampton submarine plateau and its archipelago, which supports a large number of breeding seabirds (Spaggiari *et al.* 2007; Borsa *et al.* 2022). Observations showed a wide use of the surveyed areas by seabirds, with Procellariidae and Sulidae species mostly found in pelagic waters, according to their known foraging distances (Ravache *et al.* 2020; Weimerskirch *et al.* 2020). With the exception of 'brown' terns, encounters of terns and noddies were higher near the mainland, probably reflecting their shorter foraging distances. Shearwaters were as expected, the most abundant species group, as the wedge-tailed shearwater, is by far the most abundant species among New Caledonia's breeding seabirds (0.5–1 million breeding pairs; (Baudat-Franceschi 2006, 2011, 2012; Barré *et al.* 2011). Short-tailed shearwaters, may have also been observed passing through New Caledonian waters during their seasonal migration, although they do not breed locally (Baudat-Franceschi 2012). 'Grey' petrels (mainly Gould's petrel, and black-winged petrel) were found in slightly higher numbers than expected, with an estimated abundance of 23 000–42 000 individuals compared to an approximate total colony size of 1100–10 100 breeding pairs (Spaggiari *et al.* 2007). Among the *Laridae*, the 'brown' terns (mainly sooty terns (*Onychoprion fuscatus*), and a few bridled terns (*Onychoprion anaethetus*) were the most abundant

species group (95% IC: 43 000–160 000 individuals), but their estimates are lower than the estimated population size (~300 000 individuals for the sooty tern, Barré *et al.* 2011). This is probably due to the absence of Chesterfield Reef from our study area, where 90 000–100 000 breeding pairs of sooty terns are concentrated (Baudat-Franceschi 2011). Sulidae, Fregatidae and noddies show similar discrepancies, while the numbers of 'grey' terns (roseate tern, black-naped tern, *Sterna sumatrana*; fairy tern *Sternula nereis*; and greater-crested tern, *Thalasseus bergii*) are close to land-based estimates, as all species breed mostly near the mainland in the areas included in the survey (Baudat-Franceschi 2006, 2012; Berr *et al.* 2020, 2021, 2022). White terns (here *Gygis alba*) and Phaethontidae (*Phaethon lepturus* and *Phaethon rubricauda*) are the only species for which there are important differences between at-sea observations and land-based counts that cannot be explained by the extent of the surveyed area. Both had much higher numbers in aerial surveys (5000–13 600 and 7500–14 700 individuals, respectively) than in land observations (~1500 and ~2000 suspected breeding pairs respectively; Barré *et al.* 2011). This discrepancy may reflect the cryptic on-land behaviour of the two species groups (seasonal breeding by isolated pairs in either cliffs or tall trees) and/or foraging by individuals from other locations (Fiji, Vanuatu) in New Caledonian waters.

Published data on seabirds from the Wallis and Futuna archipelago are scarce, as the only reliable monitoring campaigns were conducted in 1985–1986, 2014 and 2018–2019 (Thibault *et al.* 2014, 2015; Berr and Mathivet 2018; Berr 2019). For species groups except noddies, the abundance estimates derived from the REMMOA surveys are much higher than the land counts. The estimates for noddies (95% IC: 13 500–80 000 individuals) are consistent with surveys conducted in 2018 which reported a colony of 15 000–30 000 breeding pairs on islets north of the Wallis lagoon (Berr and Mathivet 2018). For other species, the estimated at-sea densities suggest that a large number of non-breeding seabirds use the waters of Wallis and Futuna for foraging or pass through them during migration. The frequent observations of shearwaters at sea (95% IC:8900–24 100 individuals) may explain the temporary presence of mixed species nesting on Fiji Islands (Watling 2001), as procellariid species are thought to have been nearly extirpated from all the islands of Wallis and Futuna (Thibault *et al.* 2014; Berr and Mathivet 2018; Berr 2019).

The geographical extent of French Polynesia (2.5 M km^2 EEZ) and the number of islands (>100 main islands and >1000 islets in total) contribute to the scarcity of survey data on most seabird breeding sites (Thibault and Bretagnolle 1999). Therefore, density estimates derived from the REMMOA surveys provide some new information on seabird distribution and abundance. White terns and noddies are the dominant species group among Polynesian seabirds, as they are found at all of our survey blocks, with particularly high densities in the northern Tuamotu archipelago. Sulidae

(mainly red-footed, *Sula sula* and brown boobies, *Sula leucogaster*) are also abundant in the Tuamotu archipelago, in agreement with previous land-based surveys (Thibault and Bretagnolle 1999). The high abundance of seabirds in the northern Tuamotu and southern Marquesas can be linked to the distribution of their prey: within French Polynesian waters, epipelagic micronekton biomass is highest in these two areas (Bertrand *et al.* 2002). In contrast, the southern Austral Islands have very few birds compared to the rest of the EEZ, similar to other megafaunal species.

Elasmobranchs

Approximately 50 shark species are known to occur in the waters of New Caledonia, where they inhabit reef-lagoon and open-ocean ecosystems throughout their life cycle (fishbase.org, Boussarie *et al.* 2018). Previous studies using baited cameras and environmental DNA analyses revealed higher diversity and density of sharks in remote areas, particularly in northern New Caledonia, Chesterfield and d'Entrecasteaux (Bakker *et al.* 2017; Juhel *et al.* 2018). The REMMOA surveys highlight a distribution of elasmobranchs throughout the Grande Terre with a clear preference for the west coast. The most common ray species encountered during the flights was the spotted eagle ray (*Aetobatus narinari*) while among manta rays, the reef species (*Mobula alfredi*) is dominant in New Caledonia (Lassauce 2021). This corresponds well with the location of sightings inside the lagoon during the survey in New Caledonia, unlike the other two subregions (see https://pelabox.univ-lr.fr/pelagis/PelaObs/ for species distribution).

Knowledge of elasmobranchs in the Wallis and Futuna EEZ is also very limited, but 10 species of sharks and five species of rays inhabit the waters around the islands (Williams *et al.* 2006). These include several pelagic species such as whale shark, longfin shark (*Isurus paucus*) and manta ray. Several sightings of devil rays (*Mobula* spp) were also collected during the survey. In contrast to New Caledonia, no hammerhead sharks (*Sphyrna* spp) were observed, but 20 whale sharks were detected during transects. Higher encounter rates (of individuals) were estimated around Wallis Island (including the lagoon). Pelagic and migratory species such as whale sharks and *Mobula* spp were ubiquitous in the oceanic and shallow waters north of the surveyed area. Noting that aerial surveys detect only animals at or near the sea-surface, when all species were combined, nearly 4400 sharks (95% IC: 1400–14 300) and about 900 rays (95% IC: 320–3000) were estimated for the surveyed area (corrected for availability bias only), all species combined. For the endangered whale shark, the encounter rate recorded in the Wallis and Futuna subregion is the highest of all surveyed areas covered by the REMMOA project. This area may represent a favourable zone for juveniles, as most sightings were of small individuals (5 m or less). However, none of our three subregions were highlighted in the global

map of whale shark hotspots, revealed by spatial distribution of tracked animals (Womersley *et al.* 2022).

Since 2006, the entire French Polynesian EEZ has been declared a shark sanctuary for all species (Decree No. 396 of the Environmental Code 28 April 2006 and the mako shark (*Isurus* spp) since 2012). The sanctuary prohibits fishing and trade in products of all fish belonging to the taxon Elasmobranchii, with the exception of rays (Ward-Paige 2017). Approximately 30 species of elasmobranchs have been reported through citizen science in the Marquesas (Séguigne *et al.* 2023). The Tuamotu-Gambier survey block has a density of sharks equivalent to New Caledonia, mainly encountered around the Tuamotu Archipelago. Regarding rays, this study highlighted a high density of manta rays in the Marquesas Archipelago, where the oceanic manta ray, and the reef manta ray, co-occur (Carpentier *et al.* 2019). Despite the protected status, there are concerns about bycatch in fisheries and tourism, including the development of feeding sites (Carpentier *et al.* 2019).

Sea turtles

In New Caledonia waters, leatherback sea turtle presence had only been mentioned in the Loyalty Archipelago by a telemetry study (Benson *et al.* 2011), and to our knowledge, the REMMOA survey reported the first sighting within the Grande Terre lagoon. The aerial surveys occurred during the nesting season of the critically endangered North-east Indian Ocean and East Pacific Ocean subpopulations (Petro *et al.* 2007; Robinson *et al.* 2014), which may result in underestimation of leatherback turtle presence. The REMMOA survey was conducted at the beginning of the nesting season for green (*Chelonia mydas*) and loggerhead (*Caretta caretta*) turtles, which occurs from late October to late March (Read *et al.* 2013; Fournière *et al.* 2015; Barbier *et al.* 2023; Fretey *et al.* 2023). Both species migrate between foraging and nesting areas as part of their life cycle (Read *et al.* 2014). There are no estimates for these species in the area to compare with our corrected abundance of 14 600 individuals (95% IC: 10 600–21 200) excluding the Chesterfield and Bellona Reefs, recently identified as major breeding rookeries (Fretey *et al.* 2023). REMMOA therefore provides a much needed first assessment at sea of the sea turtle community in New Caledonia.

Only the green turtle has been regularly observed in the Wallis and Futuna area, with no mention of nesting sites on the main islands (SPREP 2007) but a rising awareness of potential sites on insular, small and scattered nesting grounds (Berr 2019; B. Bouchard, pers. comm.). Our study complements the knowledge on the distribution of hard-shelled sea turtles in the area. They were mainly encountered found in the Wallis lagoon, and less frequently around Futuna and Alofi (neither of which has a lagoon) or offshore. The presence of the leatherback sea turtle was also attested with two encounters in the north of the study area.

Five species of sea turtles are in French Polynesia waters, green, hawksbill (*Eretmochelys imbricata*), leatherback, loggerhead and olive ridley turtle (*Lepidochelys olivacea*). Scientific knowledge on the distribution of sea turtles is limited, the size of the territory and the dispersion of the islands being a major obstacle. The two regularly reported species are: (1) the green turtle, which nests from November to April, with Tetiaroa (included in the Society surveyed block) being the largest known nesting site across the Windward Islands in the Society Archipelago (Petit *et al.* 2013; Laloë *et al.* 2020); and (2) and the hawksbill turtle. The flights took place at the end of the green turtle nesting season. Two other important nesting rookeries are monitored and classified as territorial reserves: Scilly and Bellinghausen Atolls (out of the study area). In addition to bycatch threats, destruction of nesting sites, pollution, and predation of hatchlings by dogs, rats or other introduced predators (Gronwald *et al.* 2019), the consumption of turtle meat is a traditional practice still on going in this subregion (Brikke 2009; Rudrud 2010), while prohibited by the environmental regulations of French Polynesia (arrêté 466 CM of 22 March 2018).

Conservation of marine megafauna

Marine megafaunal species are diverse and charismatic. They provide a source of protein for human populations and/or support regional economies and cultures and are an integral part of biodiversity. These species are valuable as ecological indicators and may play pivotal roles in assessments of marine ecosystem health (Estes *et al.* 2016). They influence their ecosystems in various way as consumers, prey, detritus sources, and nutrient vectors, and their impacts extend to all species through direct and indirect interactions over large time and space scales from coastal to oceanic food webs, providing top-down effects on marine food webs that can control community stability (Estes *et al.* 2016). Most megafaunal species are long-lived and slow to reproduce making them particularly vulnerable to all sorts of environmental change, including climate change, whose effects on vertebrates have consequences for marine ecosystem structure and services (Sydeman *et al.* 2015). Large-scale climate phenomena such as the ENSO, the major year-to-year climate signal on earth involves both the ocean and atmosphere. This variability in oceanographic mechanisms affects ecological and biological processes, and in turn foraging patterns, breeding performance and thus population dynamics of marine top predators (Nowicki *et al.* 2019). Oceanic and atmospheric conditions in the tropical Pacific fluctuate somewhat irregularly between warm El Niño phases and cold phases called La Niña in which surface waters cool across the tropical Pacific. Among the three subregions, French Polynesia was sampled by the REMMOA survey during a weak to moderate La Niña event, while Wallis and Futuna and New Caledonia were sampled during weak El Niño

conditions (2007–2020 ONI values from https://psl.noaa.gov/data/correlation/oni.data; cf. Fig. S6). This difference in general oceano-climatic conditions could have an effect on the distribution of megafauna and on our observations. Long-term datasets are crucial to assess extreme climatic events and potential impacts of climate change, but few are available due to logistical difficulties and financial costs (e.g. Simmonds and Isaac 2007; Bost *et al.* 2015). In our project, the three subregions were surveyed only once, with no opportunity to test for the effects of extreme climatic events or global change. However, in a context of rapid change in marine ecosystems, our results provide a large-scale baseline, but the need for more regular sampling in the future is critical for monitoring change in the ocean.

There is a trend to establish MPAs based on their marine megafauna, and particularly mammals or seabirds, and to use top predators as ecological indicators or focal species (Hooker and Gerber 2004; Tetley *et al.* 2022). Knowledge of the distribution and abundance of megafauna is important to better understand and manage the impacts of anthropogenic activities. The ability to monitor progress towards such goals has been constrained by the lack of robust data on MPAs. A multi-species monitoring approach provides an opportunity to collect data on multiple taxa simultaneously, which can improve cost-effectiveness and help to better understand and predict how taxa are likely to respond to or be affected by disturbances. In addition this approach can identify areas where more dedicated surveys would be important in term of the unknown presence of a species, a hot spot or human interactions.

MPAs are increasing in number and size around the world as a tool for pelagic conservation (Game *et al.* 2009). However, most MPAs have been identified as too small to encompass the complete home ranges of most highly mobile species, as shown by tracking data for five megafaunal taxa (Conners *et al.* 2022). Our multi-taxa study may also inform future designations. Indeed 30 by 30 worldwide initiative was agreed at the COP15 meeting of the Convention on Biological Diversity (https://www.cbd.int/meetings/COP-15), to designate 30% of Earth's land and ocean areas as protected by 2030 and there is now a global call to increase the coverage of MPAs. France is a major actor in marine conservation due to its numerous overseas territories scattered across the Oceans, and especially in the three subregions surveyed in our study, which account for 64% of the French EEZ (French Polynesia, 47%; New Caledonia, 14%; Wallis and Futuna, 3%). Nonetheless, according to regulation-based classification system (Horta e Costa *et al.* 2016), France currently uses a case specific, loose approach to define strong protection, with no criteria for the representativeness of protection across the French Ocean basins (Claudet *et al.* 2021). Due to their status as overseas local authorities, French Polynesia, New Caledonia and Wallis and Futuna have full authority to manage and protect the environment in their EEZ (Schaffar 2011). A standardised recurring protocol could help to assess

some species of marine megafauna (marine mammals, seabirds, sea turtles and large fish) as in the case, for example, in the European the Marine Strategy Framework Directive.

More recently, the Important Marine Mammal Areas (IMMAs) initiative, launched by the Marine Mammal Protected Areas Task Force of the International Union for the Conservation of Nature (Tetley *et al.* 2022), identifies discrete portions of habitat that are important to one or more marine mammal species, and have the potential to be delineated and managed for conservation. REMMOA surveys have contributed to the designation of several IMMAs, which were identified through a biocentric expert process independent of political and socio-economic pressure or concerns (Notarbartolo di Sciara and Hoyt 2020). Four IMMAs have been identified in New Caledonia, and three in French Polynesia, while the one for Wallis and Futuna is still under revision (www.marinemammalhabitat.org/imma-eatlas/). Similar initiatives are underway for sharks and rays (Important Sharks and Rays Areas, ISRA, https://sharkrayareas.org/) and sea turtles (Important Marine Turtles Areas, IMTA). The aerial multi-taxa protocol used here represents a powerful tool for measuring marine megafauna abundance and potential long-term changes by repeating this protocol on a regular basis.

Supplementary material

Supplementary material is available online.

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