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USO DE CÁMARAS REMOTAS SUBMARINAS PARA CARACTERIZAR ENSAMBLAJES DE DEPREDADORES EN AMBIENTES REMOTOS DEL PACÍFICO ESTE TROPICAL

Tesis sometida a la consideración de la Comisión del Programa de Estudios de Posgrado en Biología para optar al grado y título de Maestría Académica en Biología

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DEDICATORIA

A mi madre Clara Agustí y a mi padre Javier Cambra,
por darme alas para volar y mil razones para volver

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RESUMEN

Los grandes depredadores marinos son generalmente animales longevos de gran tamaño como mamíferos marinos, tiburones, rayas y grandes teleósteos que ocupan niveles superiores en la cadena trófica. Se caracterizan por tener un lento crecimiento, una madurez sexual tardía y poca descendencia. Estas características dan como resultado una baja resiliencia a perturbaciones externas y un alto riesgo de extinción, condiciones que los hacen altamente vulnerables a la sobrepesca. A nivel global, los grandes depredadores han presentado drásticos declives poblacionales como consecuencia directa de pesquerías que los han capturado desproporcionadamente durante siglos. A esto, se le suma la falta de información ecológica básica necesaria para proteger a estas especies tales como la identificación de hábitats críticos, patrones de distribución y requerimientos ambientales. La dificultad de generar ese tipo de información se relaciona principalmente con su alta movilidad y a los amplios rangos de distribución que en muchos casos incluyen ambientes remotos alejados de la costa. Dado que la disminución de grandes depredadores en ecosistemas marinos puede generar efectos negativos que se propagan a través de la cadena trófica, es fundamental generar información necesaria para establecer medidas de manejo efectivas que permitan la recuperación de sus poblaciones.

Las cámaras remotas submarinas con carnada (BRUVS, por sus siglas en inglés) han demostrado superar muchas de las dificultades para el estudio de grandes depredadores dado que representan una técnica no invasiva ni extractiva (no hay presencia humana dentro del agua y no se producen efectos negativos sobre los animales), y poseen una mayor probabilidad de detección de especies carnívoras gracias al uso de la carnada. En este estudio utilicé BRUVS para investigar cuales son las principales variables naturales (espaciales y ambientales) que determinan los patrones de distribución y abundancia de grandes depredadores en ambientes remotos del Pacífico Tropical Oriental (PTO). Concretamente, los BRUVS fueron utilizados en la Isla del Coco (Capítulo 1 y 3) y en los montes submarinos de la Cordillera del Coco que conectan las Islas Galápagos con la Isla del Coco (Capítulo 2). La información obtenida del uso de BRUVS en la Isla del Coco también fue oportunísimamente utilizada para identificar posibles hábitats y comportamientos asociados a la reproducción del tiburón tigre, uno de los mayores depredadores presentes en esta isla oceánica (Capítulo 3).

Como parte del Capítulo 1, se realizaron nueve expediciones a la Isla del Coco desde diciembre 2016 hasta octubre 2020. Se lanzaron un total de 294 BRUVS cubriendo estaciones seca y lluviosa, ambientes bentónicos someros cercanos a la costa (< 1.6 km) entre 2 – 60 m de profundidad y ambientes pelágicos alejados de la costa (2 – 7 km) entre 10 – 15 m de profundidad. Se registraron un total de 13 especies de elasmobranquios (tiburones y rayas) presentes en el 95% de los BRUVS. Se obtuvieron valores altos de riqueza (2.7 ± 1.6 especies por estación) y abundancia (6.3 ± 6.5 individuos por hora) comparados con otros ambientes remotos y protegidos, lo que realza la importancia de la isla como un verdadero refugio para elasmobranquios a nivel global. Se identificó las variables espaciales de profundidad, distancia a la costa y tipo de hábitat (pináculos, sitios costeros, bahías y ambientes pelágicos) como los factores con mayor influencia sobre la estructura comunitaria de elasmobranquios. Adicionalmente, se identificaron relaciones especie-específicas entre la abundancia de elasmobranquios y la profundidad, la distancia a la costa, el tipo de hábitat, la estación, el grado de exposición según la ubicación norte o sur en la isla, el tipo de sustrato y la temperatura. Este tipo de estudios en ambientes aislados y mínimamente afectados por actividades antropogénicas, son fundamentales para identificar áreas claves para la conservación de especies amenazadas y para predecir las consecuencias de la degradación del hábitat y del cambio climático.

Como parte del Capítulo 2, se monitorearon nueve montes submarinos de la Cordillera del Coco en una expedición de 12 días en el 2018. Se utilizó la versión pelágica de los BRUVS donde dos sets de cinco estaciones unidas con una línea superficial se suspendieron a 10 y 25 metros de profundidad y se dejaron a la deriva durante periodos de 2 horas en distintos momentos del día encima de cada monte submarino. Se obtuvieron un total de 150 videos (347.5 horas) que permitieron la detección de 21 especies pelágicas grandes en un 90.6% de los lanzamientos realizados. Los peces óseos pequeños (tamaño común < 1 m) fueron los más abundantes (14.1 ± 59.7 MaxN hr^{-1}), seguido de los peces óseos grandes (2.9 ± 4.4 MaxN hr^{-1}) y los elasmobranquios (3.3 ± 6.1 MaxN hr^{-1}) con abundancias similares. El grupo menos abundante fueron los delfines y las tortugas (1.8 ± 1.7 MaxN hr^{-1}). Se identificó la profundidad del monte submarino y el grado de aislamiento, como los dos factores con mayor influencia sobre el ensamblaje de grandes depredadores en esos ambientes. Los montes menos profundos (< 400 m) y más aislados, como Paramount (Ecuador) y West Cocos (Costa Rica), presentaron una mayor abundancia y diversidad de especies, y por lo tanto fueron identificados como posibles sitios de agregación de grandes pelágicos en ambientes remotos del PTO. Este estudio representa el primer intento de caracterizar la distribución espacial y la abundancia relativa de grandes pelágicos en los montes submarinos de la Cordillera del Coco y por lo tanto, puede servir como una importante referencia para futuros estudios en la región utilizando esta técnica de monitoreo.

En el Capítulo 3 reporto la primera observación de un posible neonato de tiburón tigre *(Galeocerdo Cuvier)* detectado en la Bahía Yglesias en octubre del 2020 por uno de nuestros BRUVS. Presento además observaciones de hembras potencialmente embarazadas de tiburón tigre y discuto la posibilidad de que este sea un evento aislado o de que algunos individuos de esta especie puedan estar utilizando los ambientes costeros de la Isla del Coco como sitio de crianza. De ser así, esto implicaría una menor necesidad de migrar a otras zonas de crianza y por lo tanto un mayor índice de residencia por parte de hembras de tiburón tigre en la Isla del Coco. Un mayor tiempo de permanencia en la Isla del Coco podría facilitar las estrategias de conservación de esta especie, así como tener implicaciones ecológicas dado el posible papel de esta especie como depredador tope en la Isla del Coco.

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LISTA DE ABREVIATURAS

AIS: Automatic Identification System
AIC: Akaike information criterion
AICc: small sample-corrected AIC
AMP: Área Marina Protegida
BRUVS: Baited Remote Underwater Video Stations
CVRE: cross-validated relative error
db-MRT: distance based Multivariate Regression Tree
DLI: Dufrêne-Legendre indicator value
EEZ: Exclusive Economic Zones
ENSO: El Niño Southern Oscilation
ETP: Eastern Tropical Pacific
GAMMs: generalized additive mixed models
GLM: generalized linear models
GIS: Geographic Information System
GPS: Global Positioning System device
IUCN: International Union for the Conservation of Nature
LPS: large pelagic species
MaxN: Relative abundance
MODIS: Moderate Resolution Imaging Spectroradiometer
MPA: Marine Protected Area
MRT: Multivariate Regression Trees
NOAA: National Oceanic and Atmospheric Administration
PCA: Principal Component Analysis
PacIOOS: Pacific Islands Ocean Observing System
PNIC: Parque Nacional Isla del Coco
PTO: Pacífico Tropical Oriental
SINAC: Sistema Nacional de Áreas de Conservación
SS-MRT: sum of squares Multivariate Regression Tree
VIF: Variance Inflation Factors

CAPÍTULO 1

Effect of natural drivers on elasmobranch assemblages at a near pristine remote island from the Eastern Tropical Pacific

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ABSTRACT

A better understanding of how natural drivers affect abundance and distribution patterns of animals in an ecosystem is essential to identify species-habitat associations and ultimately define effective conservation planning under a changing climate. Yet these relationships are often hindered by anthropogenic impacts. Remote and relatively undisturbed oceanic islands provide a unique opportunity to study the mechanisms that control spatial variation of biodiversity in response to natural drivers. This study used benthic and pelagic baited remote underwater video stations (BRUVS) to examine the effect of spatial, seasonal, and environmental drivers on elasmobranch assemblages at Cocos Island, Eastern Tropical Pacific. Overall, 13 elasmobranch species were detected in 95% (n = 277) of the BRUVS, with 2.7 ± 1.6 species recorded per station and 6.3 ± 6.5 ind hr^{-1}, exceeding values reported by BRUVS in other remote ecosystems. Through a multivariate regression tree, we identified that spatial drivers such as depth, distance to the coast and habitat type had the greatest influence on elasmobranch assemblages. This result suggests that spatial segregation may be the main strategy used by several predators that coexist in a relatively small area. In addition, generalized additive mixed models revealed previously unknown species-specific responses of elasmobranch abundance to nearest distance to the coast, depth, season, location, substrate cover and temperature. This study highlights the importance of Cocos Island as

one of the last remaining healthy predator-dominated ecosystems on earth. Long term surveys at remote habitats that hold high predator abundance are crucial since they are likely the last baselines left to understand how coral reef ecosystem function as well as help predict ecological consequences of population declines.

INTRODUCTION

Knowledge of when, how and why animals are distributed in space is essential to understand species-habitat associations, and ultimately define important areas for the conservation of threatened species (McClellan et al. 2014). A better understanding of how natural drivers (here defined as environmental and spatial factors) affect abundance and distribution patterns of a species is also important for conservation planning under a changing climate (Pittman & Brown 2011). However, given the rapid rate in which anthropogenic activities have altered many terrestrial and aquatic ecosystems, it is challenging to discern the effects of natural drivers from human-derived activities on biological communities (Mellin et al. 2016). Essentially because anthropogenic impacts, such as extraction and habitat degradation, tend to overcome the effect of natural drivers on animal abundance and distribution patterns (Ward-Paige et al. 2010).

Remote and relatively undisturbed oceanic islands a unique opportunity to study the mechanisms that control spatial variation in biodiversity in response to environmental changes (Quimbayo et al. 2019, Haupt 2020). Fish assemblages at such near-pristine locations are usually dominated by large, wide-ranging predators that have key roles in maintaining the structure and functioning of marine ecosystems (Stevenson et al. 2007). Some elasmobranchs (sharks and rays) are known to influence the behaviour and abundance of their prey through top-down control and/or fear-effects, and therefore, their absence can significantly alter community structure and function (Heithaus et al. 2008, Baum & Worm 2009). As elasmobranch populations are under increasing pressure from fisheries (Dulvy et al. 2021), habitat loss (Knip et al. 2010), pollution (Gelsleichter et al. 2005) and climate change (Chin et al. 2010), their removal is expected to have ecosystem-wide consequences (Dulvy et al. 2004).

Quantifying abundance and distribution patterns of elasmobranchs across multiple habitats and how species respond to environmental changes in the absence of human impacts can provide valuable insights for their conservation and consequently for the restoration of marine ecosystems (Tickler et al. 2017, Goetze et al. 2018). Ecological data from such near-pristine ecosystems could also represent an important baseline to evaluate human impacts on elasmobranch populations at more exploited areas (Sandin et al. 2008, Ferretti et al. 2018). However, sites with limited or no human impacts are increasingly difficult to find nowadays, even at remote and isolated locations (Graham et al. 2010). Moreover, long-term monitoring efforts at such remote sites are often expensive and challenging to maintain (Dale et al., 2011, Espinoza et al., 2020).

Cocos Island is a remote no-take Marine Protected Area (MPA) located in the Eastern Tropical Pacific realm (ETP) that harbours an abundant and diverse elasmobranch assemblage, and one of the largest fish biomass in the tropics (Friedlander et al. 2012, Quimbayo et al. 2019). Due to its geographic isolation (550 km from mainland Costa Rica) and minimum anthropogenic influence (only a small number of park rangers inhabit the island and only 60 tourists are allowed per day), Cocos Island provides a unique opportunity to study elasmobranch assemblages in a relatively near pristine coral reef ecosystem (Espinoza et al. 2020). Detailed information regarding elasmobranch distribution and abundance patterns at Cocos Island is scarce or focused on few species (Friedlander et al. 2012, Zanella et al. 2016a), and the effect of environmental drivers on elasmobranch assemblages has only been analysed using a long-term data set (1993-2013) collected by dive guides (González-Andrés et al. 2021). While this dataset has allowed monitoring broad-scale trends of elasmobranchs over time (Osgood et al., 2021; White et al., 2015), there are biases associated with shark responses to divers (usually groups of 10 divers) or affected by multiple unstandardized observers over the years (Gonzalez-Perez & Cubero-Pardo 2010, Cubero-Pardo et al. 2011). Therefore, there is a major need to complement citizen-science data with a long-term scientific based elasmobranch survey at Cocos Island.

Baited Remote Underwater Video Stations (BRUVS) have become a powerful and cost-effective technique to study large and mobile predator species in a wide range of habitats (Brooks et al., 2011; Cappo et al., 2004; Cappo et al., 2003; Espinoza et al., 2014; Spaet et al. 2016; White et al., 2013). Given that Cocos Island is one of the only remaining places in the region with large aggregations of elasmobranchs coexisting in a near-pristine ecosystem (Friedlander et al. 2012, Quimbayo et al. 2019), long-term data collection with BRUVS at this oceanic island might provide novel insights into elasmobranch ecology necessary to establish effective management and protection plans at local and regional levels. In this study, we used benthic and drifting BRUVS to examine the effect of spatial, seasonal, and environmental drivers on coastal and pelagic elasmobranch assemblages at Cocos Island.

We hypothesized that large elasmobranch (species with a common total length – TL > 2 m) would dominate pinnacles and pelagic habitats where they have access to cleaning stations, stronger currents, larger prey and deep cooler areas (Friedlander et al. 2012, Quimbayo et al. 2017), whereas the occurrence and abundance of small elasmobranchs (species with a common TL < 2 m) would increase in shallow and protected nearshore habitats (e.g. bays and coral reefs) that may offer lower predation risks and abundant food resources (Zanella et al. 2016a). Also, we expected differences in elasmobranch distribution between the north and south of Cocos Island. Small elasmobranchs typically prefer large bays, areas with high coral cover and habitats with low wave/current exposure (i.e. habitat characteristics of northern Cocos Island) (Lizano 2008a, Alvarado et al. 2016), while large elasmobranchs typically aggregate around pinnacles with cleaning stations and areas of high topographic complexity, which are present in both sides of the island (Cortés 2016a). We further hypothesized that elasmobranch assemblages vary among seasons due to an increased abundance of migratory species during the rainy season (July – November) when environmental conditions are favourable, i.e. low temperature, high productivity and strong currents (Sibaja-Cordero, 2008; White et al., 2015). Finally, we anticipated that the abundance of large elasmobranchs would decrease with higher temperatures since they have a greater ease to track for optimal conditions during water temperature changes (Osgood et al. 2021). Instead, small elasmobranchs have less capacity to redistribute with changing environmental conditions and therefore, we expected these species to be more influenced by spatial drivers such as habitat type, substrate cover and location (Richards et al. 2012).

METHODOLOGY

Study area

Cocos Island (5º 32’N – 87º 04’W) is a volcanic oceanic island located 550 km southwest from mainland Costa Rica and the only sub-aerial summit of the Cocos Volcanic Mountain Range, the largest mountain chain of Central America (Walther 2003). Due to its high level of marine endemism and biodiversity, Cocos Island was declared a National Park in 1978 although it was not until 2001 that all marine extractive activities were prohibited at 12 nautical miles around the island (Alvarado et al. 2012). Although illegal fishing at Cocos Island has become less frequent, over the last two decades it was identified as one of the main threats for sharks (Carcharhinidae, Alopiidae and Sphyrnidae) and tunnas (Scombridae) (López-Garro et al. 2016a, González-Andrés et al. 2020). These, and other migratory species such as mahi-mahi (*Coryphaena hippurus*), sea turtles (Cheloniidae) and billfishes (Istiophoridae) are also caught in large numbers as bycatch in pelagic longline and purse seine fisheries across the ETP (Dapp et al. 2013, Alava et al. 2017).

Coastal habitats around Cocos Island are characterized by a complex bottom morphology (Lizano 2012a), with soft and hard substrates, rich benthic habitats in deep waters and extensive coral reefs and coral communities at shallow depths (Guzman & Cortes 1992, Sibaja-Cordero et al. 2012). Well-developed coral reef systems at sandy bottoms are found at the north and northeast side of the island mainly along the coast and inside three large bays (Wafer, Chatham, and Weston). The south and southwest sides, in contrast, are mainly characterized by rocks covered in barnacles and other invertebrates (Sibaja-Cordero et al. 2012, Alvarado et al. 2016). The distinct shift in habitat along the north-south gradient can be explained by the northeast-southwest axis orientation of the insular platform that offers more protection from the currents and surge to the northern site of the island (Lizano 2008a). The insular platform around the island presents a higher bathymetric variation in the southwest side where many islets and submerged pinnacles can be found. In the northeast side, the insular platform is shorter with a higher slope (Lizano 2001). Islets and rocky pinnacles around the island promote highly productive habitats for a wide range of species by increasing vertical nutrient-rich fluxes and material retention (Rogers 1994).

Cocos Island is influenced by a marked seasonality with variation in environmental parameters attributed to the southern oscillation of the Intertropical Convergence Zone which determines the degree of influence of the North Equatorial Countercurrent, the main west-east current near to the equator (Lizano 2008a). During the rainy season (July – November) the effect of the North Equatorial Countercurrent is enhanced, thus increasing ocean productivity and currents, while reducing water temperature (Acuña González et al. 2008). Sea surface temperatures at Cocos Island range from 24ºC to 29ºC, although temperature levels are known to increase during El Niño Southern Oscilation (ENSO) events every 4-9 years (Osgood et al. 2021). Due to the high level of precipitation, salinity levels at Cocos Island are among the lowest of all tropical oceans (max. concentrations of 33.27 ups during the rainy season) (Lizano 2008b).

Sampling design

Nine trips to Cocos Island were conducted between December 6th 2016 and October 19th 2020 covering both dry and rainy seasons (Table S1). A total of 363 BRUVS were initially deployed in the north and the south sides of Cocos Island covering bays, inshore reefs, pinnacles, and pelagic habitats (Fig. 1). Due to restrictions imposed by Cocos Island officials, rocky pinnacles (n = 12) and other coastal sites (n = 7) used for tourist-related diving activities (Fig. 1) were only surveyed until 2018, after which all BRUVS had to be deployed at a minimum distance of 300 m from touristic sites. Such restrictions lead to a higher survey effort at pinnacles before 2018 and a higher survey effort at inshore sites after that year (Table S1). Surveys at pelagic sites also started in 2018 when the necessary equipment was acquired and the logistics of this type of survey were addressed.

Each BRUVS consisted of a stainless-steel frame with a single high-definition GoPro camera (Hero 4-7; 1080 res, 60 frames/sec) encased in an underwater housing. All units were equipped with a bait arm of 85 cm length, to which a perforated 30 cm PVC bait container was attached. Two types of benthic BRUVS were used to survey benthic habitats based on habitat topography following the methodology of Espinoza et al. (2020): (i) a pyramid-shaped steel frame for sites with flat or less irregular seafloor, and (ii) a triangle-shape steel frame anchored on the seafloor but suspended at 1 m off the bottom with an intermediate buoy for sites with irregular rocky/coral reef substrates and steep slopes, which prevented the rig from getting tangled and resulting in a better (i.e. less obstructed) field of view.

Benthic BRUVS were deployed from a small vessel using a stratified random design to cover a wide range of habitats (coral and rocky reefs, sandy bottoms, rhodolite beds, pinnacles, bays) and depths (2–60 m; mean ± SD: 18.4 ± 9.4 m) between 6 m and 1.6 km (mean ± SD = 0.32 ± 0.34 km) from the coast of Cocos Island. A minimum distance of 300 m (mean ± SD = 356.9 ± 321.6 m) between neighbouring BRUVS was anticipated to reduce potential movement of elasmobranchs between stations due to bait flume overlap (Cappo 2010). Yet, due to logistical reasons and the relatively small size of some sites such as pinnacles, 32% of benthic stations (n =

69) were deployed at closer distances from each other (mean ± SD = 107.2 ± 83.1 m). Effective soak time (the actual time each BRUVS recorded on the bottom) for benthic BRUVS ranged from 8 to 197 min (mean ± SD: 84.5 ± 25 min).

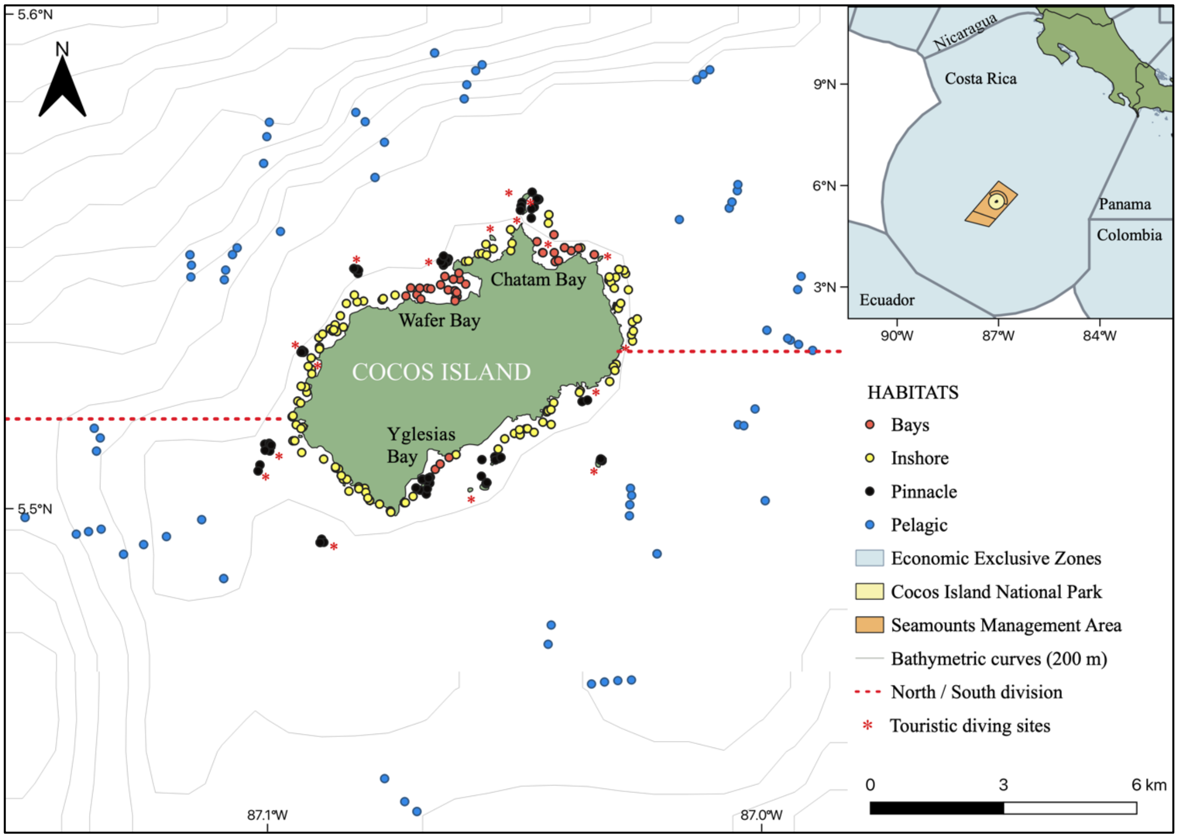

Fig 1. Sampling locations of Baited Remote Underwater Video Stations (BRUVS) deployed at Cocos Island National Park between December 6th 2016 to October 19th 2020. Coloured dots represent the location of BRUVS at different habitat types. Coloured rectangles represent the extension of the Economic Exclusive Zone of Costa Rica and the extension of Cocos Island National Park and the Seamounts Management Marine Area during the time range of this study (both MPAs have been recently expanded in January 2022). The red dashed line represents the north south division of Cocos Island used in our sampling design. Red stars indicate the location of the touristic diving sites. Coordinates were plotted using base and raster layers from the Costa Rican Geographic Information System (GIS) Atlas open-access project in QGis 3.22.2. Bathymetry curves were plotted on a 15 arc-second grid using the GEBCO_2020 Grid (GEBCO Compilation Group, 2020).

We also used drifting BRUVS not anchored to the bottom to survey elasmobranchs in pelagic habitats between 2 and 7 km from Cocos Island (mean ± SD = 4.1 ± 1.1 km). This technique has been proven to effectively survey predator species in open water ecosystems (Bouchet & Meeuwig 2015, Cambra et al. 2021a). Drifting-pelagic BRUVS (hereafter referred as pelagic BRUVS) consisted of sets of four or five BRUVS deployed simultaneously resembling a long-line system (Cambra et al., 2021). BRUVS attached to the pelagic long-line system were separated by 150 to 200 m and suspended at 10-25 m depth (mean ± SD: 10.9 ± 3.2 m). Effective soak time for pelagic BRUVS ranged from 21 to 144 min (mean ± SD: 99 ± 18.6 min). All BRUVS deployments were conducted between 8:00 and 15:30 hrs. Approximately 1.7 kg of crushed chub mackerel (*Scomber japonicus*) was used as bait.

Spatial and environmental drivers

Natural drivers included in this study were divided between spatial and environmental drivers (Table 1). Mean water temperature was measured with a datalogger (ONSET Hobo Pendant® UA) attached to each BRUVS to monitor temperature at 1-min intervals. The minimum distance of each BRUVS to the coast was calculated using layers from the Costa Rican Geographic Information System (GIS) Atlas open-access project (https://repositoriotec.tec.ac.cr/handle/2238/6749) in ArcMap 10.4 software. Depth of benthic BRUVS was measured using a manual depth sounder whereas for drifting BRUVS it was estimated using the Navionics application (Geocore version 18.0.1). Additional information such as date, time and location were also recorded by each BRUVS.

Table 1. Natural drivers used in multivariate analysis and statistical modeling in this study

Drivers	Predictors	Type	Range or categories	Mean ± SD
Spatial	Region	Categorical	North; South	NA
	Habitat *	Categorical	Bay; Inshore reef; Pinnacle; Pelagic	NA
	Depth	Continuous	2 – 60 m	17.8 ± 9.7 m
	Distance	Continuous	0.01 – 6.9 km	1.3 ± 1.8 km
Environmental	Season	Categorical	Dry; Rainy	NA
	Temperature	Continuous	18.4 – 29.8 ºC	26.7 ± 1.9 ºC
	PC1 (rock)	Continuous	-0.2 – 0.5	0 ± 0.1
	PC2 (sand)	Continuous	-0.3 – 0.4	0 ± 0.1
	PC3 (coral)	Continuous	-0.6 – 0.4	0 ± 0.1

(*) Habitat was included in multivariate analysis but not in statistical modeling

The division between north and south was based on the northeast-southwest axis orientation of Cocos Island and was used as a proxy for current exposure (Fig. 1). Higher exposures would be expected in the south compared to the north. To test that hypothesis, daily estimates of current direction provided on a 1/4-degree grid for the Pacific were extracted from the Pacific Islands Ocean Observing System (PacIOOS) (https://www.pacioos.hawaii.edu/, last accessed July 2022). The function *rxtracto* from the R package *rerddapXtracto* (Mendelssohn, 2021) was used to extract current data using the ERDDAP data server (https://coastwatch.pfeg.noaa.gov /erddap/index.html, last accessed July 2022) from the National Oceanic and Atmospheric Administration (NOAA). Currents followed a predominant southwest towards southeast direction as is expected in Cocos Island (Lizano 2008a). Approximately 72% of the BRUVS in the south were highly exposed to currents (upstream location) compared to only 23% of the stations in the north, the majority of which were protected from currents. Therefore, the division between north and south regions were kept as predictors during the statistical analysis.

Habitat types were divided in 4 categories (Table 1). 'Inshore reefs' included all BRUVS deployed in coastal areas of Cocos Island, except those located inside bays (Fig 1). Only large bays with river discharges (i.e. Chatham, Wafer and Yglesias; Fig. 1) were classified as such given the relationship that exists between the more turbid waters and the use of these areas as nursery grounds for elasmobranchs (Cambra et al., 2021; Zanella et al., 2016). Therefore, those BRUVS located in any of the smaller bays of Cocos Island with no or little river discharge were classified as 'inshore reefs' in this study. 'Pinnacles' included all structurally complex rocky structures separated from the coast that rise from the seabed including islets, pinnacles, and seamounts (Fig 1). 'Pelagic sites' included all pelagic BRUVS deployed between 10 and 15 m depth in the water column (Fig 1). Season was considered an environmental driver and was divided between dry and rainy seasons. 'Dry season' included all data collected between December and June and 'rainy season' between July and November.

Substrate cover associated to each replicate was categorized using a collection of reference images from each video following Espinoza et al. (2020). All types of substrates present on each image were classified into six categories: 'bare rock with encrusting organisms' (mainly encrusting calcareous algae), 'reef-building coral', 'rock with turf', 'macroalgae', 'sand/rubble' (including small rubble), and 'others' (i.e. anemones, barnacles, cyanobacteria, octocoral, sponges, softcoral and tunicates). Rugosity, visibility, and depth of field (i.e. level of image obstruction by some type of substrate) were also qualitatively evaluated (1-3; low to high) by the two observers using the same reference images. ‘Low rugosity’ (1) was assigned at those substrates dominated by sand or rubble (> 80% of the image), ‘medium rugosity’ (2) was assigned at substrates with sand in combination with some rocks of similar medium size or substrates partially covered in coral reefs, and ‘high rugosity’ (3) was assigned at those substrates dominated by large rocks with steep walls or substrates completely covered in coral reefs. ‘Low visibility’ (1), ‘medium visibility’ (2) and ‘high visibility’ (3) indicated estimated visibility of < 3 m, 3 - 10 m, > 10 m, respectively. Finally, ‘low depth of field’ (1), ‘medium depth of field’ (2) and ‘high depth of field’ (3) were assigned when < 33%, 33 – 66% or > 66% of the image was water column or far distances substrates, respectively. Those BRUVS with a very low depth of field and visibility (average between observers < 1.5) were removed from the analysis (n = 17).

A principal component analysis (PCA) was performed at the BRUVS level to reduce the dimensions of substrate cover types, explaining the major variability among replicates (Jorgenses & Fath 2018). The PCA was calculated on a matrix with the percentages of each substrate cover using the function *rda* from the vegan package (Oksanen et al. 2020). This reduced the number of substrate cover classes that explained 84% of the variability among BRUVS into three major principal scores: PC1, PC2 and PC3 representing 47.2%, 24.7% and 12% of variance, respectively (Table S2; Fig S1). The axis PC1 was defined by the dominance of bare rock with incrusting organisms and absence of sand, and was mainly associated to pinnacles. The axis PC2 was characterized mainly by sand with a smaller contribution of rock and absence of coral and turf, and was mainly associated to inshore reefs and bays. The axis PC3 was associated with substrate covers dominated by coral reefs and absence of turf, and was also associated to inshore reefs and bays (Figs S2, S3). The resulting principal scores were used as predictor variables for multivariate analysis and statistical models allowing the reduction on the predictors while improving the independence of the coefficients and increasing the power and stability of multiple regression (Jorgenses & Fath 2018).

A Spearman’s correlation index test was used to evaluate the degree of correlation between predictor variables before performing any statistical analysis. A high correlation value (> 0.5) was detected between rugosity and PC1, therefore, they were considered proxies of one another (Booth 1995). Since PC1 provided information on substrate cover and, indirectly the level of rugosity, this variable was kept in all statistical analyses while rugosity was removed (Table 1). The linear dependencies of continuous explanatory variables were also explored by computing variance inflation factors (VIF) using the function *vif.cca* from the R *vegan* package (Oksanen et al. 2020). For all predictors, VIF's values below 10 indicated low collinearity between explanatory variables and therefore all variables were retained (Borcard et al. 2011). Finally, a total of nine predictor variables were used in the statistical analysis of this study including, three categorical (habitat, location, and season) and six continuous (temperature, distance, depth, PC1, PC2 and PC3) variables.

Video analysis

The software EventMeasure (SeaGIS®) was used to record species richness, occurrence and abundance of each video footage obtained from BRUVS. We estimated the frequency of occurrence as the percentage of BRUVS that recorded elasmobranchs. To avoid repeat counts of individuals re-entering the field of view, the maximum number of individuals from each species appearing together in a single frame (MaxN) was recorded as a conservative estimate of relative abundance (Cappo et al. 2004). Differences in sampling effort between replicates were reduced by removing replicates with soak times less than 50 min (n = 15). In addition, we excluded species recorded in BRUVS with soak times greater than 90 min (n = 6). Species were identified to the lowest taxonomic level possible using local fish guides and expert criteria when needed. Due to the high survey effort of this study, the video analysis was carried out by a total of 16 different observers, all of which were previously trained with the same protocol and were accompanied by an expert until the necessary skills to ensure a standardized and robust video analysis were acquired. All resulting files were reviewed and corrected, if necessary, by an expert. Unidentifiable individuals, due to distance from the camera, overexposure, or turbidity, were excluded from further analysis.

Spatial and environmental divers at the assemblage level

We used multivariate regression trees (MRT) to investigate the differences in the structure of the elasmobranch assemblage at Cocos Island based on spatial and environmental drivers (Table 1). This clustering technique represents an alternative to many traditional statistical techniques for analysis of complex ecological data that may include lack of balance, missing values, non-linear relationships between variables and high-order interactions (De'ath & Fabricius 2000). MRTs were used to evaluate which of the nine predictors best explained the elasmobranch assemblage at Cocos Island based on relative abundance (MaxN) values of species per replicate. Only species detected more than two times in the whole study were included in the species matrix. Replicates with no elasmobranchs (n = 17) were not included in the analysis.

Multivariate trees can be formulated to work from a species data matrix based on the sum of squared Euclidean distances (sum of squares MRT or SS-MRT) or from a dissimilarity matrix using a specific measure of ecological distance (distance based MRT or db-MRT) (De'ath & Fabricius, 2000). In order to retain the MRT with the best predictive power, different types of SS-MRT and db-MRT computed with different types of data transformation were compared (Table S3). In all cases, cross-validation of each tree was used to select tree size based on the smallest predicted mean square error (De'ath 2002). The resulting MRTs were initially compared by its cross-validated relative error (CVRE) (De'ath 2002, Borcard et al. 2011). Values of CVRE close to 0 were associated to perfect predictors and values close to 1 to a poor set of predictors (De'ath 2002). A high percentage of species variance (equivalent to a low relative error) was also used as an indicative of good predictive performance. All statistical analysis in this study were performed using R software (v 3.6.3; R Core Team 2022). The function to perform MRTs was *mvpart* from the *mvpart* R package (Therneau et al. 2014) and the results of each tree (i.e. species variance) were extracted using the function *MRT* from the *MVPARTwrap* R package (Ouellette, 2011). Tree size of each MRT was selected based on the tree with the best predictive error (minimum CVRE).

From the selected MRT, we used the Dufrêne-Legendre indicator value (DLI) to show species that best characterized each terminal node (Dufrêne & Legendre, 1997). This index combines species mean abundances and frequencies of occurrence in the groups to identify indicator species that dominates each terminal node (Borcard et al. 2011). The DLI values can range from 0 to 1, where values close to 1 indicate a combination of a large mean abundance within a group compared to the other groups (specificity) and presence in most sites of that group (fidelity) (Borcard et al. 2011). Barplots of DLI values by species were presented at each terminal node, highlighting those species with the highest DLI values or the species with its maximum DLI value among all terminal nodes. Significance of DLI was determined with 1000 permutation test using the function *indval* of the *labdsv* R package (Roberts, 2019). Species with p values < 0.05 were considered indicator species or species closely related to the ecological conditions of their group.

Spatial and environmental drivers at the species level

Generalized additive mixed models (GAMMs) were used to investigate the effect of the predictors on the relative abundance (MaxN) of elasmobranchs at the species level. Only those species recorded in over 25% of BRUVS were included in these analyses. Predictors included in the models were the same ones used in the MRT, except for habitat type (Table 1). The exclusion of habitat type allowed the reduction of model complexity and potential correlation with other predictors. Distance to the coast for benthic models and bottom depth for pelagic models were square root transformed to normalize their right skewed distribution. To allow for potential spatial correlation between replicates (Harvey et al. 2021), all benthic BRUVS simultaneously deployed in the water and at shorter distances than 1 km were grouped under the same 'deployment' as well as pelagic BRUVS that were connected to the same line. Each 'deployment' was then used as a random effect in all models. Replicates with large aggregation of individuals (n = 3) and those at the limit of the maximum sampling depth (60 m) of this study (n = 1) were removed from the models.

Poisson and negative binomial GAMMs were examined for benthic and pelagic elasmobranch species. The negative binomial distribution was used as an alternative to the Poisson distribution to handle overdispersion of the data (variance larger than the mean) (Borcard et al. 2011). Overdispersion in Poisson models was tested with the function *dispersion test* of the *AER* package (Kleiber & Zeileis, 2008). Both models were also compared with likelihood ratio tests and diagnostic plots of the residuals (Zuur et al. 2009a). To account for differences in soak time (hr) between deployments, log (soak time; hr) was used as an offset for all models examined (Zuur et al. 2009a). A cubic regression spline was used as the smoothing function for each continuous predictor variable in the models to ensure smoothness of the response curve at the points where the individual segments connect (Wood, 2006). The maximum number of degrees of freedom was set to four (k = 4) to allow some complexity in the functions while avoiding overfitting the data (Zuur et al. 2009a).

Model selection was based on the small sample-corrected AIC (AICc), recommended for small samples (Burnham & Anderson 2002). Models were ranked based on minimum AICc, detailing the difference in AICc with respect to the top ranked model (delta AIC or ΔAICc). Models with values of ΔAICc < 2 were presented for each species based on recommendations by Burnham & Anderson (2004). The predictor variables included in the most parsimonious model and the lowest AICc among models with values of ΔAICc < 2 were plotted against the response variable (Lester et al. 2022). ΔAICc was also used to calculate the Akaike weight (w_i; range from 0–1) of each model. The cumulative model weights were used to reduce the amount of candidate models to a 95% confidence set of models (sum of Akaike weights = 0.95) (Symonds & Moussalli 2011). Model weights were also used to measure the relative importance of each variable by summing the Akaike weights ($\sum w_i$) from each model in which the variable occurred (McAlpine et al. 2006). The closer the sum of the weight value was to 0.95, the higher probability that predictor must be a component of the best model (Burnham & Anderson 2002).

Deviance residuals were plotted against fitted values and against all predictor variables included in the full model to evaluate the goodness of fit of the resulting models and to determine whether model assumptions were met. The *gam* function in the R package *mgvc* (Wood, 2011) was used to fit the GAMs and the function *lrtest* from the R package *lmtest* (Zeileis & Hothorn, 2002) was used to apply likelihood ratio tests for model comparisons. The function *gam.check* from *mgcv* R package (Wood, 2011) was used to run diagnostic plots of the models. The function *dredge* from the *MuMIn* package (Barton, 2022) was used to rank models according to AICc.

RESULTS

After removing non-valid replicates (low visibility, low field of view or soak time below 50 min), a total of 294 BRUVS (~ 434 hours) remained for the analysis (81%) (Table S1). From these, 218 were benthic BRUVS deployed in benthic environments (inshore reefs, bays and pinnacles) and 76 were pelagic BRUVS deployed in pelagic environments (Fig 1). Elasmobranchs were detected in 94.2% of all replicates with a higher frequency of occurrence in benthic (99.5%) than pelagic (78.9%) environments. A total of 13 elasmobranch species were detected at Cocos Island, four of which were found in both benthic and pelagic environments (Table 2). The number of species detected per hour ranged from 0 to 6 in benthic environments (mean ± SD: 2.5 ± 1.1 species hr^{-1})

and from 0 to 2.1 in pelagic environments (mean ± SD: 0.7 ± 0.5 species hr^{-1}). The relative abundance (MaxN hr^{-1}) per station ranged from 0 to 33.6 ind hr^{-1} in benthic environments (mean ± SD: 6.9 ± 5.1 ind hr^{-1}) and from 0 to 26.5 ind hr^{-1} in pelagic environments (mean ± SD: 2.3 ± 4.4 ind hr^{-1}). Cumulative species curves per habitat indicated that the rate of species accumulation was higher at inshore reefs where a total of 12 species were detected, followed by pinnacles (9 species), bays (11 species) and pelagic sites (9 species) (Fig S3). The cumulative curve in pelagic sites failed to reach an asymptote, suggesting that a higher sampling effort in that area is still needed (Fig S3).

The whitetip reef shark (*Triaenodon obesus)* and the scalloped hammerhead shark (*Sphyrna lewini*) were the most frequently observed and abundant species in benthic environments, accounting for 38.4% and 30.1% of the total elasmobranch abundance (sum MaxN = 2055), respectively (Table 2). The Galapagos shark (*Carcharhinus galapagensis*), the silvertip shark (*Carcharhinus albimarginatus*) the marble ray (*Taeniurops meyeni*), and the tiger shark (*Galeocerdo cuvier*) presented relatively similar values of frequency of occurrence and abundance (Table 2). The least observed and abundant shark species in benthic environments were (in descending order) the blacktip shark (*Carcharhinus limbatus*), the blacktip reef shark (*Carcharhinus melanopterus*) and the silky shark (*Carcharhinus falciformis*). *Carcharhinus falciformis* and *S. lewini* were the most abundant and most frequently observed species in pelagic environments, accounting for 29% and 65.7% of the total elasmobranch abundance (sum MaxN = 280). Overall, observations of pelagic and bentho-pelagic rays were uncommon in benthic environments. The thresher shark *(Alopias pelagicus*) was detected only once in pelagic BRUVS over the course of this study (Table 2).

Several elasmobranch species were more abundant during the rainy season, particularly at inshore reefs from the north side of Cocos Island (Table S4). The mean depth of all elasmobranchs detected by benthic BRUVS was 19.7 ± 9.8 (mean ± SD); *C. melanopterus* was the species recorded in the shallowest waters (10.9 ± 5.6 m); *C. falciformis* was recorded in at the greatest measured depth (26.2 ± 11.1 m) in benthic environments (Table S5). Mean bottom water temperature ranged from 25.7 ± 2.1ºC for *C. falciformis* in benthic environments to 28.1 ± 0.4 ºC for *C. galapagensis* in pelagic environments (Table S5). Mean nearest distance to the cost ranged from 0.03 km for the giant manta ray (*Mobula birostris*) in benthic environments to 6.52 km for *A. pelagicus* in pelagic environments (Table S5).

Table 2. Summary of occurrence (N), mean, maximum and sum of relative abundance (MaxN) and conservation status (CS) of elasmobranch species detected in benthic and pelagic environments (Env) of Cocos Island by Baited Remote Underwater Video Stations (BRUVS). Conservation status of each species (LC – Least Concern, NT – Near Threatened, VU – Vulnerable, EN – Endangered, and CR – Critically Endangered) is presented based on current International Union for the Conservation of Nature Red List Assessments (IUCN 2022). Species are ranked by sum of MaxN.

Env	**Species**	**Common name**	**N**	**% N**	**MaxN**			**CS**
					mean ± SD	**max**	**sum**	
Benthic	*Triaenodon obesus*	White tip reef shark	164	75.20	4.82 ± 3.5	24	790	VU
	Sphyrna lewini	Scalloped hammerhead shark	114	52.30	5.42 ± 9.3	70	618	CR
	Carcharhinus galapagensis	Galapagos shark	84	38.50	1.88 ± 1.3	8	158	LC
	Carcharhinus albimarginatus	Silvertip shark	79	36.20	1.65 ± 1.3	8	130	VU
	Taeniurops meyeni	Marble ray	86	39.40	1.33 ± 0.8	5	114	VU
	Galeocerdo cuvier	Tiger shark	85	39.00	1.15 ± 0.6	5	98	NT
	Carcharhinus limbatus	Blacktip shark	42	19.30	1.24 ± 0.7	5	52	VU
	Carcharhinus melanopterus	Blacktip reef shark	31	14.20	1.39 ± 0.8	4	43	VU
	Carcharhinus falciformis	Silky shark	20	9.20	1.65 ± 1.2	5	33	VU
	Aetobatus laticeps	Eagle ray	11	5.00	1.36 ± 0.7	3	15	VU
	Mobula birostris	Giant manta ray	2	0.90	1.00	1	2	EN
	Mobula tarapacana	Sicklefin devil ray	2	0.90	1.00	1	2	EN
Pelagic	*Sphyrna lewini*	Scalloped hammerhead shark	42	55.30	4.38 ± 8.1	34	184	CR
	Carcharhinus falciformis	Silky shark	38	50.00	2.13 ± 2.6	16	81	VU
	Carcharhinus galapagensis	Galapagos shark	7	9.20	1.14 ± 0.4	2	8	LC
	Carcharhinus limbatus	Blacktip shark	3	3.90	1.00	1	3	VU
	Galeocerdo cuvier	Tiger shark	2	2.60	1.00	1	2	NT
	Alopias pelagicus	Pelagic tresher shark	1	1.30	1.00	1	1	EN
	Carcharhinus albimarginatus	Silvertip shark	1	1.30	1.00	1	1	VU

Spatial and environmental divers at the assemblage level

A Bray-Curtis distance-based MRT with log-transformed MaxN data was selected as the MRT with the best predictive performance (CVRE = 0.68), the lowest relative error (RE = 0.57) and the highest percentage of explained species variance (R2 = 42.47%) (Table S3; Fig. 2). Although five-terminal nodes were identified by cross-validation as the tree size with the smallest estimated predictive error, a tree with six terminal nodes was selected to increase species variance while maintaining a similar CVRE (Table S3; Fig S4). The selected MRT was constrained by minimum distance to the coast, depth, mean temperature, and habitat (Fig. 2). Distance was the only predictor variable selected by all MRT, while depth and habitat were selected by most of them (Table S3).

The first split in the MRT divided the elasmobranch community of Cocos Island between benthic sites (terminal nodes one to five) located closer than 1.6 km from the coast and pelagic sites (terminal node 6) located farther than 1.6 km from the coast (Fig. 2). All replicates from pelagic environments were clustered at node 6 reiterating clear differences among elasmobranch assemblages between benthic and pelagic environments (Table 3). *Carcharhinus falciformis* was identified as the only significant indicator species in pelagic sites (DLI = 0.38; pval = 0.001). *Sphyrna lewini* was the second species closely related to this terminal node (DLI = 0.17) (Fig 2).

The second split separated shallow (< 16.7 m) and deep (> 16.7 m) elasmobranch assemblages. The shallow assemblages were further divided by cold (< 27.7 ºC) and warm (> 27.7 ºC) water temperatures. Cold elasmobranch assemblages (terminal node 1) grouped replicates from all habitats with similar representations between locations and seasons. Instead, warm elasmobranch assemblages (terminal node 2) grouped mainly replicates with the following characteristics bays and inshore sites, north location, dry season, shallow depths, close distances from the coast and high coral reef cover (PC3) (Table 3). Although the eagle ray (*Aetobatus laticeps*) had the maximum DLI value (DLI = 0.04) in the terminal node 1 (cold sites), this species was not a significant indicator species (pval = 0.21) (Fig 2). Warm elasmobranch assemblages were clearly dominated by *T. obesus* (DLI = 0.37) and *C. melanopterus* (DLI = 0.44), both identified as significant indicator species (p = 0.001) (Fig 2). Deep elasmobranch assemblages were divided by the presence of pinnacles (terminal node 3) and inshore reefs and bays (terminal nodes 4 and 5). All the replicates within the terminal node 3 were deployed at pinnacles, at the farthest distances from the coast, deepest depth levels and highest percentage of rocky substrates compared to the replicates grouped at other terminal nodes (Table 3). Pinnacles were dominated by *S. lewini* (DLI = 0.32) and *T. meyeni* (DLI = 0.21), both selected as significant indicator species (p = 0.001).

The last split of the MRT divided elasmobranch assemblages at close distances (< 200 m) from bays and inshore reefs from those at further distances (> 200 m) from it (Fig 2). Both terminal nodes 4 (close sites) and 5 (far sites) grouped replicates from inshore reefs and bays with substrates dominated by sand at similar depths and temperatures. The main differences were a higher number of replicates from the south and a mean distance of 100 m from the coast for the terminal node 4, whereas the terminal node 5 had a higher number of replicates located at the north and a mean distance of 300 m from the coast (Table 3). Close sites (terminal node 4) at inshore habitats or bays were dominated by *C. albimarginatus* (DLI = 0.20) although, *G. cuvier* was the only species that obtained its maximum DLI value in this cluster (DLI = 0.13). Since there were other species with similar DLI values in this terminal node, *G. cuvier* was marginally significant as an indicator species (p = 0.03). Far sites (terminal node 5) at inshore reefs or bays were dominated by *C. albimarginatus* (DLI = 0.32) and *C. galapagensis* (DLI = 0.21) both of which were significant indicator species of this cluster (p = 0.001). In this cluster, *C. limbatus* had its maximum DLI value (DLI = 0.08), but it was not a significant indicator species (p = 0.13) (Fig 2). The species *A. pelagicus, M. tarapacana* and *M. birostris* were not included in the MRT since they were detected in less than three replicates (Table 2).

The last split of the MRT divided elasmobranch assemblages at close distances (< 200 m) from bays and inshore reefs from those at further distances (> 200 m) from it (Fig 2). Both terminal nodes 4 (close sites) and 5 (far sites) grouped replicates from inshore reefs and bays with substrates dominated by sand at similar depths and temperatures. The main differences were a higher number of replicates from the south and a mean distance of 100 m from the coast for the terminal node 4, whereas the terminal node 5 had a higher number of replicates located at the north and a mean distance of 300 m from the coast (Table 3). Close sites (terminal node 4) at inshore habitats or bays were dominated by *C. albimarginatus* (DLI = 0.20) although, *G. cuvier* was the only species that obtained its maximum DLI value in this cluster (DLI = 0.13). Since there were other species with similar DLI values in this terminal node, *G. cuvier* was marginally significant as an indicator species (p = 0.03). Far sites (terminal node 5) at inshore reefs or bays were dominated by

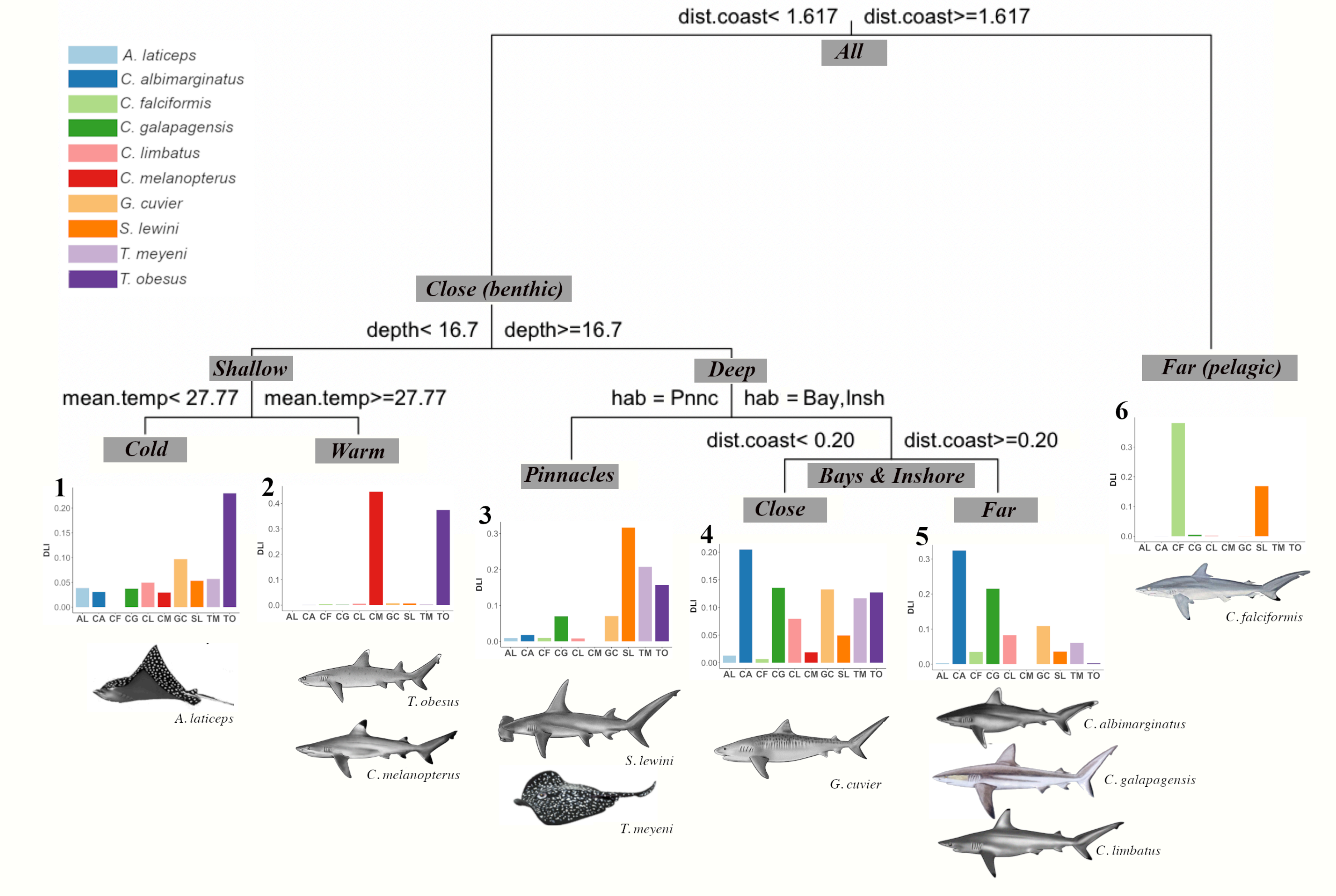
A. laticeps
C. albimarginatus
C. falciformis
C. galapagensis
C. limbatus
C. melanopterus
G. cuvier
S. lewini
T. meyeni
T. obesus
dist.coast< 1.617
dist.coast>=1.617
All
Close (benthic)
depth< 16.7
depth>=16.7
Far (pelagic)
Shallow
Deep
mean.temp< 27.77
mean.temp>=27.77
hab = Pnnc
hab = Bay,Insh
Cold
Warm
Pinnacles
dist.coast< 0.20
dist.coast>=0.20
Bays & Inshore
Close
Far
1
2
3
4
5
6
DLI
AL CA CF CG CL CM GC SL TM TO
A. laticeps
T. obesus
C. melanopterus
S. lewini
T. meyeni
G. cuvier
C. albimarginatus
C. galapagensis
C. limbatus
C. falciformis

Fig 2. Bray-Curtis distance-based multivariate regression tree based on a log-transformed relative abundance (MaxN) matrix. The predictor variables dividing elasmobranch assemblages were: nearest distance to the coast (km), depth (m), mean temperature (ºC) and habitat type (pinnacles, bays or inshore). The terminal leaves are indicated in bold numbers from 1 to 6. The Dufrêne-Legendre indicator value (DLI) of each species is shown in histograms below each terminal node. The elasmobranch images represent each of the species included in the analysis: *Aetobatus laticeps, Carcharhinus albimarginatus, C. falciformis, C. galapagensis, C. limbatus, C. melanopterus, Galeocerdo cuvier, Sphyrna lewini, Taeniurops meyeni* and *Triaenodon obesus.*

Table 3. Ecological conditions of replicates clustered at each terminal node of the Multivariate Regression Tree (Fig 2). The amount of total replicates (N) and the amount of replicates per season (dry, rainy), location (north, south) and habitat (bays, inshore, pinacle, pelagic) is shown at each node. Mean values of distance, temperature, depth, PC1 (rocky), PC2 (sandy) and PC3 (coral reef) are calculated among all replicates from the same node.

Node	N	Season		Location		Habitat				Distance (km)	Temp (ºC)	Depth (m)	PC1	PC2	PC3
		D	R	N	S	B	I	Pi	Pe						
1	60	13	47	34	26	12	34	14	0	0.22 ± 0.2	26.82 ± 0.8	11.25 ± 3.6	0.008	-0.056	0.020
2	24	19	5	22	2	9	14	1	0	0.10 ± 0.1	28.31 ± 0.3	8.96 ± 3.3	0.003	-0.108	0.063
3	58	23	35	30	28	0	0	58	0	0.66 ± 0.4	26.14 ± 2.2	27.76 ± 8.8	0.089	0.043	-0.020
4	40	23	17	15	25	4	36	0	0	0.10 ± 0.1	25.74 ± 2.6	25.17 ± 5.8	-0.073	0.037	-0.034
5	34	14	20	22	12	8	26	0	0	0.32 ± 0.1	25.76 ± 2.2	26.34 ± 6.7	-0.083	0.059	-0.008
6	60	22	38	31	29	0	0	1	59	3.90 ± 1.1	27.67 ± 0.7	225.7 ±	-0.011	-0.104	0.027

C. albimarginatus (DLI = 0.32) and *C. galapagensis* (DLI = 0.21) both of which were significant indicator species of this cluster (p = 0.001). In this cluster, *C. limbatus* had its maximum DLI value (DLI = 0.08), but it was not a significant indicator species (p = 0.13) (Fig. 2). The species *A. pelagicus, M. tarapacana* and *M. birostris* were not included in the MRT since they were detected in less than three replicates (Table 2).

Spatial and environmental drivers at the species level

Generalized Additive Mixed Models were performed on the relative abundance of six elasmobranch species in benthic habitats and two elasmobranch species in pelagic habitats (Fig. 3). Results from likelihood ratio tests indicated a better performance of negative binomial GAMMs over the Poisson distribution models, except for *S. lewini* in benthic habitats (Table S6). However, a negative binomial distribution was also chosen for this species to address the overdispersion detected in the Poisson GAMM. Diagnostic plots also indicated a better fit of the negative binomial model for *S. lewini*. All species presented right skewed MaxN distributions due to a higher number of replicates with 0 or few individuals, with some variations observed between species (Fig S5). The mean amount of model combinations within the 95% confidence set ($\sum w_i = 95$) for all species models was 155 ± 167.11 (mean ± SD) ranging from 39 models for *S. lewini* in the pelagic environment to 194 models for *T. obesus,* indicating high levels of model uncertainty that varied depending on the species (Table S7). The number of candidate models with ΔAICc < 2 also varied per species ranging from 5 models for *C. albimarginatus* to 24 models for *T. obesus* (Table S7). The relative influence of each predictor variable based on summed Akaike weights ($\sum w_i$) varied by species indicating species specific responses to the natural drivers included in the models (Fig 4).

The abundance of *S. lewini* was modelled in benthic and pelagic environments. The most parsimonious model in benthic environments included distance, location and season (Table S7). The abundance of *S. lewini* was significantly higher at farther distances from the coast, at the north side of the island and during the rainy season (Figs 3, 4). The full model had an explained deviance of 54.7% which increased to 54.8% for the most parsimonious model. In pelagic environments, location was the only variable included in the most parsimonious model (Table S7). The abundance of *S. lewini* in pelagic environments was significantly higher in the south compared to the north side of Cocos Island (Fig. 3). The full model had an explained deviance of 65.7% and the most parsimonious model of 61.7%. The random effect of deployment had the highest relative importance on the abundance of *S. lewini* in both benthic and pelagic environments, compared to other species (Fig. 4).

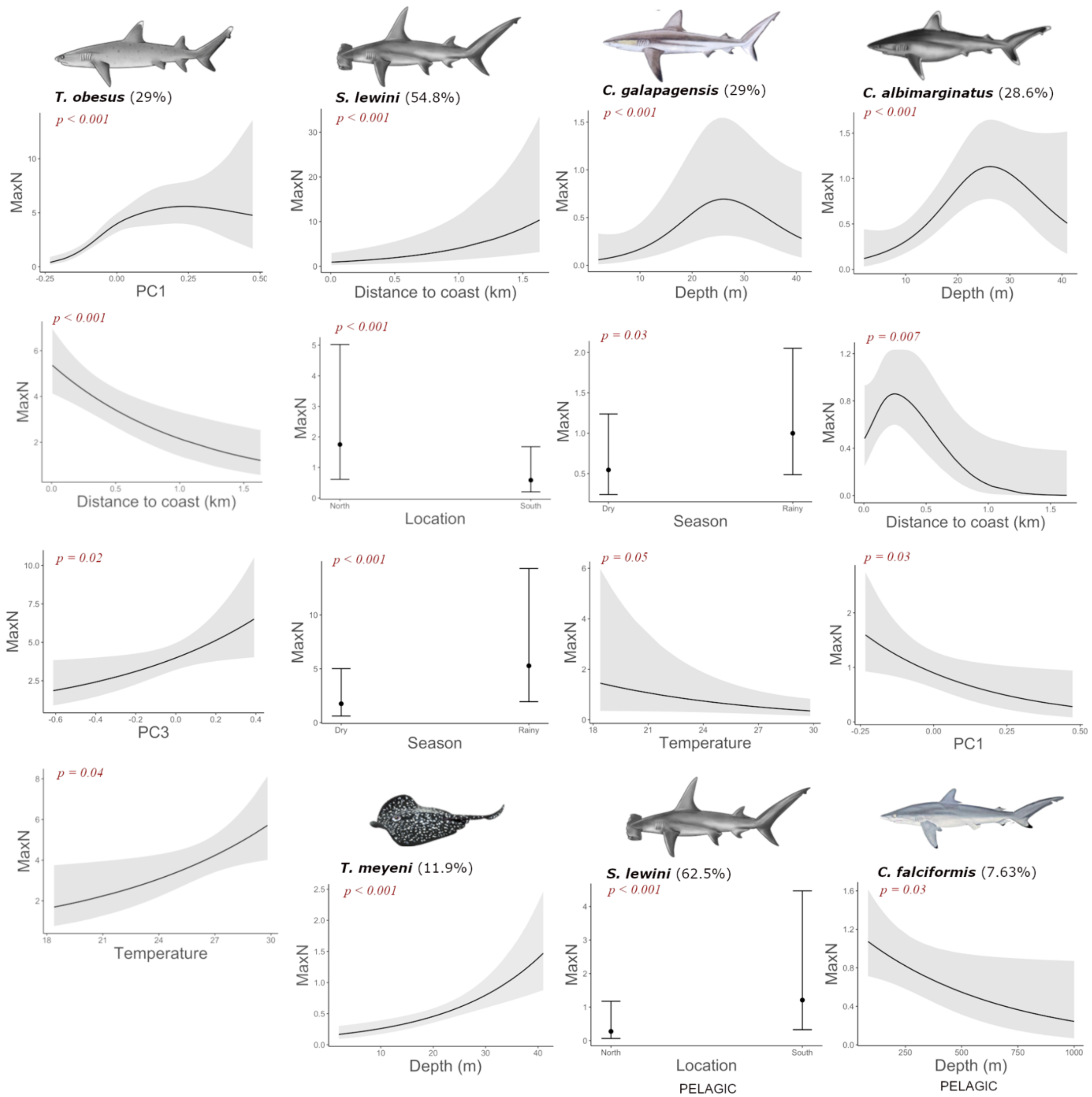

Fig 3. Summed effects of the predicted relative abundance (MaxN) against the variables present in the most parsimonious Generalized Additive Mixed Model (GAMM) for each species. The percentage of explained deviance of each model and the p values of each variable (in red) within the model are also included.

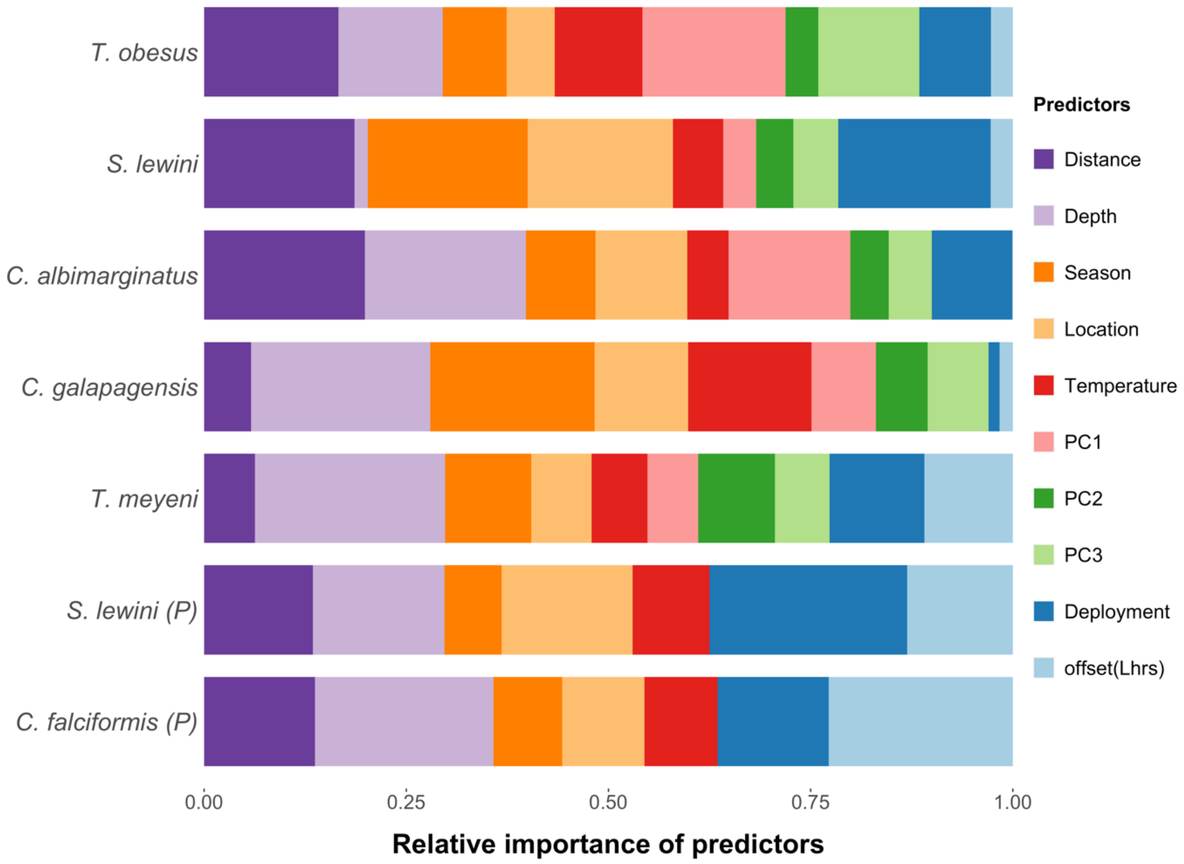

Fig 4. Relative importance of each predictor variable used in Generalized Additive Mixed Models (GAMMs) based on the summed Akaike weights ($\sum w_i$) of the 95% confidence set of models in which the variable occurred. Models performed based on species abundance in pelagic environments are indicated by (P).

Depth, season and mean temperature were included in the most parsimonious model for *C. galapagensis* (Table S7)*,* although only depth and season were significant (Fig 3). The abundance of *C. galapagensis* was significantly higher between 20 and 30 m depth and at rainy season. However, it decreased with increasing temperatures (Fig. 3). The full model for *C. galapagensis* had an explained deviance of 36% which dropped to 33.9% in the most parsimonious model.

The most parsimonious model for the abundance of *T. obesus* included distance, temperature, PC1 and PC3 as significant predictor variables (Table S7). The abundance of *T. obesus* significantly decreased with distance to the coast and increased with mean temperature, PC1 and PC3 (Fig 3). Relative important scores also highlighted these, in addition to depth, as the most influential predictor variables (Fig 4). The full model had an explained deviance of 32.5% which dropped to 29% in the most parsimonious model.

The most parsimonious model for *C. albimarginatus* included depth, distance and PC1 (Table S7). Depth and distance had the highest relative importance on the abundance of *C. albimarginatus* (Fig 4), which was significantly higher at distances between 500 and 800 m of the coast (square root of 0.26 and 0.74) and at depths between 20 and 30 m. However, it significantly decreased with increasing values of PC1 (Fig 3). The full model had an explained deviance of 38.1 % which dropped to 28.6% in the most parsimonious model.

Depth was the variable with the highest relative importance for the abundance of *T. meyeni* (Fig 4), and the only one included in the most parsimonious model (Table S7). The abundance of *T. meyeni* significantly increased with increasing depth levels (Fig 3). The explained deviance of the full model for this species was 16.8 % and for the most parsimonious model was 11.9 %.

Depth was the only variable included in the most parsimonious model for *C. falciformis* (Table S7) and the variable with the highest influence on its abundance (Fig 4). The abundance of *C. falciformis* decreased significantly with increasing seafloor depth levels (Fig 3). The full model on the abundance *C. falciformis* had an explained deviance of 17.2%, which dropped to 7.63% in the most parsimonious model.

DISCUSSION

Anthropogenic impacts can hinder our understanding of the relationships between species and the environment (Ward-Paige et al. 2010). By investigating the interaction between elasmobranchs and their environment at a remote and relatively undisturbed oceanic island, we were able to identify key drivers that may be shaping how these assemblages are structured. Long term surveys at remote habitats with minimum anthropogenic impacts that hold high predator biomass are crucial since they are likely the last natural baselines remaining to understand how healthy coral reef ecosystems function (Knowlton & Jackson 2008, Juhel et al. 2018).

This study identified spatial drivers (i.e., distance to the coast, depth and habitat) as the factors with the greatest influence dividing benthic and pelagic elasmobranch assemblages, particularly those that inhabit shallow inshore sites and deep coastal areas in benthic environments. These results indicate that spatial segregation might be the main strategy used by a highly diverse and abundant elasmobranch community to coexist in a relatively small area (Tews et al. 2004, White & Potter 2004). The underlying processes determining habitat partitioning and segregation patterns of elasmobranchs are often related to predator avoidance and the reduction of intra- and inter-specific resource competition (Sims 2003). Small islands where elasmobranch multi-species aggregations occur, provide an ideal opportunity to examine spatial partitioning and other inter-specific interactions that are necessary to understand the role of these predators in marine ecosystems (Speed et al. 2011).

Depth and habitat have been identified as important predictors for elasmobranch assemblages at different geographical scales (Menni et al. 2010, Guisande et al. 2013). Our study revealed a significant association of large elasmobranchs with deep areas (> 16 m) and small elasmobranchs with shallow areas (< 16 m), which agrees with our initial hypothesis. Deep areas of Cocos Island are in closer proximity to pinnacles and offshore environments where shark cleaning stations and higher concentrations of plankton occur, therefore increasing cleaning and foraging opportunities for apex predators (Friedlander et al., 2012). Shallow areas instead, are associated with inshore sites and bays characterized with extensive coral reef formations and lower exposure to waves and currents especially at the north side of the island (Cortés 2016a). These conditions offer a higher degree of protection from predators and easier access to prey to smaller elasmobranchs commonly found in those environments (Espinoza et al. 2014a, Osgood & Baum 2015).

At deep areas, we found a strong association between *S. lewini* and pinnacles, as it has been already described in other oceanic islands (Hearn et al. 2010, Acuña-Marrero et al. 2018), and offshore seamounts from the ETP (Cambra et al., 2021). This behavior is thought to be associated to energy optimization, to social behaviors and cleaning activities or as an orientation strategy during long-range foraging excursions or migrations (Klimley & Nelson 1984, Klimley 1987). Fish species that aggregate around seamounts, especially large fishes with long life spans, slow growth and later sexual maturation such as sharks, are highly vulnerable to exploitation (Morato et al. 2006). Therefore, identifying and protecting threatened species that are known to form large aggregations around seamounts such as S. *lewini* is critical to reduce population declines (Cambra et al. 2021a).

At shallow areas instead, *T. obesus* and *C. melanopterus* were identified as the only significant indicator species with preference for higher temperatures and structurally complex substrate covers dominated by coral reefs or rocks. These results are also in agreement with our initial hypothesis where small elasmobranch species would be more influenced by substrate cover than large elasmobranchs. Small-scale factors such as benthic cover may be important to shallow water species that interact most directly with the reef either for food or shelter (Chabanet et al. 1997). Whereas for wide-ranging large-bodied species, small-scale differences in benthic cover are likely less important (Richards et al. 2012).

Besides the similarities found between these two reef-associated shark species, our results suggest a higher specificity of *C. melanopterus* to shallow depths, coral reefs, north location, bays and inshore sites. Instead, *T. obesus* presented a much broader distribution at both north and south sides of the island including bays, inshore sites and pinnacles. By maintaining a small home range, *C. melanopterus* may facilitate the use of local resources such as feeding sites, predator refuges and breeding sites (Speed et al. 2011), and may also increase opportunities for complex social interactions (Mourier et al., 2012). On the other hand, the small size of Cocos Island combined with the high intraspecific competition of *T. obesus* usually occurring at oceanic islands (Whitney et al. 2012)*,* may have led to the expansion of its distribution towards the south and pinnacles, where rocky substrates dominate over coral reefs (Sibaja-Cordero et al. 2012, Alvarado et al. 2016). While many studies indicate the high association of *T. obesus* with coral reefs (Zanella et al. 2012, Espinoza et al. 2014a, Lester et al. 2022), our results indicated a stronger association with rocky reefs. Both coral reefs and caves and crevices in rocky reefs might provide important resting areas during the day or between foraging excursions to *T. obesus* and reduce predation from larger sharks (Randall 1977).

Although temperature has traditionally been identified as a determining factor of the abundance and distribution of elasmobranchs (Guisande et al. 2013, Schlaff et al. 2014), only the abundance of two species was significantly affected by temperature. Cocos Island is influenced by the mass of tropical surface waters north of the equator (Fiedler & Talley 2006) and, therefore, is not exposed to major changes in temperature as other larger islands such as the Galapagos Islands, where colder currents have a greater influence on elasmobranch assemblages (Acuña-Marrero et al., 2018). During the study period, the island was affected by small fluctuations in temperature derived from weak (2017 – 2018) and moderate (2020 - 2021) La Niña events (cooler) and by a weak El Niño event (2018 – 2019) (warmer) (NOAA 2022). However, our results suggest that these anomalies were not drastic enough to induce a significant effect on the abundance of most elasmobranch species.

The only clear relationships found between temperature and elasmobranchs at the assemblage level was the affinity of *C. melanopterus* and *T. obesus* for high temperatures in shallow inshore sites and bays. This result might indicate their limited capacity to respond to extreme temperatures compared to large, mobile elasmobranch species (Osgood et al. 2021). Additionally, inshore daytime aggregations and habitat selection associated with higher water temperatures in small reef sharks have been found to increase embryonic development, favor digestive efficiency, or optimize other physiological processes (Hight & Lowe 2007, Speed et al. 2012).

We also anticipated a stronger influence of temperature on the movements of large elasmobranchs compared to small elasombranchs, and hence a higher abundance of large elasombranchs during the rainy season when water temperature is lower. A significant effect of temperature on large elasmobranchs was found for *C. galapagensis* whose abundance decreased with increasing temperature. However, a significant effect of seasonality potentially associated with temperature, was found for *C. galapagensis* and *S. lewini*. Seasonal patterns in the abundance of these two species have been reported at Cocos Island (White et al., 2015) and at other oceanic islands of the ETP (Hearn et al., 2014; Lara-Lizardi, 2018) where, similar to this study, greater abundances were recorded during the cooler months. Such seasonal patterns might be associated with their preference for the weaker stratification of the water column, the deeper thermocline and the higher productivity present during the rainy season which increases foraging opportunities and facilitates thermoregulation (Lizano 2008a, Ketchum et al. 2014a). Given that adults of *C. galapagensis* can perform long migrations (Lara-Lizardi 2018), it is possible that many individuals migrate during the warmest months in the dry season, which coincide with the coldest months at some other oceanic islands of the region (Soler et al. 2013, Lara-Lizardi 2018). Females of *S. lewini* may also migrate to pupping areas at other oceanic islands or near the coast during the dry season (Klimley 1987, Bessudo et al. 2011).

It is very likely that this study did not capture a strong effect of seasonality on elasmobranch assemblages because the field work during the dry season was carried out in June every year (except for few days of survey in December 2016), during the transition between dry and rainy seasons (Acuña González et al. 2008). Given that all the species were detected in both dry and rainy seasons, our results indicate that seasonal differences in elasmobranch assemblages at Cocos Island may be associated to changes in species abundance rather than in species composition.

Distance was identified as an important predictor not only to differentiate elasmobranch assemblages between benthic and pelagic environments, but also between close (< 200 m) and far deep coastal areas at Cocos Island. These results agree with a previous study using diving data from Cocos Island, which found distance to be one of the main predictors of habitat selection by elasmobranchs and a general negative association to increasing distance from the coast for all species (González-Andrés et al. 2021). Here, in contrast, we identified species-specific responses of elasmobranch abundance to increasing distances from the coast providing a more comprehensive overview of elasmobranch distribution patterns at Cocos Island. For example, the abundance of *T. obesus* increased at shallow waters close to the coast while the abundance of *S. lewini* increased at deep areas far from the coast. The high abundance of *T. obesus* generally found at closer distances from the coast (Espinoza et al. 2014a, Lester et al. 2022) may be explained by the species' high metabolic cost of activity (Osgood et al. 2021), which limits its movements during the day to small centers of activity close to feeding or aggregation sites (Barnett et al. 2012). A higher abundance of *S. lewini* at farther distances from the coast is probably related to its preference for pinnacles with cleaning stations located at deeper depth levels (Friedlander et al. 2012, Nalesso et al. 2019).

A clearer pattern was found for *C. albimarginatus* which was significantly more abundant at sandy areas between 500 and 800 m off the coast, showing a similar pattern to what was found at the Great Barrier Reef in Australia (Espinoza et al. 2015). With this particular distribution, *C. albimarginatus* could increase predator avoidance by larger predators at pinnacles or at shallow coastal sites (frequented by *G. cuvier* according to this study) while reducing inter-specific competition for resources with other reef-associated shark species. Another explanation could be the easier access that this distribution offers to benthic and pelagic prey since both have been found to be important parts of their diet (Curnick et al., 2019). The low relative importance of coral reefs in our models is in agreement with previous studies that classify *C. albimarginatus* as a transient reef-associated species with a lower dependence on coral reefs compared to smaller and less mobile reef-associated species (Espinoza et al. 2014a, 2015, Tickler et al. 2017).

Differences in elasmobranch distribution between the north and south of Cocos Island were less evident than expected. For example, *S. lewini* and *C. melanopterus* were the only species that had a high association with northern areas of Cocos Island. Permanent shark cleaning stations at Cocos Island exist in both north and south sides of Cocos Island offering similar opportunities to *S. lewini* for cleaning activities around the island. However, pinnacles with cleaning stations located in the north offer a higher protection from currents which might promote energy optimization during the resting phase of the species' diel cycle (Klimley & Nelson 1984). In pelagic environments, in contrast, we found a significant higher abundance of *S. lewini* in the upstream southern areas of Cocos Island. The schooling behavior of *S. lewini* in upstream southern offshore areas of Cocos Island could represent a strategy to reduce energy costs in the presence of strong currents and to benefit from higher productivity levels usually present in the south, similar to what has been reported in the Galapagos and Malpelo Islands (Hearn et al. 2010, Bessudo et al. 2011, Ketchum et al. 2014a). Here, we present the first evidence of schooling behaviour of *S. lewini* at offshore (> 1 km) pelagic environments off Cocos Island, a behavior that increases its vulnerability to pelagic longline fisheries in the ETP.

In contrast to benthic environments where five species were identified as significant indicators of specific habitat types, *C. falciformis* was the only indicator species in pelagic environments. Seafloor depth was the only significant predictor on the abundance of this species which was highest at the minimum recorded sea bottom depth of 200 m and decreased above deeper sea levels. This species is known to use the edge of continental and insular shelves over deep water reefs and around islands possibly to benefit from higher food sources compared to more open ocean sites (Camhi et al. 2008). This could explain the higher relative abundance of this species found at the north side of Cocos Island, where the insular platform extends farther compared to the shorter insular platform in the south side (Lizano 2001). However, the low explained variance obtained (7.6%) indicates that other variables may be more important at explaining the abundance and distribution patterns of *C. falciformis*. Given that spatial distributions of many pelagic species are closely related to dynamic oceanic processes, current speed and direction, kinetic energy, chlorophyll-*a* concentration, dissolved oxygen and pH may be important variables to include in future models (Lopez et al. 2016, Andrzejaczek et al. 2019).

This is the first study at Cocos Island describing the community structure of elasmobranchs in the pelagic environment. Our findings revealed that *S. lewini* and *C. falciformis* were the most frequent species, accounting for 96.7% of the total elasmobranch abundance. The association of *S. lewini* and *C. falciformis* to pelagic environments (Camhi et al. 2008) in addition to the high commercial interest of their fins in Asian markets (Dent & Clarke 2015, Ross et al. 2019) make these species one of the most vulnerable to longline fishing (Whoriskey et al. 2011, Clarke et al. 2013). Increasing survey effort in pelagic environments around Cocos Island (Cambra et al. 2021a) along with effective conservation schemes, is necessary to identify important areas for the conservation of pelagic elasmobranch species and protect them from further population declines (Soler et al. 2013, White et al. 2015).

The use of BRUVS has demonstrated to overcome biases associated with fish avoidance to divers, increasing counts of larger-bodied predatory species and therefore providing a higher statistical power compared to diving survey transects (Langlois et al. 2010, Eisele et al. 2021). Important differences can be observed when comparing the frequency of occurrence of elasmobranch species obtained by BRUVS in this study with diving data at Cocos Island (Fig 5). The higher frequency of occurrence of some species reported by dive guides is probably associated with (i) a low efficiency of benthic BRUVS to detect filter-feeding elasmobranch species (Bruns & Henderson 2020), and (ii) the preference of those species for pinnacles, where most of the diving activities occur (Sibaja-Cordero 2008). Since BRUVS are currently not allowed at touristic sites, unbaited video stations might be used at pinnacles with shark cleaning stations (M. Espinoza, unpubl. data) to investigate the association of elasmobranchs with these unique environments. On the other hand, it is likely that the species that were most frequently detected by our BRUVS are (i) species that are negatively affected by the presence of divers (Dale et al. 2011) or (ii) species with a higher occurrence at inshore sites where diving activities are not allowed. These results highlight the efficacy of BRUVS to provide accurate data on elasmobranch abundance and distribution patterns at a wider depth range and in habitat types not as frequented by or as accessible to divers. The use of BRUVS also allowed us to report, for the first time, the presence of *A. pelagicus* at offshore pelagic environments of Cocos Island.

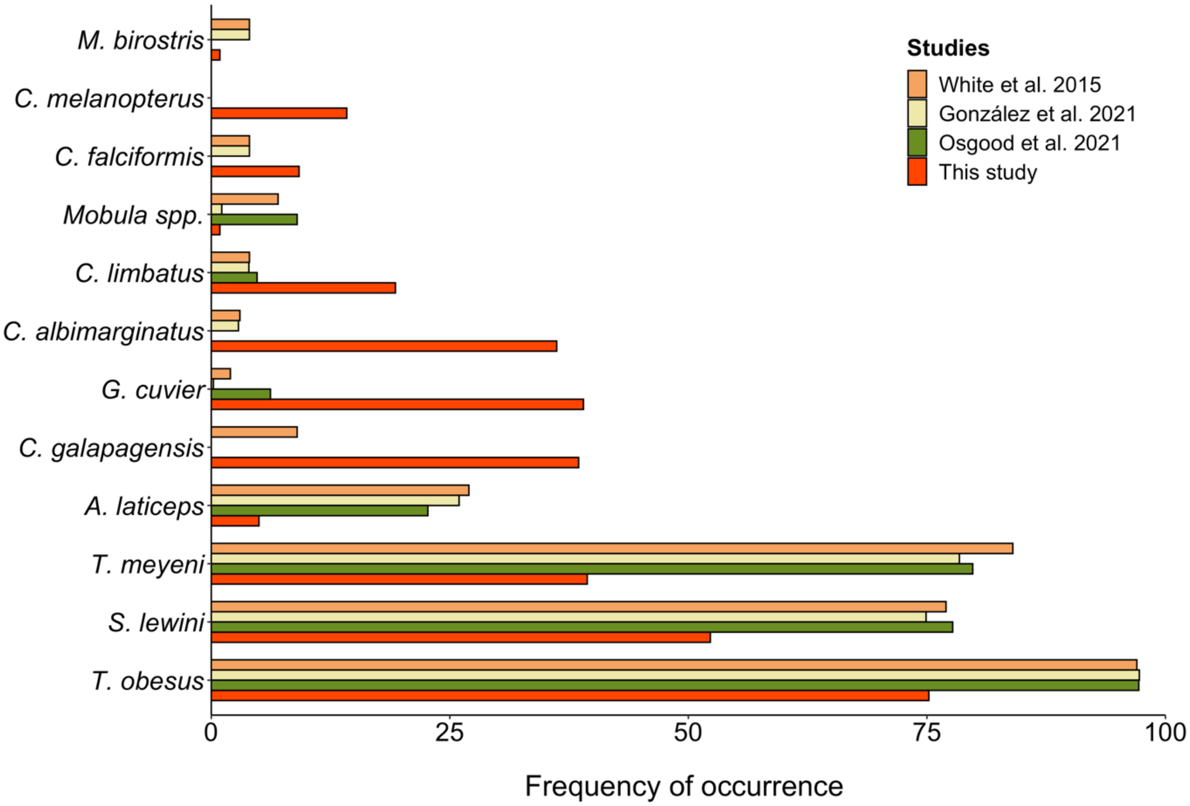

Fig. 5. Comparison of the frequency of occurrence (%) of elasmobranch species detected by Baited Remote Underwater Video Stations of this study and the same data set collected by dive guides of Cocos Island between 1993 and 2013 (White et al. 2015, González-Andrés et al. 2021) and between 1993 and 2019 (Osgood et al. 2021). Values of 0 in frequency of occurrence for some species indicate that the study did not include that species in the analysis.

CONSERVATION IMPLICATIONS

Eleven of the 13 elasmobranch species detected by BRUVS in this study are classified as threatened species based on IUCN Red List criteria (IUCN 2022). Diving data collected at Cocos Island from 1991 to 2013 (White et al., 2015) and from 1991 to 2019 (Osgood et al. 2021) documented decreases in relative abundance of at least 10 of these species with population declines between 50 and 89% in most cases. Population declines of elasmobranch species have also occurred at other oceanic islands of the region such as Galapagos and Malpelo Islands (Soler et al. 2013, Peñaherrera-Palma et al. 2015). Pelagic longline fishing in offshore areas of the ETP (Dapp et al. 2013) and illegal fishing inside MPAs (Arias & Pressey 2016, López-Garro et al. 2016a, González-Andrés et al. 2020) have been identified as the main cause associated with these declines

(White et al., 2015). However, climate change has also been found to interact with fisheries exploitation affecting long-term trends of elasmobranchs at Cocos Island (Osgood et al. 2021). Given the crucial ecological role of many elasmobranchs in marine ecosystems (Baum & Worm 2009), urgent management actions are required to prevent these species from further population declines.

Despite the severe degree of population declines reported for many elasmobranch species at Cocos Island (White et al. 2015, Osgood et al. 2021), in this study, elasmobranchs were detected in 95% of BRUVS deployments, with 2.7 ± 1.6 species per station and 6.3 ± 6.5 ind hr^{-1}. These values largely exceed the global median expected value of 0.3 ind hr^{-1} (MacNeil et al. 2020), as well as the relative abundance reported by benthic BRUVS in other remote and relatively undisturbed oceanic islands which ranged from 0.7 to 4.2 ind hr^{-1} (Acuña-Marrero et al., 2018; Goetze et al., 2018; Goetze & Fullwood, 2013; Spaet et al. 2016; Juhel et al., 2018; Lara-Lizardi, 2018; Speed et al., 2018; Tickler et al., 2017). This results, highlight the importance of Cocos Island as one of the last remaining healthy predator dominated ecosystem in the ETP and probably on earth (Friedlander et al. 2012, Edgar et al. 2014, Alvarado et al. 2016, Fourriére et al. 2019).

In January 2022, the size of Cocos Island National Park no-take MPA was expanded from 2,034 km^2 to 54,844 km^2 in order to mitigate the negative effects of fishing and increase the resilience of marine ecosystems to climate change. In addition, the previous Marine Management Area (currently called the Bicentennial Marine Management Area) that excluded purse-seine fisheries around the no-take MPA, changed from 9,649 km^2 to 106,285 km^2. Collectively, these two new areas could provide additional protection to key habitats for pelagic and migratory species that connect Cocos Island with remote seamounts and other oceanic islands of the ETP (Cambra, et al., 2021; Peñaherrera-Palma et al., 2018). Given the lack of detailed ecological data for elasmobranch species at near-pristine ecosystems in the ETP, this study provides a valuable contribution to the understanding of species-specific habitat associations in response to spatial, seasonal and environmental drivers. This type of information will be necessary to identify priority areas for conservation (Agardy et al. 2011) and predict consequences of habitat degradation and climate change (Bruno et al. 2018) at coastal and pelagic environments of MPAs of the ETP. Furthermore, our data could be used as a reference baseline from which to evaluate changes in the community structure, abundance and distribution patterns of elasmobranchs after the expansion of Cocos Island National Park.

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SUPPLEMENTARY MATERIAL

Table S1. Survey effort at each expedition to Cocos Island between 2016 and 2020 represented with the number of Baited Remote Underwater Video Stations (BRUVS) in total (N), per region and per habitat type. Minimum, maximum and average (mean ± SD) BRUVS depth and nearest distance to the shore is also presented.

Month	**Year**	**Season**	**N**	**Region**		**Habitat**				**Depth (m)**		**Distance (km)**	
				North	South	Bay	Inshore	Pinnacle	Pelagic	Range	Mean	Range	Mean
December	2016	Dry	8	8	0	6	2	0	0	5 – 30	15.6 ± 8	0.05 – 0.3	0.2 ± 0.1
June	2017	Dry	24	16	8	0	4	20	0	11 – 60	27.7 ± 12	0.1 – 1.5	0.5 ± 0.4
October	2017	Rainy	35	21	14	0	2	26	7	9 – 40	23.3 ± 7.7	0.02 – 4.4	1.4 ± 1.2
September	2018	Rainy	55	33	22	8	16	16	15	3 – 41	16.2 ± 8.6	0.01 – 3.7	1.2 ± 1.3
June	2019	Dry	36	19	17	2	18	3	13	3 – 49	17.7 ± 10.4	0.01 – 4.9	1.5 ± 1.8
October	2019	Rainy	49	27	22	9	22	5	13	3 – 38	17.2 ± 9.5	0.01 – 5	1.2 ± 1.7
June	2020	Dry	52	27	25	6	30	2	14	2 – 30	15.4 ± 7.8	0.01 – 6.2	1.4 ± 2.1
October	2020	Rainy	35	15	20	3	16	2	14	2 – 28	13.3 ± 7.4	0.04 – 6.9	2.1 ± 2.5
TOTAL			294	166	128	34	110	74	76	2 – 60	17.8 ± 9.7	0.01 – 6.9	1.3 ± 1.8

Table S2. Summary of the Principal Component Analysis (PCA) results for the six major habitat types.

	PC1	**PC2**	**PC3**
Eigenvalues	0.038	0.020	0.009
Proportion explained	0.472	0.247	0.120
Cumulative proportion	0.472	0.718	0.838
Habitat scores			
Rock with encrusting organisms	1.227	0.445	-0.010
Sand or rubble	-0.667	0.796	-0.064
Hard coral	-0.007	-0.304	0.374
Rock with turf	0.050	-0.301	-0.587
Macroalgae	0.004	0.001	0.001
Others	0.024	-0.084	0.081

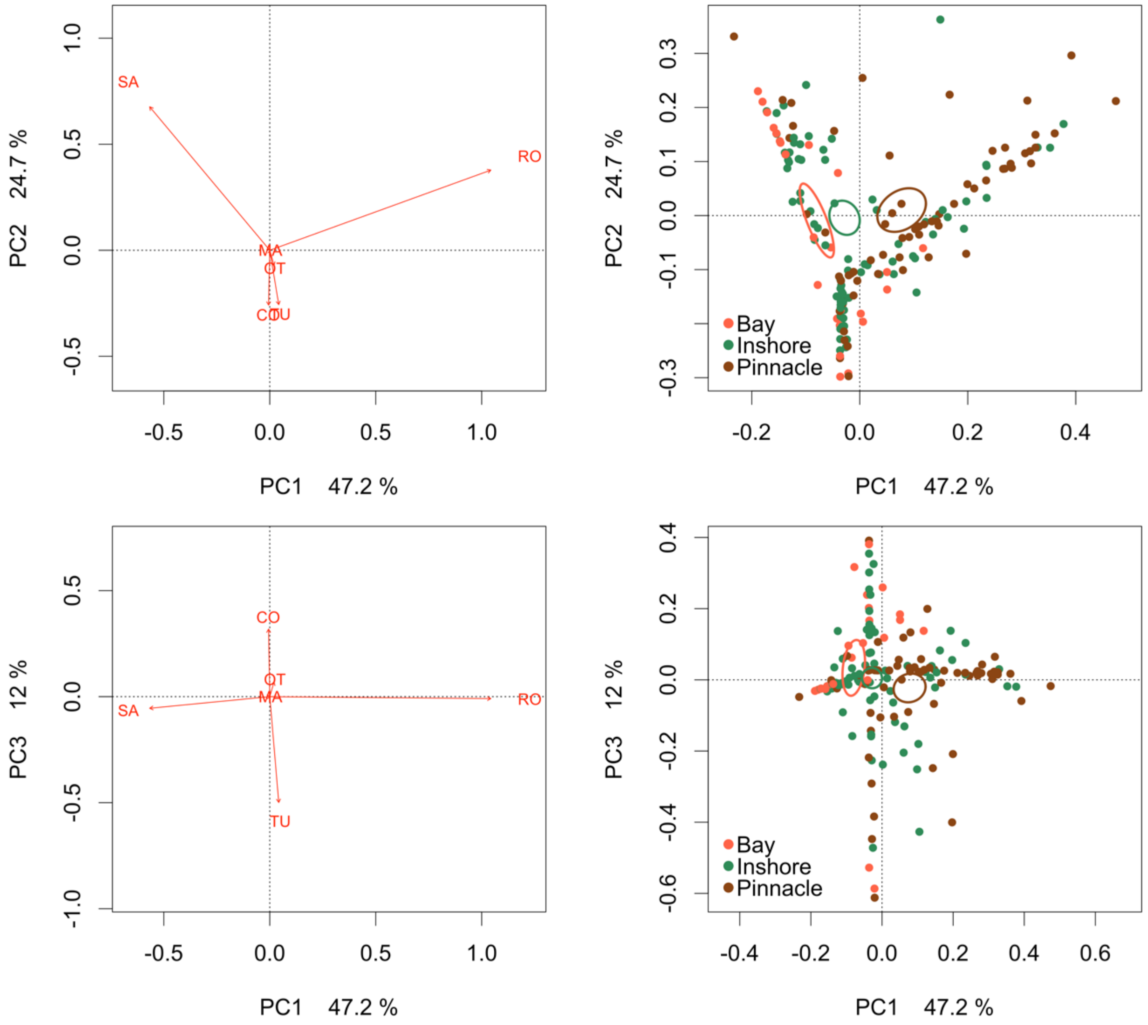

Fig. S1. Principale Component Analyis (PCA) indicating the main substrate cover classes contributing to axes PC1 and PC2 (left – top) and axes PC1 and PC3 (left – bottom): RO) bare rock with encrusting organisms; SA) sand and rubble; MA) macroalgae; TU) rock with turf; OT) other organisms including anemones, barnacles, cyanobacteria, octocoral, sponges, softcoral and tunicates. The coordinates of each Baited Remote Underwater Video Station (BRUVS) replicate are plotted associated to axes PC1 and PC2 (right – top) and axes PC1 – PC3 (right – bottom). Habitat types in the ordination diagram are differenciated by colors. Ellipses represent the 95% confidence interval based on Standard Error.

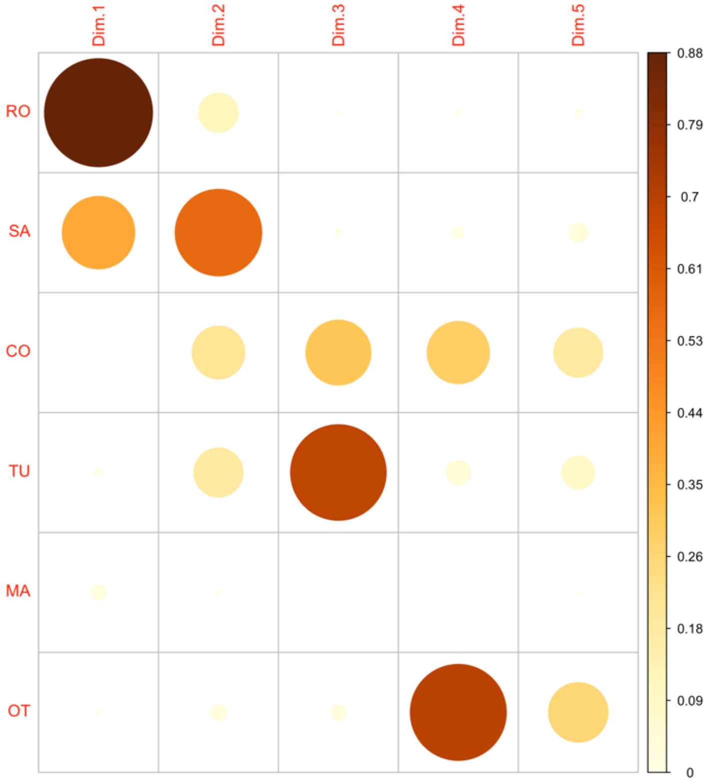

Fig. S2. Correlation plot indicating the percentatge of contribution of each substrate cover type to the Principal Component Analysis (PCA) dimensions: rock (RO), sand (SA), coral (CO), turf (TU), macroalgaes (MA), other sesile invertebrates (OT). Larger circles of darker color indicate a higher percentatge of contribution.

Table S3. Comparison of sums of squares and distance based multivariate regression trees (MRT) of elasmobranch relative abundance (MaxN) at Cocos Island explained by the set of predictor variables included in this study. Relative error (RE), cross-validated error (CVRE) and the percentage of species variance explained by each tree allowed the selection of the best MRT (highlighted in bold). The number of terminal nodes and the main predictor variables used to split the elasmobranch community in each MRT are also shown. Numbers next to some of the variables indicate the number of times each variable was used on that tree. The selection process of each MRT was based on the minimum CVRE, except for the last tree which was 1 SE from the tree size with the minimum CVRE (Fig S4).

Types of MRT		RE	CVRE	Variance	Clusters	Predictors
Sums of squares MRT	Raw data	0.53	5.16	47.39 %	3	Distance; PC1
	Chord transformed data	0.61	0.77	37.17 %	8	Distance ^{3}; Depth; Habitat ^{2}; Location;
	Hellinger transformed data	0.72	0.78	28.06%	4	Distance; Depth; Habitat
Distance-based MRT	Chord distance-based matrix	0.67	0.71	32.88 %	3	Distance; Depth
	Hellinger distance-based matrix	0.60	0.68	40.1 %	5	Distance ^{2}; Depth; Habitat
	Bray-Curtis distance-based matrix (log-transformed)	0.59	0.67	41 %	5	Distance ^{2}; Depth; Habitat
	Bray-Curtis distance-based matrix (log-transformed) *CRVE + 1 SE*	**0.57**	**0.68**	**42.47%**	**6**	**Distance ^{2};** **Depth;** **Temperature;** **Habitat;**

Chord (abundance data normalized to length 1) and Hellinger (square-root of standardized abundance values) transformations were applied to the species matrix and then used in SS-MRT (Legendre & Gallagher, 2001). These pre-transformations expressed the data as relative abundances per sites and are appropriate alternatives giving low weights to rare species (Legendre & Gallagher 2001, Borcard et al. 2011). Raw abundance data was also used in SS-MRT for the comparison with pre-transformed data. Three types of db-MRTs were performed using Euclidean and Bray-Curtis distances on a MaxN species matrix. The calculation of Euclidean distances preceded the Chord and Hellinger transformations in order to preserve the asymmetrical distance among sites (i.e. treat double zeroes as indicators of dissimilarity among sites) (Legendre & Gallagher, 2001). The Bray-Curtis db-MRT was performed on a log1p transformed abundance data (natural logarithm of abundance plus 1 to keep absence as zero) in order to reduce the importance of observations with very high values and to normalize a strongly right-skewed abundance data (Legendre & Gallagher 2001).

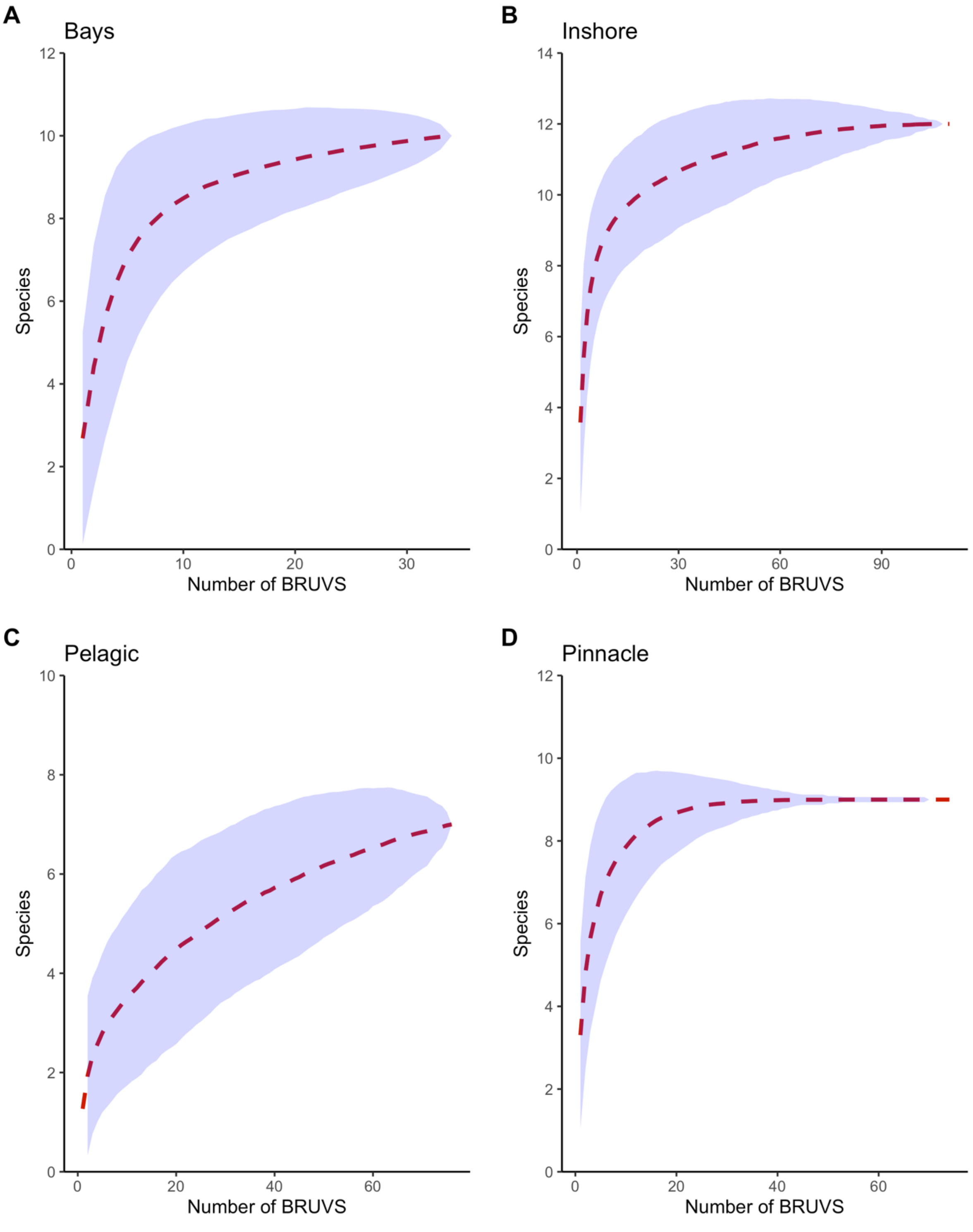

Fig. S3 Species accumulation curves per habitat over the number of Baited Remote Underwater Video Stations deployed at Cocos Island. Shaded colors represent 95% confidence intervals.

Table S4. Sum of relative abundance per hour (MaxN hr^{-1}) for each elasmobranch species by season, location and habitat captured by Baited Remote Underwater Video Stations (BRUVS) at Cocos Island. The total soak time (hrs) per season, location and habitat are also represented. Species are ranked by total sum of relative abundance (MaxN). The colour pattern degrades from dark colours (high abundance) to pale colours (low abundance).

Env	**Species**	**SEASON**		**LOCATION**		**HABITAT**			
		Dry	**Rainy**	**North**	**South**	**Bay**	**Inshore**	**Pinnacle**	**Pelagic**
Benthic	*Triaenodon obesus*	260.91	316.07	347.28	229.69	69.50	314.82	192.65	0
	Sphyrna lewini	62.66	380.43	332.33	110.77	15.38	110.44	317.28	115.55
	Carcharhinus galapagensis	28.84	87.32	69.86	46.30	5.31	81.80	29.06	4.87
	Carcharhinus albimarginatus	44.88	56.26	46.96	54.18	20.58	66.67	13.89	0.61
	Taeniurus meyeni	46.68	39.42	53.97	32.13	8.24	30.80	47.06	0
	Galeocerdo cuvier	24.94	48.80	42.72	31.01	10.11	38.64	24.99	1.34
	Carcharhinus limbatus	14.42	26.54	18.45	20.65	4.28	27.93	6.89	1.86
	Carcharhinus melanopterus	17.70	11.92	21.53	8.08	9.90	19.72	0	0
	Carcharhinus falciformis	7.2	16.23	8.53	14.89	0.80	15.60	7.04	49.20
	Aetobatus laticeps	4.20	6.94	5.30	5.83	1.50	5.13	4.50	0
	Mobula birostris	0	1.28	0	1.28	0	1.28	0	0
	Mobula tarapacana	0	1.51	1.51	0	0	1.51	0	0
Pelagic	*Sphyrna lewini*	65.98	49.57	17.87	97.67*	443.09			115.55
	Carcharhinus falciformis	10.91	38.28	33.69	15.50	23.43			49.20
	Carcharhinus galapagensis	2.53	2.33	2.90	1.97	116.17			4.87
	Carcharhinus limbatus	0.60	1.26	1.13	0.73	39.10			1.86
	Galeocerdo cuvier	0.72	0.62	1.34	0	73.73			1.34
	Alopias pelagicus	0	0.72	0.72	0	0			0.72
	Carcharhinus albimarginatus	0	0.61	0	0.61	101.14			0.61
TOTAL MaxN hr^{-1}		592.6	1084.9	1006.1	671.3	145.6	714.3	643.3	174.1
TOTAL SOAK TIME (hrs)		173.9	259.9	236.8	196.9	48.1	155	125.1	105.6

Sum MaxN hr^{-1}

> 200
100 - 200
50 - 100
26 - 50
1 - 25
0 - 0.9

Table S5. Mean, minimum and maximum values of temperature, bottom depth and minimum distance to the coast at which elasmobranch species were detected by Baited Remote Underwater Video Stations (BRUVS) in benthic and pelagic environments (Env) of Cocos Island.

Env	**Species**	**Depth (m)**			**Temperature (ºC)**			**Distance (km)**		
		Mean ± SD	**Min**	**Max**	**Mean ± SD**	**Min**	**Max**	**Mean ± SD**	**Min**	**Max**
Benthic	*Triaenodon obesus*	18.7 ± 9.4	2	41	26.6 ± 1.9	18.4	29.1	0.33 ± 0.37	0.01	1.60
	Sphyrna lewini	22 ± 9.6	3	49	26.3 ± 2.1	19	29.8	0.40 ± 0.39	0.01	1.63
	Carcharhinus galapagensis	23.1 ± 7.8	6	41	25.8 ± 2.3	18.4	29.8	0.39 ± 0.42	0.01	1.63
	Carcharhinus albimarginatus	23.6 ± 9	6	60	26.1 ± 2.1	18.5	28.9	0.24 ± 0.17	0.01	0.93
	Taeniurus meyeni	22.8 ± 9.7	2	49	26.1 ± 2.1	18.4	28.7	0.34 ± 0.35	0.01	1.50
	Galeocerdo cuvier	21.5 ± 10.1	5	60	26.2 ± 2	19.3	28.9	0.31 ± 0.29	0.01	1.60
	Carcharhinus limbatus	21.3 ± 10.1	3	49	26.1 ± 2.4	18.5	28.9	0.29 ± 0.23	0.01	0.95
	Carcharhinus melanopterus	10.9 ± 5.6	2	24	27.7 ± 1.1	23.6	29.1	0.10 ± 0.08	0.01	0.29
	Carcharhinus falciformis	26.2 ± 11.1	7	60	25.7 ± 2.1	19.7	28.3	0.40 ± 0.38	0.04	1.50
	Aetobatus laticeps	19.5 ± 11.7	2	40	26.5 ± 1.5	22.9	28.4	0.19 ± 0.09	0.08	0.35
	Mobula birostris	12 ± 2.8	10	14	26.5 ± 1.1	25.7	27.3	0.03	0.03	0.04
	Mobula tarapacana	11.1 ± 3.4	9	13.5	26.2 ± 0.2	26.1	26.4	0.07	0.07	0.07
Pelagic	*Sphyrna lewini*	215 ± 169	87	740	27.6 ± 0.7	26.2	28.6	3.94 ± 1.20	2.39	6.89
	Carcharhinus falciformis	219 ± 241	84	1000	27.6 ± 0.7	26.2	28.6	3.82 ± 0.86	2.00	6.89
	Carcharhinus galapagensis	227 ± 178	87	500	28.1 ± 0.4	27.7	28.4	3.85 ± 0.89	3.10	5.36
	Carcharhinus limbatus	92 ± 3	88	95	27.5 ± 1.1	26.2	28.5	3.20 ± 0.87	2.39	4.12
	Galeocerdo cuvier	102 ± 3	100	104	27.3 ± 1.2	26.5	28.2	4.32 ± 0.68	3.84	4.80
	Alopias pelagicus	390	390	390	27.6	27.6	27.6	6.52	6.52	6.52
	Carcharhinus albimarginatus	96	96	96	26.2	26.2	26.2	2.73	2.73	2.73

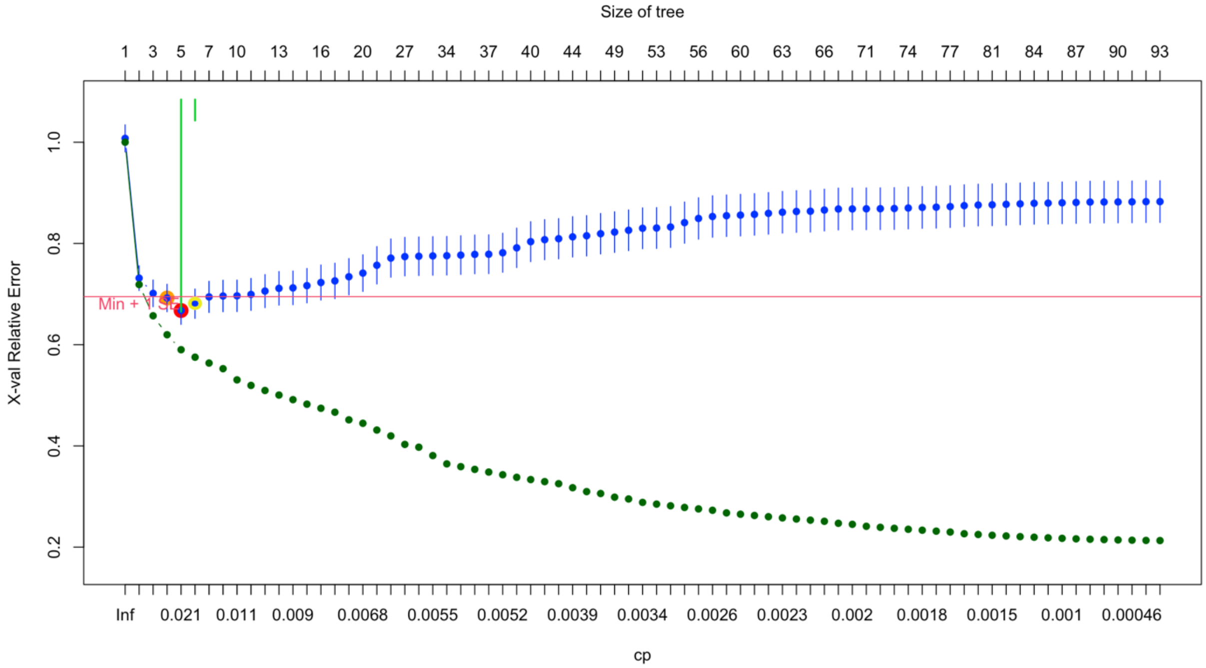

Fig. S4 Graph of the possible tree sizes solutions resulting from a Bray Curtis distance-based Multivariate Regression Tree with log-transformed relative abundance (MaxN). For each solution the relative error RE (green dots) and the cross-validated relative error CVRE (blue dots) with its associated standard error SE (blue lines) are shown. The solution with the smallest CVRE is considered the best fitting model and is indicated with the red point. The smallest tree with a CVRE within 1SE of the best fitting model is indicated with an orange point (Borcard et al. 2011). The tree size selected in this study is indicated with a yellow point.

Table S6. Results from likelihood ratio test to compare between negative binomial and poisson distributions in Generalized Additive Mixed Models (GAMMs) to model the effect of natural drivers on the relative abundance (MaxN) of elasmobranch species at benthic and pelagic environments

Env	Species	Df	LogLik	Df	Chisq	p
Benthic	*Triaenodon obesus*	44.79	-431.98			
		10.98	-466.57	-33.9	69.20	<0.001***
	Sphyrna lewini	58.89	-348.53			
		33.58	-334.95	-25.31	27.16	0.35
	Carcharhinus albimarginatus	34.85	-164.87			
		13.50	-191.83	-21.35	53.92	<0.001***
	Carcharhinus galapagensis	40.54	-176.42			
		23.85	-208.76	-16.69	64.70	<0.001***
	Galeocerdo cuvier	14.54	-169.4			
		9.46	-186.32	-5.08	22.57	<0.001***
	Taeniurops meyeni	11.78	-185.56			
		10.06	-195.04	-1.73	18.96	<0.001***
Pelagic	*Sphyrna lewini*	24.04	-128.58			
		14.26	-117.27	-9.78	22.63	0.012 *
	Carcharhinus falciformis	6.85	87.91			
		6.17	-89.95	-0.67	4.07	0.04 *

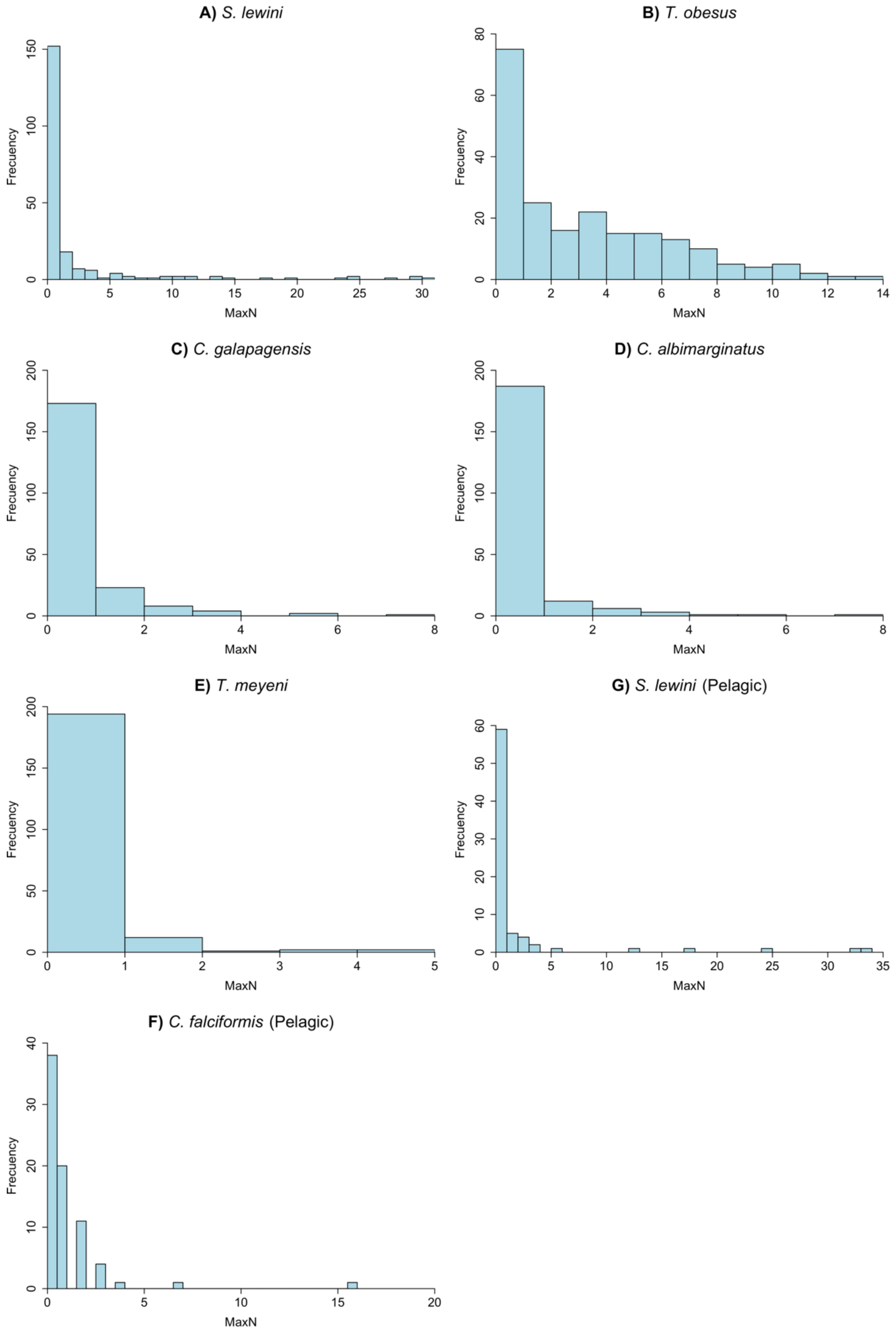

Fig. S5 Frequency of relative abundance (MaxN) values recorded in Baited Remote Underwater Video Stations (BRUVS) of each species.

Table S7. Candidate Generalized Additive Mixed Models (GAMMs) for predicting the relative abundance (MaxN) of six elasmobranch species against a set of predictor variables measured in benthic and pelagic environments of Cocos Island. The difference between the lowest reported Akaike Information Criterion corrected for small sample size (AICc), AICc weights (wAICc), variance explained (R^2), adjusted variance explained ($adjR^2$) and estimated degrees of freedom (DF) are reported for model comparison. Candidate models are ranked based on AICc. Only candidate models with delta AICc < 2 are shown per each elasmobranch species. The most parsimonious model is shown in orange and was defined as the model that contains the fewest variables within two units of the lowest AICc. The relative importance of each predictor variable is calculated based on the sum of the wAICc from the 95% confidence set of models (not shown here).

1) *TRIAENODON OBESUS*

(Intercept)	Location	Depth	Distance	Temperature	PC1	PC2	PC3	Season	Deployment	offset(Lhrs)	adjR^2	R^2	DF	LogLik	AICc	delta AICc	Weight
1.049	NA	+	+	+	+	NA	+	NA	+	NA	0.274	0.272	7	-466.690	949.428	0.000	0.029
1.049	NA	+	+	+	+	NA	+	NA	NA	NA	0.274	0.272	7	-466.689	949.428	0.000	0.029
1.198	NA	+	+	NA	+	NA	+	+	+	NA	0.273	0.271	7	-466.856	949.746	0.319	0.025
1.198	NA	+	+	NA	+	NA	+	+	NA	NA	0.273	0.271	7	-466.856	949.747	0.319	0.025
1.057	NA	NA	+	+	+	NA	+	NA	NA	NA	0.265	0.263	6	-467.901	949.883	0.455	0.023
1.057	NA	NA	+	+	+	NA	+	NA	+	NA	0.265	0.263	6	-467.902	949.883	0.455	0.023
1.058	NA	+	+	NA	+	NA	+	NA	NA	NA	0.266	0.264	6	-467.784	949.887	0.460	0.023
1.058	NA	+	+	NA	+	NA	+	NA	+	NA	0.266	0.264	6	-467.784	949.888	0.461	0.023
1.056	NA	+	+	+	+	NA	NA	NA	NA	NA	0.266	0.263	6	-467.874	950.296	0.869	0.019
1.056	NA	+	+	+	+	NA	NA	NA	+	NA	0.266	0.263	6	-467.874	950.297	0.869	0.019
0.957	+	+	+	+	+	NA	+	NA	NA	NA	0.278	0.276	8	-466.050	950.324	0.896	0.019
0.957	+	+	+	+	+	NA	+	NA	+	NA	0.278	0.276	8	-466.051	950.324	0.896	0.019
1.154	NA	+	+	+	+	NA	+	+	NA	NA	0.278	0.275	8	-466.152	950.536	1.109	0.017
1.154	NA	+	+	+	+	NA	+	+	+	NA	0.278	0.275	8	-466.152	950.537	1.110	0.017
0.964	+	NA	+	+	+	NA	+	NA	+	NA	0.270	0.268	7	-467.254	950.742	1.315	0.015
0.964	+	NA	+	+	+	NA	+	NA	NA	NA	0.270	0.268	7	-467.251	950.744	1.316	0.015
1.126	+	+	+	NA	+	NA	+	+	+	NA	0.276	0.274	8	-466.425	951.049	1.622	0.013
1.125	+	+	+	NA	+	NA	+	+	NA	NA	0.276	0.274	8	-466.425	951.049	1.622	0.013
1.213	NA	+	+	NA	+	NA	NA	+	+	NA	0.260	0.258	6	-468.653	951.230	1.802	0.012
1.213	NA	+	+	NA	+	NA	NA	+	NA	NA	0.260	0.258	6	-468.651	951.231	1.803	0.012
0.985	+	+	+	NA	+	NA	+	NA	+	NA	0.270	0.268	8	-467.274	951.293	1.865	0.012
0.985	+	+	+	NA	+	NA	+	NA	NA	NA	0.270	0.268	8	-467.273	951.294	1.866	0.012
1.158	NA	+	+	+	+	NA	NA	+	+	NA	0.267	0.265	7	-467.617	951.340	1.912	0.011
1.158	NA	+	+	+	+	NA	NA	+	NA	NA	0.267	0.265	7	-467.615	951.341	1.913	0.011
Relative importance	**0.31**	**0.70**	**0.91**	**0.59**	**0.95**	**0.20**	**0.69**	**0.42**	**0.48**	**0.12**					**Cumulative wAICc**		**0.95**

Total candidate models within the 95% confidence set	**194**
Total candidate models with delta AIC <2	**24**

2) *SPHYRNA LEWINI* (Benthic)

(Intercept)	Location	Depth	Distance	Temperature	PC1	PC2	PC3	Season	Deployment	offset(Lhrs)	adjR^2	R^2	DF	LogLik	AICc	delta AICc	Weight
-0.070	+	NA	+	NA	NA	NA	NA	+	+	NA	0.658	0.648	28	-332.149	729.426	0.000	0.105
-0.128	+	NA	+	+	NA	NA	NA	+	+	NA	0.658	0.648	28	-332.161	729.489	0.063	0.102
-0.112	+	NA	+	+	NA	NA	+	+	+	NA	0.647	0.637	25	-335.260	729.567	0.141	0.098
-0.058	+	NA	+	NA	NA	+	NA	+	+	NA	0.660	0.651	29	-331.325	730.860	1.433	0.051
-0.041	+	NA	+	NA	NA	NA	+	+	+	NA	0.648	0.638	26	-335.057	730.872	1.446	0.051
-0.095	+	NA	+	+	NA	+	+	+	+	NA	0.649	0.639	26	-334.755	731.286	1.860	0.042
-0.115	+	NA	+	+	NA	+	NA	+	+	NA	0.659	0.650	29	-331.619	731.309	1.883	0.041
-0.126	+	NA	+	+	+	NA	+	+	+	NA	0.649	0.639	26	-334.723	731.389	1.963	0.039
Relative importance	**0.89**	**0.08**	**0.91**	**0.55**	**0.19**	**0.30**	**0.38**	**0.94**	**0.92**	**0.11**				**Cumulative wAICc**			**0.95**

Total candidate models within the 95% confidence set	**61**
Total candidate models with delta AIC <2	**8**

3) *CARCHARHINUS GALAPAGENSIS*

(Intercept)	Location	Depth	Distance	Temperature	PC1	PC2	PC3	Season	Deployment	offset(Lhrs)	adjR^2	R^2	DF	LogLik	AICc	delta AICc	Weight
-0.925	+	+	NA	+	NA	NA	NA	+	NA	NA	0.241	0.217	6	-218.301	450.248	0.000	0.065
-1.053	NA	+	NA	+	NA	NA	NA	+	NA	NA	0.230	0.208	5	-219.603	450.688	0.441	0.052
-0.970	+	+	NA	+	+	NA	NA	+	NA	NA	0.245	0.221	7	-217.878	451.481	1.234	0.035
-0.921	+	+	NA	+	NA	NA	+	+	NA	NA	0.252	0.227	8	-216.952	451.708	1.460	0.031
-1.097	NA	+	NA	+	+	NA	NA	+	NA	NA	0.234	0.211	6	-219.132	451.794	1.547	0.030
-1.042	NA	+	NA	+	NA	NA	+	+	NA	NA	0.243	0.219	7	-218.036	451.807	1.559	0.030
-0.938	+	+	NA	+	NA	+	NA	+	NA	NA	0.242	0.219	7	-218.156	452.060	1.812	0.026
-1.060	NA	+	NA	+	NA	+	NA	+	NA	NA	0.233	0.210	6	-219.333	452.217	1.969	0.024
Relative importance	**0.51**	**0.95**	**0.24**	**0.69**	**0.36**	**0.27**	**0.32**	**0.89**	**0.10**	**0.05**				**Cumulative wAICc**			**0.95**

Total candidate models within the 95% confidence set	163
Total candidate models with delta AIC <2	8

4) *CARCHARHINUS ALBIMARGINATUS*

(Intercept)	Location	Depth	Distance	Temperature	PC1	PC2	PC3	Season	Deployment	offset(Lhrs)	adjR^2	R^2	DF	LogLik	AICc	delta AICc	Weight
-1.255	+	+	+	NA	+	NA	NA	NA	+	NA	0.291	0.254	8	-187.837	393.030	0.000	0.051
-1.255	+	+	+	NA	+	NA	NA	NA	NA	NA	0.291	0.254	8	-187.837	393.030	0.000	0.051
-1.479	+	+	+	NA	+	NA	NA	+	+	NA	0.298	0.261	9	-186.913	393.418	0.388	0.042
-1.479	+	+	+	NA	+	NA	NA	+	NA	NA	0.298	0.261	9	-186.913	393.418	0.388	0.042
-1.036	NA	+	+	NA	+	NA	NA	NA	+	NA	0.280	0.245	7	-189.199	393.743	0.713	0.036
-1.036	NA	+	+	NA	+	NA	NA	NA	NA	NA	0.280	0.244	7	-189.199	393.743	0.713	0.036
-1.245	NA	+	+	NA	+	NA	NA	+	+	NA	0.287	0.251	8	-188.329	394.218	1.188	0.028
-1.245	NA	+	+	NA	+	NA	NA	+	NA	NA	0.287	0.251	8	-188.329	394.218	1.188	0.028
Relative importance	**0.55**	**0.95**	**0.95**	**0.22**	**0.74**	**0.21**	**0.23**	**0.41**	**0.47**	**0**					**Cumulative wAICc**		**0.95**

Total candidate models within the 95% confidence set	**93**
Total candidate models with delta AIC <2	**8**

5) *TAENIUROPS MEYENI*

(Intercept)	Location	Depth	Distance	Temperature	PC1	PC2	PC3	Season	Deployment	offset(Lhrs)	adjR^2	R^2	DF	LogLik	AICc	delta AICc	Weight
-0.766	NA	+	NA	NA	NA	NA	NA	NA	NA	NA	0.087	0.075	2	-198.152	400.361	0.000	0.022
-0.766	NA	+	NA	NA	NA	NA	NA	NA	+	NA	0.087	0.075	2	-198.151	400.361	0.000	0.022
-0.618	NA	+	NA	NA	NA	NA	NA	+	NA	NA	0.093	0.080	3	-197.550	401.217	0.856	0.014
-0.618	NA	+	NA	NA	NA	NA	NA	+	+	NA	0.093	0.080	3	-197.550	401.217	0.856	0.014
-0.902	NA	+	NA	NA	NA	+	NA	+	NA	+	0.115	0.099	5	-195.374	401.481	1.120	0.012
-0.902	NA	+	NA	NA	NA	+	NA	+	+	+	0.115	0.099	5	-195.373	401.481	1.120	0.012
-0.770	NA	+	NA	+	NA	NA	NA	NA	NA	NA	0.090	0.077	3	-197.886	401.889	1.528	0.010
-0.770	NA	+	NA	+	NA	NA	NA	NA	+	NA	0.090	0.077	3	-197.886	401.889	1.528	0.010
-0.708	+	+	NA	NA	NA	NA	NA	NA	NA	NA	0.089	0.076	3	-197.995	402.107	1.746	0.009
-0.708	+	+	NA	NA	NA	NA	NA	NA	+	NA	0.089	0.076	3	-197.995	402.107	1.746	0.009
-0.770	NA	+	NA	NA	NA	+	NA	NA	NA	NA	0.091	0.078	3	-197.756	402.108	1.747	0.009
-0.770	NA	+	NA	NA	NA	+	NA	NA	+	NA	0.091	0.078	3	-197.756	402.109	1.748	0.009
-0.767	NA	+	NA	NA	NA	NA	+	NA	NA	NA	0.088	0.076	3	-198.042	402.202	1.841	0.009
-0.767	NA	+	NA	NA	NA	NA	+	NA	+	NA	0.088	0.076	3	-198.042	402.202	1.841	0.009
-1.100	NA	+	NA	NA	NA	NA	NA	NA	NA	+	0.077	0.067	2	-199.076	402.209	1.848	0.009
-1.100	NA	+	NA	NA	NA	NA	NA	NA	+	+	0.077	0.067	2	-199.075	402.210	1.849	0.009
-0.905	NA	+	NA	NA	NA	NA	NA	+	NA	+	0.088	0.075	3	-198.071	402.257	1.896	0.008
-0.905	NA	+	NA	NA	NA	NA	NA	+	+	+	0.088	0.075	3	-198.070	402.258	1.897	0.008
-1.116	NA	+	NA	NA	NA	+	NA	NA	NA	+	0.098	0.085	4	-197.022	402.302	1.941	0.008
-1.116	NA	+	NA	NA	NA	+	NA	NA	+	+	0.098	0.085	4	-197.021	402.303	1.942	0.008
-0.767	NA	+	+	NA	NA	NA	NA	NA	NA	NA	0.087	0.075	3	-198.118	402.353	1.992	0.008
-0.767	NA	+	+	NA	NA	NA	NA	NA	+	NA	0.087	0.075	3	-198.118	402.353	1.992	0.008
Relative importance	**0.08**	**0.46**	**0.04**	**0.07**	**0.04**	**0.15**	**0.06**	**0.21**	**0.22**	**0.20**				**Cumulative wAICc**			**0.46**

Total candidate models within the 95% confidence set	**63**
Total candidate models with delta AIC <2	**22**

6) *SPHYRNA LEWINI* (Pelagic)

(Intercept)	Location	Depth	Distance	Temperature	Season	Deployment	offset(Lhrs)	adjR^2	R^2	DF	LogLik	AICc	delta AICc	Weight
-0.917	+	+	+	+	NA	NA	NA	0.587	0.578	6	-124.354	262.896	0.000	0.090
-0.877	+	+	+	NA	NA	+	NA	0.709	0.698	15	-111.650	263.130	0.233	0.080
-0.434	NA	NA	NA	NA	NA	+	+	0.723	0.711	16	-109.878	263.259	0.363	0.075
0.057	NA	NA	NA	NA	NA	+	NA	0.721	0.710	16	-110.081	263.388	0.492	0.070
-1.370	+	+	+	NA	NA	+	+	0.710	0.698	15	-111.564	263.713	0.817	0.060
-0.564	+	NA	NA	NA	NA	+	NA	0.699	0.688	15	-112.832	263.743	0.847	0.059
-1.071	+	NA	NA	NA	NA	+	+	0.699	0.688	15	-112.812	263.915	1.019	0.054
-0.302	NA	NA	NA	NA	+	+	+	0.721	0.710	17	-110.081	264.886	1.990	0.033
Relative importance	**0.52**	**0.52**	**0.43**	**0.29**	**0.21**	**0.79**	**0.41**				**Cumulative wAICc**			**0.95**

Total candidate models within the 95% confidence set	**39**
Total candidate models with delta AIC <2	**8**

7) ***CARCHARHINUS FALCIFORMIS*** (Pelagic)

(Intercept)	Location	Depth	Distance	Temperature	Season	Deployment	offset(Lhrs)	adjR^2	R^2	DF	LogLik	AICc	delta AICc	Weight
-0.796	NA	+	+	NA	NA	+	+	0.149	0.138	3	-91.113	188.564	0.000	0.046
-0.796	NA	+	+	NA	NA	NA	+	0.149	0.138	3	-91.113	188.564	0.000	0.046
-0.749	NA	+	NA	NA	NA	NA	+	0.118	0.109	2	-92.337	188.841	0.278	0.040
-0.749	NA	+	NA	NA	NA	+	+	0.118	0.109	2	-92.337	188.841	0.278	0.040
-0.543	+	+	NA	NA	NA	NA	+	0.142	0.132	3	-91.390	189.119	0.555	0.035
-0.543	+	+	NA	NA	NA	+	+	0.142	0.132	3	-91.390	189.119	0.555	0.035
-0.803	NA	+	+	+	NA	+	+	0.162	0.150	4	-90.587	189.745	1.182	0.025
-0.803	NA	+	+	+	NA	NA	+	0.162	0.150	4	-90.587	189.746	1.182	0.025
-1.031	NA	+	NA	NA	+	NA	+	0.134	0.124	3	-91.715	189.768	1.204	0.025
-1.031	NA	+	NA	NA	+	+	+	0.134	0.124	3	-91.715	189.768	1.204	0.025
-0.758	NA	+	NA	+	NA	NA	+	0.132	0.122	3	-91.800	189.939	1.375	0.023
-0.758	NA	+	NA	+	NA	+	+	0.132	0.122	3	-91.800	189.939	1.375	0.023
-0.644	+	+	+	NA	NA	+	+	0.159	0.147	4	-90.715	190.003	1.439	0.022
-0.644	+	+	+	NA	NA	NA	+	0.159	0.147	4	-90.715	190.003	1.439	0.022
-1.012	NA	+	+	NA	+	+	+	0.159	0.147	4	-90.724	190.069	1.505	0.022
-1.012	NA	+	+	NA	+	NA	+	0.159	0.147	4	-90.720	190.071	1.507	0.022
-0.540	+	+	NA	+	NA	NA	+	0.158	0.146	4	-90.754	190.080	1.516	0.022
-0.540	+	+	NA	+	NA	+	+	0.158	0.146	4	-90.754	190.080	1.516	0.022
-0.822	+	+	NA	NA	+	NA	+	0.157	0.145	4	-90.804	190.179	1.616	0.021
-0.822	+	+	NA	NA	+	+	+	0.157	0.145	4	-90.804	190.179	1.616	0.021
-0.722	NA	NA	+	NA	NA	+	+	0.097	0.089	2	-93.177	190.522	1.958	0.017
-0.722	NA	NA	+	NA	NA	NA	+	0.097	0.089	2	-93.177	190.522	1.958	0.017
Relative importance	**0.35**	**0.79**	**0.47**	**0.30**	**0.27**	**0.48**	**0.81**				**Cumulative wAICc**			**0.95**

Total candidate models within the 95% confidence set	**80**
Total candidate models with delta AIC <2	**22**

CAPÍTULO 2

A first assessment of the distribution and abundance of large pelagic species at Cocos Ridge seamounts (Eastern Tropical Pacific) using drifting pelagic baited remote cameras

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ABSTRACT

Understanding the link between seamounts and large pelagic species (LPS) may provide important insights for the conservation of these species in open water ecosystems. The seamounts along the Cocos Ridge in the Eastern Tropical Pacific (ETP) ocean are thought to be ecologically important aggregation sites for LPS when moving between Cocos Island (Costa Rica) and Galapagos Islands (Ecuador). However, to date, research efforts to quantify the abundance and distribution patterns of LPS beyond the borders of these two oceanic Marine Protected Areas (MPAs) have been limited. This study used drifting-pelagic baited remote underwater video stations (BRUVS) to investigate the distribution and relative abundance of LPS at Cocos Ridge seamounts. Our drifting-pelagic BRUVS recorded a total of 21 species including elasmobranchs, small and large teleosts, dolphins and one sea turtle; of which four species are currently threatened. Depth of seamount summit was the most significant driver for LPS richness and abundance which were significantly higher at shallow seamounts (< 400 m) compared to deeper ones (> 400m). Distance to nearest MPA was also a significant predictor for LPS abundance, which increased at increasing distances from the nearest MPA. Our results suggest that the Cocos Ridge seamounts, specifically Paramount and West Cocos which had the highest LPS richness and abundance, are important aggregation sites for LPS in the ETP. However, further research is still needed to demonstrate a positive association between LPS and Cocos Ridge seamounts. Our findings showed that drifting pelagic BRUVS are an effective tool to survey LPS in fully pelagic ecosystems of the ETP. This study represents the first step towards the standardization of this technique throughout the region.

INTRODUCTION

Quantifying the spatial distribution and abundance of pelagic species (hereafter referred to as species that spend the majority of their lives inhabiting the upper layers of the water column in oceanic waters) is critical to effectively manage and protect their populations in the open oceans (Worm et al. 2003, 2005, McCauley et al. 2015). Overexploitation of the open ocean by industrial fisheries is driving many large pelagic species (LPS) (reported common length in Froese & Pauly (2022) > 1m) such as elasmobranchs, teleosts, sea turtles and cetaceans to dangerously low levels (Myers & Worm 2003, McCauley et al. 2015), raising global concerns about the potential top-downs effects on marine ecosystems (Dulvy et al. 2004, Ruppert et al. 2013). Seamounts have been recognized as productive and unique features in open water-systems where highly migratory LPS tend to aggregate, thus becoming vulnerable areas to overfishing (Morato et al. 2006, 2010). Understanding the link between seamounts and LPS may be fundamental to identify regional hotspots of biological production, and therefore, to guide management and conservation efforts in open water ecosystems (Taranto et al. 2012).

The Cocos Ridge is a chain of seamounts in the Eastern Tropical Pacific (ETP) ocean that connects Cocos Island (Costa Rica) and the Galapagos archipelago (Ecuador) (Fig. 1) (Walther 2003). These two oceanic island groups are considered biodiversity hotspots in the ETP because of their high apex predator biomass (Hearn et al. 2010, Friedlander et al. 2012). They are also important no-take Marine Protected Areas (MPAs) and UNESCO World Heritage Sites within the ETP (Dirección del Parque Nacional Galápagos 2014, SINAC 2016). Previous studies have shown a higher degree of movement connectivity between Cocos and Galapagos Islands relative to other regions of the ETP, suggesting that LPS may be using this area as a migratory corridor (Bessudo et al. 2011, Ketchum et al. 2014b, Acuña-Marrero et al. 2017, Peñaherrera-Palma et al. 2018, Nalesso et al. 2019). The Cocos Ridge seamounts are thought to be ecologically important aggregation sites for LPS during their migratory movements between both MPAs (Peñaherrera-Palma et al. 2018). However, most research effort on LPS in the ETP have concentrated inside MPAs (Soler et al. 2013, Hearn et al. 2014b, White et al. 2015, Acuña-Marrero et al. 2018), and there is currently limited information available on the role that seamounts play on the population structure and dynamics of LPS in this region (although see Chávez et al., (2020)).

As populations of LPS continue to decrease in the ETP (Soler et al. 2013, White et al. 2015), there is a greater need to survey the pelagic ecosystem beyond the borders of MPAs to effectively guide marine spatial planning (Secretariat of the Convention on Biological Diversity 2009, Peñaherrera-Palma et al. 2018). Information outside the protection boundaries of Cocos and Galapagos Islands is scarce and restricted to fishery dependent data (Martínez-Rincón 2012, Dapp et al. 2013, Martínez-Ortiz et al. 2015) or to movement studies on sharks (Bessudo et al. 2011, Ketchum et al. 2014b, Acuña-Marrero et al. 2017, Nalesso et al. 2019, Chávez et al. 2020), teleosts (Domeier 2006) and sea turtles (Seminoff et al. 2008, Shillinger et al. 2011). Despite the valuable information acquired from biotelemetry to understand individual habitat preferences, movements and migrations, this technique relies on the catch of a high number of individuals from various species in order to understand how the pelagic community is distributed in the open ocean (Hussey et al. 2015). Furthermore, such studies can be invasive, expensive and logistically challenging (Letessier et al. 2013). Fisheries data also present some limitations as they are usually biased by temporally and spatially uneven sampling effort, gear selectivity and lack of robust reports (Schnute & Richards 2001, Hilborn et al. 2020).

Drifting-pelagic baited remote underwater video stations (BRUVS) have demonstrated a promising potential for studying pelagic wildlife in open water ecosystems (Bouchet & Meeuwig 2015, Bouchet et al. 2018, Letessier et al. 2019). Drifting-pelagic BRUVS are an adaptation of the benthic BRUVS where an anchoring system is no longer needed, thus enabling dynamic sampling over deep and topographically complex pelagic areas (Bouchet & Meeuwig 2015). The odor of the bait triggers bait-search behavior in nearby fish assemblages, increasing the probability of detecting predatory species in the vicinity of the BRUVS (Cappo et al. 2004). A reduced amount of zeros (i.e. less absences from count data) derived from bait use increases the statistical power of BRUVS compared to traditional survey techniques (Kingsford 1999, Langlois et al. 2010, Rees et al. 2015). Although studies using drifting-pelagic BRUVS are scarce (Bouchet & Meeuwig 2015, Letessier et al. 2017, 2019), this technique offers a powerful framework to overcome the difficulties associated to effectively survey pelagic assemblages (Bouchet et al. 2018). For example, drifting-pelagic BRUVS units can be simultaneously deployed reducing the survey effort while generating permanent high-definition images on species composition, behavior and relative abundance at different depth levels and for long periods of time (Bouchet & Meeuwig 2015). Additionally, they are affordable and easy to operate allowing the participation of non-expert stakeholders into field work. In this study, we used drifting-pelagic BRUVS for the first time in offshore waters of the ETP to investigate the distribution and relative abundance of LPS at Cocos Ridge seamounts. This study may serve as an important baseline reference on the future use of drifting-pelagic BRUVS at a regional level.

METHODOLOGY

Study area

The Cocos Ridge is an underwater mountain range located in the Northwestern Panama basin of the ETP, which originated more than 30 million years ago as a result of volcanic activity from the Galapagos Ridge hot spot (Walther 2003). The Cocos Ridge rises about 2000 m above the seafloor and extends more than 1000 km from the Galapagos Islands to Cocos Island, and from Cocos Island to the Pacific coast of Costa Rica (Walther 2003, Lizano 2012b, Rojas & Alvarado 2012). Although the depth and total number of seamounts along the Cocos Ridge is not available on global bathymetric databases, there are at least 14 seamounts that have been identified in this region (Lizano 2012b, Peñaherrera-Palma et al. 2018). All the seamounts along the Cocos Ridge are located within the Exclusive Economic Zones (EEZs) of either Ecuador or Costa Rica (Fig. 1).

The variable and dynamic oceanographic conditions surrounding the waters of Cocos Ridge seamounts are mainly attributed to the southern oscillation of the Intertropical Convergence Zone, which is also associated to seasonal changes on wind patterns and the convergence of different ocean currents (Lizano 2008b, Peñaherrera-Palma et al. 2018). The North Equatorial Current (east – west), the South Equatorial Current (east – west) and the Equatorial Countercurrent (west – east)

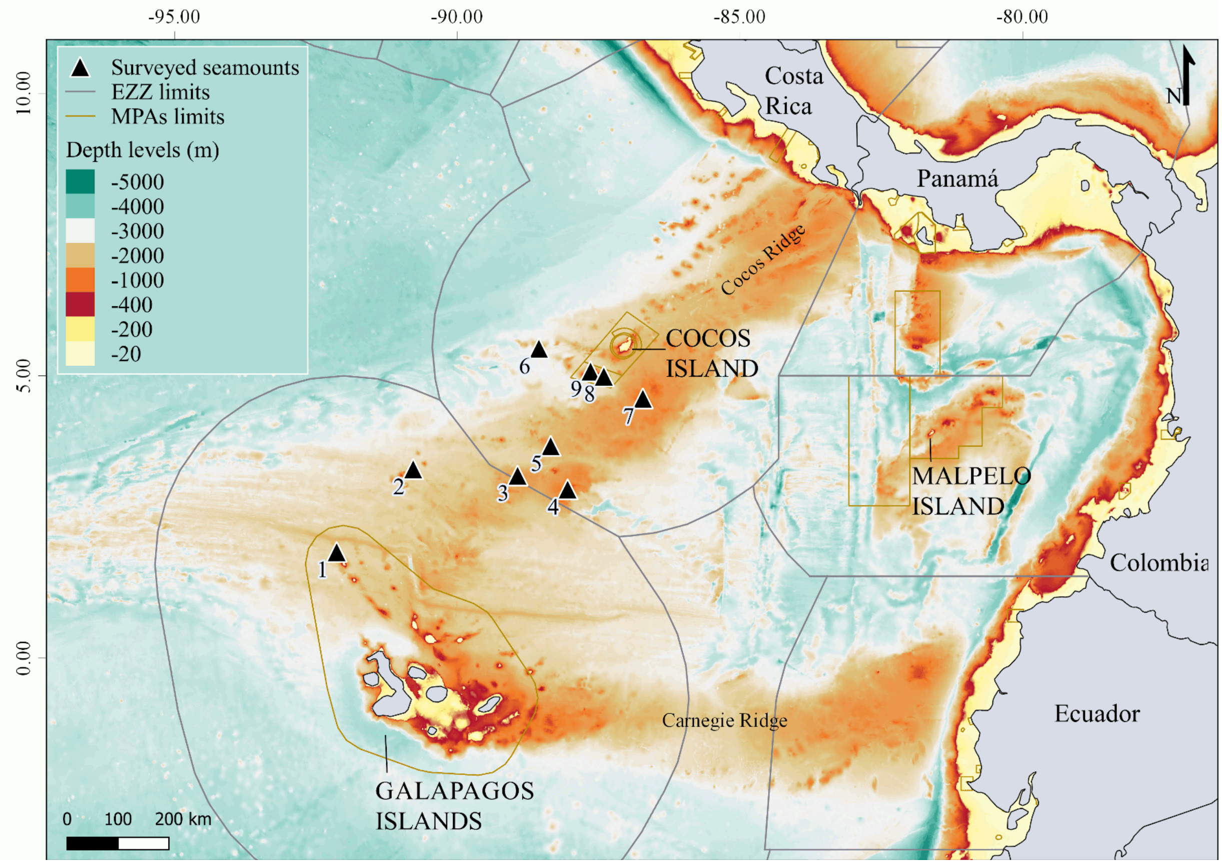

Fig. 1. Location of seamounts surveyed along the Cocos Ridge between Cocos Island and the Galapagos Islands. Numbers indicate surveyed seamounts: (1) NW Darwin; (2) Paramount; (3) Medina 1; (4) Medina 2; (5) Medina 3; (6) West Cocos; (7) East Cocos; (8) Las Gemelas 1; (9) Las Gemelas 2. Limits of the Marine Protected Areas (MPAs) in the Economic Exclusive Zone (EEZ) of each country are shown. Bathymetry data was obtained from ETOPO1 1 Arc-Minute Global Relief Model (Amante & Eakins 2009, NOAA National Geophysical Data Center 2009) under a CC BY license, with permission from NOAA National Centers for Environmental Information, original copyright 2009.

are the main surface currents affecting the Cocos Ridge seamounts (Fiedler & Lavín 2017). Although the central region of the ETP is characterized by warm waters (average 27.5ºC), the Humboldt Current (the southern limit of the ETP) and the Cromwell undercurrent (west – east) can bring cooler waters (down to ~18ºC and ~12ºC, respectively) potentially affecting seamounts closer to Galapagos Islands (Fiedler & Lavín 2017). Oceanographic variability is accentuated by the increase of the average sea temperature during the El Niño–Southern Oscillation Phenomenon, which occurs at irregular intervals of 2 – 7 years (Fiedler 2002). Chlorophyll-a concentrations along the marine corridor between Cocos and Galapagos Islands respond to seasonal variations typically oscillating between 0.15 and 0.22 mg m^{-3} (Peñaherrera-Palma et al. 2018). The ETP is also characterized by a shallow thermocline (often at 25 m) above a permanent barrier of cold hypoxic water which may limit the available physical habitat for some predator species (Prince & Goodyear 2007, Vedor et al. 2021).

Sampling method

Nine seamounts along the Cocos Ridge were surveyed from April 3rd to April 11th of 2018 (Fig. 1) when the ETP was transitioning from La Niña (cooler-than-average-waters) to ENSO-neutral conditions (sea surface temperatures near the long-term average) (Becker 2018). The survey was conducted under the research permit PC-24-18 issued by the Galapagos National Park Directorate. Permits to survey seamounts in Costa Rica were not necessary because none of them were located inside Cocos Island National Park. Seamount selection was based on the depth of each seamount summit. We prioritized the shallowest seamounts in the study area to increase the probability of LPS observation rates in subsurface waters (10 and 25 m deep) based on results from (Morato et al. 2008) and (Letessier et al. 2019), where shallower seamounts (< 400 m) showed significant effects on the aggregation of LPS. The depth of each seamount was previously determined using the Seamount Catalog of EarthRef (https://earthref.org/SC/) and the National Center for Environmental Information of the National Oceanic and Atmospheric Administration (NOAA) (https://www.ncei.noaa.gov/). The depth sounder of the research vessel used during the expedition provided more accurate locations for seamounts shallower than 600 m (depth sounder maximum capacity). Additional information regarding seamount bathymetry was accessed during the expedition from boat navigation charts and from offline nautical charts of Navionics application (Geocore version 18.0.1).

The drifting-pelagic BRUVS used in this study are an adaptation of designs used elsewhere by (Santana-Garcon et al. 2014a, Bouchet 2015). Our design consists of a triangle shaped stainless-steel frame that supports a single high-definition GoPro Hero 4 camera encased in an underwater housing (Fig. 2). Each camera was provided with a backpack battery to extend its recording time between 2 and 3 hours. Cameras were set to record at 60 frames per second/1080p resolution in wide field of view to maximize detection rates. All units had a baited arm to hold a perforated PVC bait container. A total of 1.5 kg of yellowfin tuna (*Thunnus albacares*) was used per each BRUVS during approximately 2.5 hr of soak time (mean ± SD: 140 ± 13.4 min) considering the little signs of species accumulation captured in the open ocean using drifting-pelagic BRUVS after 180 minutes (Letessier et al. 2013, Bouchet & Meeuwig 2015). Once thawed, the bait was cut into approximately 5 cm pieces and lightly crushed once inserted into the perforated PVC container before each deployment. Drifting pelagic BRUVS were manually launched and retrieved from the vessel.

The drifting-pelagic BRUVS units were connected with a superficial tether line resembling a long-line system to maximize survey effort while minimizing the risk of loss and the amount of the tracking devices needed. Two long-lines with 5 drifting-pelagic BRUVS separated 150 meters each were simultaneously deployed several times at each seamount during the expedition (Fig. 2). Hereon, we refer to each long-line with 5 connected BRUVS units as one deployment. To assess differences in species detectability between depth levels, simultaneous deployments were suspended at 10 m (shallow) and 25 m (deep) (Fig. 2). To assess the effect of time of day on species richness and abundance, deployments were conducted during morning (6:00 – 10:00 am) and afternoon (1:00 – 3:00 pm) at each seamount. All deployments entered the water upstream of each seamount to ensure that the sound of the vessel engine was not present when the units drifted over the sampling sites. A sea anchor was used to stabilize deployments and avoid entanglements (Fig. 2). The average distance left among simultaneous deployments was 1.6 ± 1.04 km (mean ± SD).

Differences in temperature between shallow and deep deployments per seamount were obtained attaching a temperature datalogger (ONSET Hobo Pendant® UA) to each BRUVS unit. The drifting distance of each deployment was measured fitting each deployment with a Global Positioning System device (GPS). An Automatic Identification System track device (AIS) was also attached to each deployment to capture its position while drifting with the current (Fig. 2). Missing temperature and drifting distance values for some BRUVS (8% and 6.7% respectively) were obtained calculating the average of those values between the two nearest stations. Mean concentrations of chlorophyll-a around each BRUVS unit (spatial resolution of 4.64km) were gathered by the Moderate Resolution Imaging Spectroradiometer (MODIS) from NASA's Goddard Space Flight Center and the Ocean Biology Processing Group. The data was extracted using the ERDDAP open-source data server with the *rxtracto* function from the *rerdappXtracto* package (Mendelson, 2021). Additional information such as date, time, location and duration of each deployment was recorded on the field.

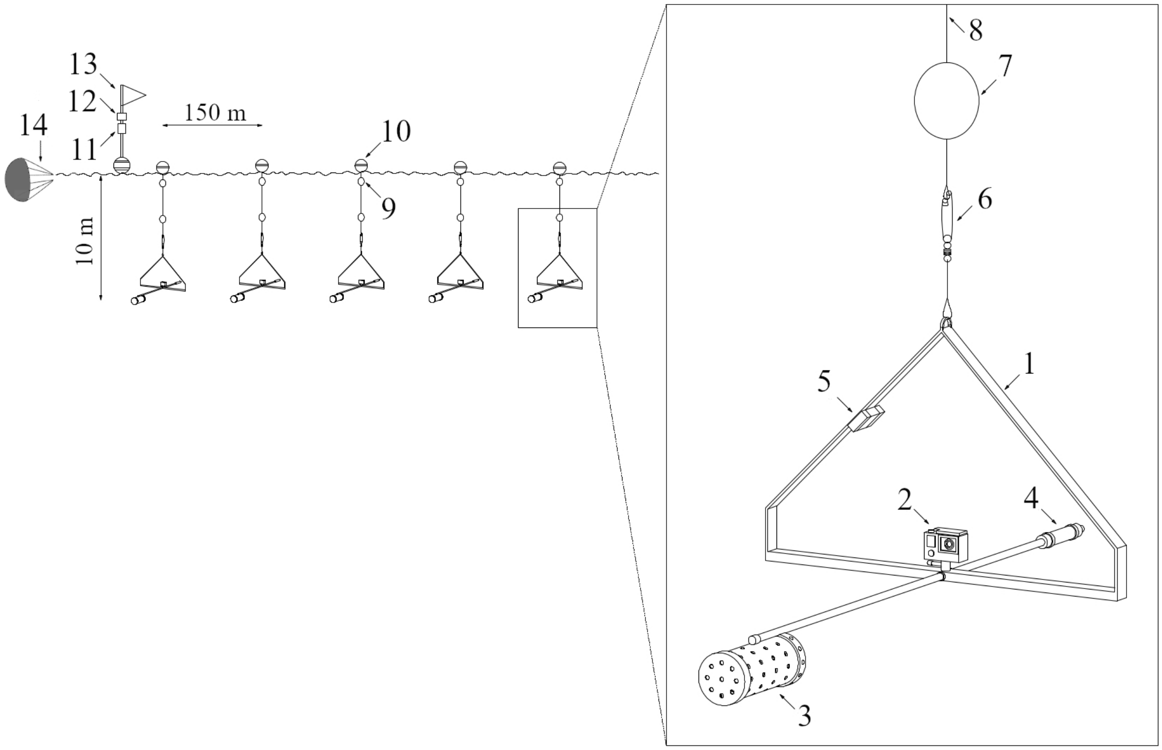

Fig. 2. Diagram of a shallow (10 m depth) drifting-pelagic Baited Remote Underwater Video Stations (BRUVS) deployment. Numbers show closer details of a BRUVS unit: (1) Triangle-shaped stainless-steel frame; (2) GoPro camera; (3) Perforated PVC bait container; (4) Counterweight; (5) Temperature sensor; (6) Stainless steel tuna fishing swivel clip; (7) Small intermediate buoy; (8) 10 m or 25 m line; (9) Small surface buoy; (10) Big surface buoy; (11) Global Positioning System device (GPS); (12) Automatic Identification System (AIS) track device; (13) Flag; (14) Sea anchor. The configuration of the deep deployment is the same as the shallow, but BRUVS units are at 25m depth.

Video and data analysis

The software EventMeasure (SeaGIS®) was used to analyze the video footage and calculate the relative abundance of each observed species. Relative abundance was defined as the maximum number of individuals from each species observed in a single frame of the video (MaxN). The MaxN is a conservative estimate of the total number of individuals present in the deployment area because it avoids repeat counts of animals reentering the field of view and because only a proportion of the species present in the deployment area will positively respond to the bait plume by entering the camera's field of view (Cappo et al. 2003, Heagney et al. 2007). Species were identified to the lowest taxonomic level possible using local identification guides and expert knowledge if required. Species were classified in ecological groups according to taxonomy and reported common sizes (Froese & Pauly 2022) into elasmobranchs, large teleosts (species with common total length > 1m), small teleosts (species with common total length < 1m), dolphins and turtles. For some graphical representations, dolphins and sea turtles were pooled together as "Other LPS" since only one species from each group was observed. Small teleost richness and abundance data were described, but not included in the statistical comparisons since their higher abundance could mask the distribution and abundance patterns of LPS which are the group of interest of this study. For statistical purposes, LPS were pooled together.

Differences in sampling effort were standardized across deployments and seamounts by dividing MaxN of each species obtained per BRUVS unit by soak time (effective time of BRUVS recording), expressed as MaxN hr^{-1}. The accumulation rate of MaxN for all organisms and for LPS increased continuously with soaktime without reaching an inflection point (Fig. S1), allowing us to use MaxN hr^{-1} without underestimating relative abundance. Considering that BRUVS from the same long-line were only separated 150 m from each other, we considered each deployment (one long-line with 5 connected BRUVS) as an independent replicate. Therefore, the MaxN hr^{-1} considered for each species was the maximum value recorded among the five connected BRUVS of the same deployment. To compare the relative abundance across ecological groups and seamounts, the MaxN hr^{-1} of each group per deployment was summed. Temperature, chlorophyll-a, latitude, longitude and soak time values were averaged among the five connected BRUVS of each deployment (Table S1). Missing temperature and distance values for some BRUVS (8% and 6.7%, respectively) were obtained calculating the average of those values between the two nearest stations. Measures of dispersion of observed means were reported as mean ± standard deviation (SD).

Cumulative species richness curves were used to examine temporal accumulation of LPS species per group by deployment and soak time. The order in which species were analyzed was randomized 999 times and the cumulative number of new species per deployment was counted for each randomization. The function *specaccum* with "random" method from the vegan statistical package (Oksanen et al. 2020) was used to calculate the rate of species accumulation. The same function but with "*rarefaction*" method was used to calculate the rate of MaxN accumulation per soak time.

Poisson and Negative binomial generalized linear models (GLM) were used to examine relationships between a set of predictors and LPS richness and relative abundance (MaxN). A

Negative binomial model was used as an alternative of a Poisson model when overdispersion was detected (variance larger than the mean) (Zuur et al. 2009b). Overdispersion was assessed using Pearson residuals, where a score of close to 1 is indicative of a lack of over-dispersion (Zuur et al. 2009b). Since soak time differed per deployment, the log transformed values of soaktime (hours) was used as an offset for all models (Zuur et al. 2009b, Espinoza et al. 2014b). The categorical predictors selected include i) time of day (morning: 6:00–10:00 am; afternoon: 1:00–3:00 pm), since it might affect the vertical movement of pelagic species in offshore habitats (Scott & Cattanach 1998, Musyl et al. 2003, Weng & Block 2004, Nasby-Lucas et al. 2009); ii) camera depth level (shallow: 10 m; deep: 25 m), since changes in water temperature and dissolved oxygen are often associated to shallow thermoclines (often at 25 m) in the ETP, and thus may be an important predictor of LPS distribution (Prince & Goodyear 2007, Ketchum et al. 2014a); and iii) seamount depth based on summit depth level (shallow: < 400 m; deep: > 400 m), since marine predators in other regions have shown a higher tendency to be associated with features shallower than 400 m (Morato et al. 2008, Letessier et al. 2019). The continuous predictor variables included in the model were i) drifting distance of each deployment during the soaktime (0.8 – 8.9 km) as a proxy of current intensity, since this parameter could influence the abundance of hammerheads and other shark species (Hearn et al. 2010, Ketchum et al. 2014b, Papastamatiou et al. 2021); ii) MPA distance defined as the minimum distance of each seamount to the boundaries of the nearest MPA (0 – 275.5 km), either Cocos or Galapagos Islands, both centers of marine diversity and abundance of LPS in the ETP (Hearn et al. 2010, 2014b, Cortés 2012, Edgar et al. 2014); iii) mean water temperature at the camera depth level (22.8 – 29.7 ºC), an important determinant of LPS distribution (Smith & Brown 2002, Gonzáles-Andrés et al. 2016); and iv) mean chorophyll-a concentration (0.13 – 0.31 mg m^{-3}), an indicator of primary productivity and available trophic energy (Smith & Brown 2002, Martínez-Rincón 2012). As visibility was always between 10 and 15 m in all samples, this parameter was not considered as an influencing factor when making comparisons between replicates. The Variance Inflation Factor (VIF) did not show signs of correlation among continuous predictor variables (VIF < 3) and therefore, all predictor variables were included in the full model for LPS richness and LPS relative abundance (Zuur et al. 2007).

The distribution of the response and predictor variables was examined prior to perform models using diagnostic plots such as histograms, cleveland plots, pairplots and boxplots (Zuur et al. 2009b). Model selection was based on the small sample-corrected Akaike's information criterion

(AICc). This approach has been suggested as a useful option for small samples where the ratio of observations to model parameters is low (e.g $N/K < 40$) (Hurvich & Tsai 1989, Burnham & Anderson 2002). Models were ranked based on minimum AICc, detailing changes in AICc with respect to the top ranked model (ΔAICc) and model weights (wAICc) (Burnham et al. 2011, Symonds & Moussalli 2011). Models with values of ΔAICc ≤ 2 were presented, since values within this threshold can have similar explanatory power (Richards 2005, Symonds & Moussalli 2011). Model weights were computed as a measure of each model's strength of evidence where the smaller the wAICc, the lower probability the model is true (Burnham & Anderson 2002). The cumulative wAICc was used to identify a 95% confidence set of models and to measure the relative importance of each variable (Zuur et al. 2009b). The larger the sum of the weight value ($\sum w_i$), the more important the variable is relative to the other variables (McAlpine et al. 2006, Zuur et al. 2009b). Residual deviance and GLM diagnostic plots of standard residuals were used to evaluate the goodness of fit of the resulting models and to determine wheatear models assumptions were met (Zuur et al. 2009b). The R packages *psych* (Revelle, 2022), *car* (Fox & Weisberg, 2019), *pscl* (Jackman, 2020), *MuMIn* (Barton, 2022), *MASS* (Venables & Ripley, 2002) and *lmtest* (Zeileis & Hothorn, 2002) were used to examine data and to perform model selection. All statistical analysis in this study were performed using R software (v 3.6.3; R Core Team 2021).

RESULTS

A total of 347.5 hours of video footage from 32 deployments (150 BRUVS units) were recorded in 9 seamounts along the Cocos Ridge (S1 Data). Although we aimed to conduct 4 deployments (20 BRUVS units) per seamount, due to logistic limitations, equipment losses or video failures, the total survey effort per seamount ranged from 11.7 to 55.1 hours (mean ± SD: 32.5 ± 13.3 hours) (Table 1).

Table 1. Survey effort, location, depth and environmental data associated with seamounts surveyed along the Cocos Ridge.

Seamounts	D (N)	Hrs	Lat	Long	Dist (km)	Depth (m)	Temp (ºC)	Drift (km h^{-1})	Chl-a (mg m^3)
Gemelas 2	2 (9)	17.5	5.069	-87.634	79	-172	27.5	0.65	0.18
Gemelas 1	4 (20)	39.9	4.985	-87.401	70	-198	28.5	0.86	0.21
East Cocos	4 (20)	31.3	4.600	-86.720	109	-775	29.1	0.97	0.16

West Cocos	4 (20)	55.1	5.467	-88.533	162	-283	29.2	0.47	0.13
Medina 3	4 (18)	26.5	3.334	-88.268	276	-445	27.9	2.19	0.21
Medina 2	4 (15)	38.4	2.990	-88.050	324	-688	27	3.08	0.28
Medina 1	4 (19)	29.8	3.235	-88.935	327	-818	27.4	1.91	0.31
Paramount	4 (19)	43.1	3.349	-90.781	227	-188	27.9	1.11	0.14
NW Darwin	2 (10)	11.7	1.881	-92.134	27	-1200	24.6	1.95	0.20

D – number of deployments; N – number of valid BRUVS units; Hrs – recorded hours with baited remote underwater video stations (BRUVS); Dist (km) – minimum distance to closest MPA (Cocos or Galapagos Islands); Depth (m) – depth of seamount summit; Temp – mean temperature (ºC); Drift – mean drifting speed (km h^{-1}) of pelagic-BRUVS deployments; Chl-a – mean concentration of chlorophyll-a (mg m^{-3}). Seamounts are ordered with increasing distance from Cocos Island. Shallow seamounts (depth < 400m) are shown in italics

Richness and abundance

Our cameras detected LPS on 90.6% of all deployments (n = 32) or 48% of individual BRUVS (n = 150), with the number of species per deployment ranging from 1 to 6 (mean ± SD: 1.8 ± 1.3 species). Twenty-one species were identified from BRUVS footage, from which 13 species (62%) were LPS, including 6 teleosts (4 families), 3 sharks (3 families), 2 pelagic rays (2 families), 1 dolphin and 1 sea turtle (Table 2, Fig. 3). Some species were only identified at the genus level (*Mobula* spp. and *Decaptreurs* spp.). Six species of small teleost from 4 families were also recorded (Table 2). Approximately, 56% of all small teleost sighted could not be identified due to their small size and/or low video resolution, hereafter referred to as "unidentified". Of all LPS identified to species level (n=12), 33% were threatened species (n=4), 58% were non threatened (n=7) and only 9% (n=1) were not evaluated based on current assessments from the International Union for the Conservation of Nature (IUCN) (IUCN 2021) (Table 2). All small teleosts recorded were classified as either Least Concern or Not Evaluated (Table 2).

Small teleosts were the most abundant (14.1 ± 59.7 MaxN hr^{-1}) and commonly sighted (94% of all deployments) group. Large teleosts and elasmobranchs occurred at 59% and 50% of all deployments, respectively, and showed similar relative abundances (large teleosts: 2.9 ± 4.4 MaxN hr^{-1}; elasmobranchs: 3.3 ± 6.1 MaxN hr^{-1}). The least sighted and abundant groups were dolphins, occurring at 28% of all deployments (1.8 ± 1.7 MaxN hr^{-1}), and sea turtles, occurring at 3.1% of all deployments with only 1 individual detected (0.4 MaxN hr^{-1}).

The scalloped hammerhead shark (*Sphyrna lewini*) dominated the elasmobranch group, representing 91.5% of the group's MaxN. Furthermore, this species showed the highest frequency of observation among all elasmobranchs (34.4% of all deployments) (Table 2). The common dolphinfish or mahi-mahi (*Coryphaena hippurus*) was the most abundant large-bodied teleost (91.8% of the group's MaxN) and the most frequently observed among all large-bodied teleosts (43.8% of all deployments) (Table 2). Among the small teleosts, the green jack (*Caranx caballus*) was the most abundant species (79.6% of the group's MaxN) and the pilot fish (*Naucrates ductor*) was the most frequently observed species (50% of all deployments) (Table 2). The bottlenose dolphin (*Tursiops truncatus*) and the black sea turtle (*Chelonia mydas)* were the only species of dolphins and sea turtles, respectively (Table 2).

The slope of the species accumulation curve indicated that the number of species for all groups increased gradually with number of BRUVS deployments and soak time, with some differences found between groups (Fig. S2). Although still increasing, the species accumulation curve for small teleosts nearly reached an asymptote after 180 min of soak time, whereas elasmobranchs and other marine megafauna species showed signs of stabilization after 90 min of soak time. The curve for large teleosts continued to increase at a maximum soak time of 140 min. Species richness accumulation curves increased at a faster rate for small teleosts and elasmobranchs (sharp increase during the first 20 min), followed by large teleosts and ultimately by other LPS (dolphins and 1 sea turtle) at a much slower rate (Fig. S2).

Table 2. Summary of occurrence, relative abundance (MaxN and MaxN hr^{-1}) and conservation status of all species classified by groups recorded on baited remote underwater video stations (BRUVS) along Cocos Ridge seamounts.

EG / Family	Species	Common name	D	% D	MaxN		MaxN hr^{-1} (mean ± SD)	Rank	Status
					max	sum			
Sphyrnidae	*Sphyrna lewini*	Scalloped hammerhead	11	34.4	60	162	6.3 ± 8	H	CR
Carharhinidae	*Carcharhinus falciformis*	Silky shark	5	15.6	2	7	0.6 ± 0.2	M	VU
Alopiidae	*Alopias pelagicus*	Pelagic tresher shark	3	9.4	1	3	0.4	L	EN
Mobulidae	*Mobula spp.*	Mobula ray	2	6.2	2	3	0.6 ± 0.3	L	-
Dasyatidae	*Pteroplatytrygon violacea*	Pelagic stingray	2	6.2	1	2	0.4	L	LC
Total elasmobranchs			**16**	**50**	**-**	**177**	**3.3 ± 6**	**-**	**-**
Coryphaenidae	*Coryphaena hippurus*	Common dolphinfish	14	43.8	28	134	4.6 ± 5.1	H	LC
Istiophoridae	*Kajikia audax*	Sriped marlin	5	15.6	1	5	0.5 ± 0.2	M	NT
	Istiompax indica	Black marlin	1	3.1	1	1	0.4	L	DD
	Istiophorus platypterus	Sailfish	1	3.1	1	1	0.4	L	LC
Scombridae	*Thunnus albacares*	Yellowfin tuna	2	6.2	3	4	0.8 ± 0.5	L	NT
Alepisauridae	*Alepisaurus ferox*	Long snouted lancetfish	1	3.1	1	1	0.4	L	LC
Total large teleosts			**19**	**59**	**-**	**146**	**2.9 ± 4**	**-**	**-**
Delphinidae	*Tursiops truncatus*	Bottlenose dolphin	9	28.1	10	33	1.8 ± 1.7	M	LC
Cheloniidae	*Chelonia mydas*	Pacific black sea turtle	1	3.1	1	1	0.4	L	EN
Total other large pelagic species			**9**	**28**	-	**34**	**1.7 ± 2**		
Carangidae	*Naucrates ductor*	Pilot fish	16	50	37	105	2.7 ± 3.4	H	LC
	Caranx caballus	Green Jack	4	12.5	500	553	55.4 ± 95.2	M	LC
	Seriola peruana	Fortune jack	3	9.4	12	19	2.6 ± 2.2	M	LC
	Seriola rivoliana	Pacific amberjack	1	3.1	6	6	2.5	L	LC
	Decapterus spp.	Scads	1	3.1	1	1	0.4	L	NE
Monacanthidae	*A. monoceros*	Unicorn filefish	2	6.2	3	4	0.7 ± 0.5	L	LC

Coryphaenidae	*Coryphaena equiselis*	Pompano dolphinfish	1	3.1	4	4	1.8	L	LC
Scombridae	*Sarda orientalis*	Striped bonito	1	3.1	3	3	1.2	L	LC
Unidentified	Unidentified	Unidentified	31	96.9	1000	1301	17.9 ± 74.9	H	-
Total small teleosts			**30**	**94**	**-**	**1996**	**14.1 ± 59**		

Species are organized by families and ecological groups (EG). D: number of BRUVS deployments with a species. Relative abundance is expressed as (i) MaxN: maximum number of individuals of a species per deployment (one deployment with 5 connected BRUVS is considered an independent sample) and (ii) MaxN hr^{-1}: MaxN divided by soak time (hours). Species are ranked based on the frequency of occurrence: H – high (>30% of deployments); M – medium (10-30% of deployments); and L – low (<10% of deployments). Conservation status of each species (DD – data deficient, LC – least concern, NT – near threatened, VU – vulnerable, EN – endangered, and CR – critically endangered) is presented based on current IUCN Red List Assessments (IUCN Red List of Threatened Species).

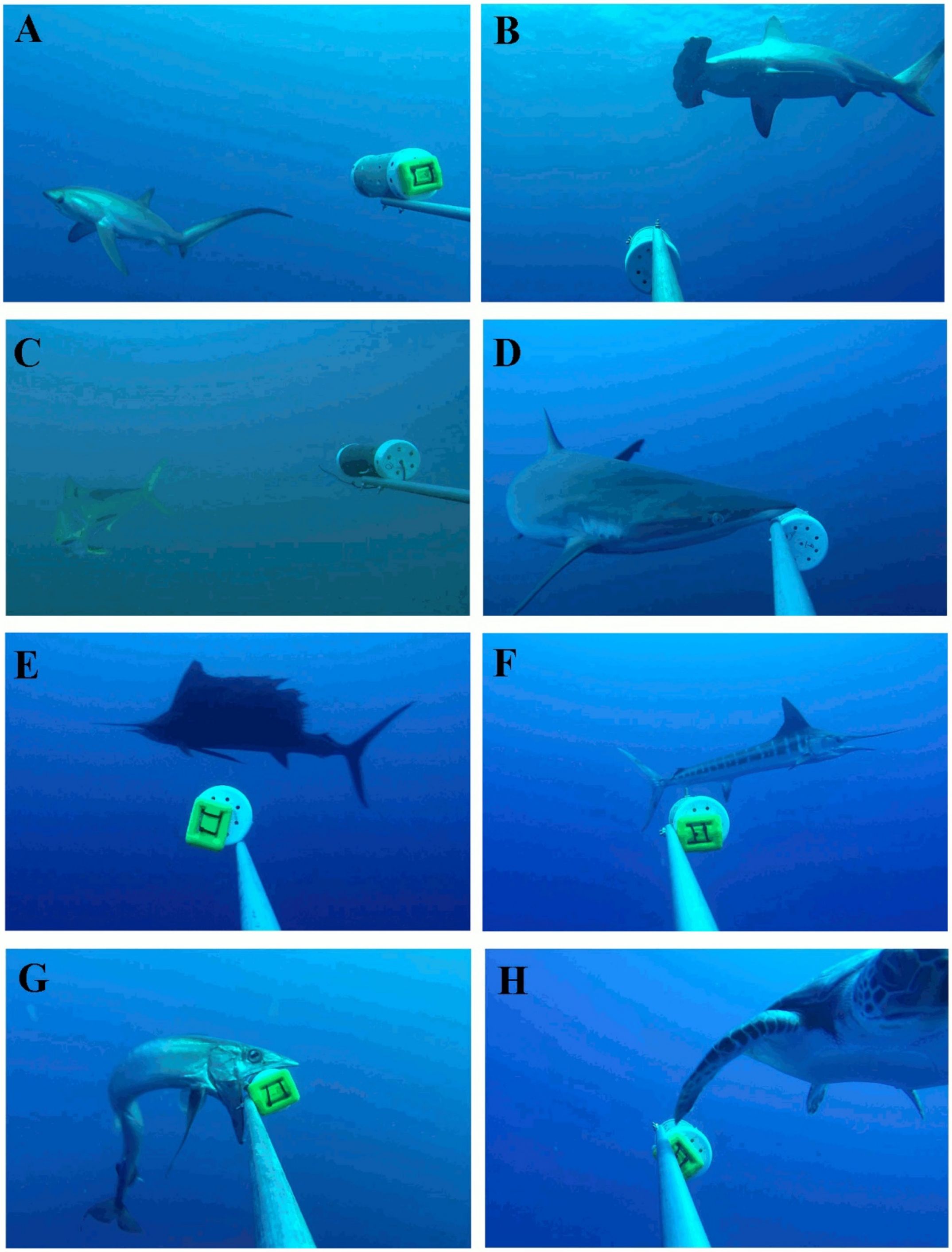

Fig. 3. Images of large pelagic species detected by baited remote underwater video stations (BRUVS). A) Thresher shark *(Alopias pelagicus)*. B) Hammerhead shark *(Sphyrna lewini)*. C) Mahi-mahi *(Coryphaena hippurus)*. D) Silky shark *(Carcharhinus falciformis)*. E) Sail fish *(Istiophorus platypterus)*. F) Stripped marlin *(Kajikia audax)*. G) Lancet fish *(Alepisaurus ferox)*. D) Pacific black sea turtle *(Chelonia mydas)*.

The slope of the species accumulation curve indicated that the number of species for all groups increased gradually with number of BRUVS deployments and soak time, with some differences found between groups (Fig. S2). Although still increasing, the species accumulation curve for small teleosts nearly reached an asymptote after 180 min of soak time, whereas elasmobranchs and other marine megafauna species showed signs of stabilization after 90 min of soak time. The curve for large teleosts continued to increase at a maximum soak time of 140 min. Species richness accumulation curves increased at a faster rate for small teleosts and elasmobranchs (sharp increase during the first 20 min), followed by large teleosts and ultimately by other LPS (dolphins and 1 sea turtle) at a much slower rate (Fig. S2).

Spatial distribution across seamounts

The highest richness and relative abundance of LPS were found at West Cocos (3.8 ± 1.5 species; 12.8 ± 6.2 MaxN hr^{-1}) and Paramount (2.5 ± 1 species; 9.1 ± 9.9 MaxN hr^{-1}) seamounts, whereas the lowest values were found at Medina 3 (0.5 ± 0.6 species; 0.2 ± 0.3 MaxN hr^{-1}) and NW Darwin (0.5 ± 0.7 species; 0.2 ± 0.4 MaxN hr^{-1}) seamounts (Fig. 4; Table S2). The number of LPS ranged from 1 species at NW Darwin to 8 species at West Cocos (Fig. 4A; Table S2). Elasmobranchs were detected at all seamounts except for Medina 1 and NW Darwin, whereas large teleosts were not detected at Paramount and Las Gemelas 2. Other LPS such as dolphins and sea turtles were only reported at seamounts close to Cocos Island including Las Gemelas seamounts, West Cocos and East Cocos (Fig. 4A). The highest elasmobranch richness was reported in Paramount, whereas the highest richness of large teleosts were reported at West Cocos (Fig. 4A).

Elasmobranchs were more abundant at West Cocos and Paramount seamounts (Fig. 4B), where large schools of *S. lewini* of up to 40 and 60 individuals were observed in a single deployment, respectively (Table S2). Few individuals of *S. lewini* were also detected in Medina 3 and Gemelas 2 (Table S2). Large teleosts were more abundant at Las Gemelas 1 and Medina 1 (Fig. 4B), where our BRUVS reported schools of 27 and 28 individuals of *C. hippurus* in a single deployment, respectively (Table S2). However, the highest abundance of *T. albacares* and billfishes (*Istiompax indica, Istiophorus platypterus* and *Kajikia audax*) was reported at West Cocos (Table S2). Dolphins and sea turtles were more abundant at West Cocos and Las Gemelas 1 (Fig. 4B), where our BRUVS recorded groups of up to 6 and 10 *T. truncatus*, respectively (Table S2). The only individual of *C. mydas* was reported at West Cocos (Table S2).

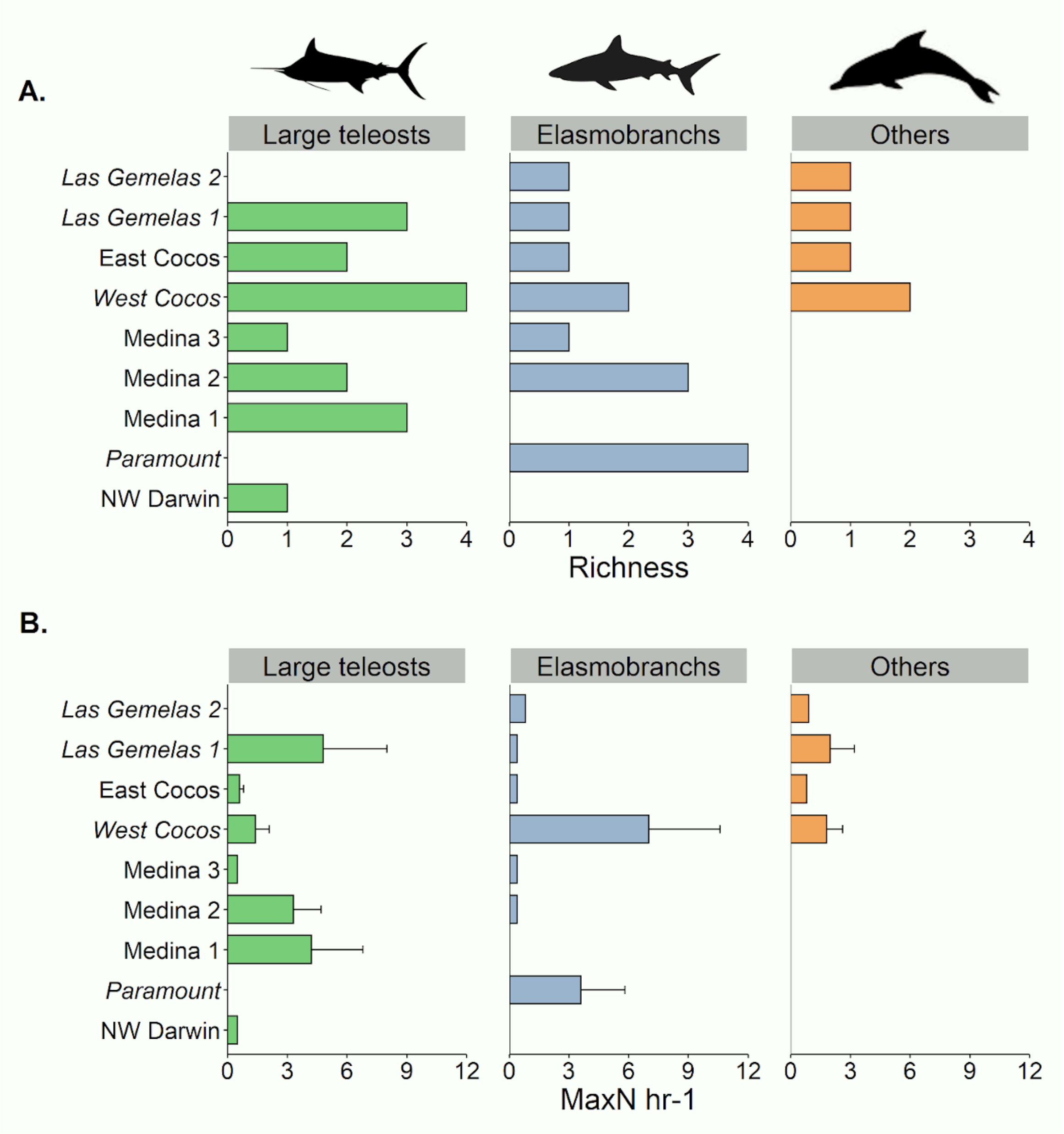

Fig. 4. Comparison of (A) species richness and (B) relative abundance (MaxN hr^{-1}) among ecological groups. Seamounts are ordered from bottom to top according to the distance from Galapagos Islands (bottom) to Cocos Island (top). Error bars represent the 95% confidence intervals. Shallow seamounts (<400 m) are shown in italics.

Drivers of large pelagic species

Based on the GLMs examined, LPS richness and relative abundance (MaxN) followed a Poisson and a Negative Binomial distribution, respectively. The large number of models in the 95% confidence set of models ($\sum w_i = 0.95$) for both LPS richness (66 models; Table S3) and LPS relative abundance (27 models; Table S4) indicated a considerable model uncertainty regarding the identity of the best approximating model. The low wAICc of the top ranked models ($\Delta AIC \leq 2$) for both response variables is another indicative of model uncertainty (Table 3). The Poison GLM with the highest wAICc included seamount depth and minimum distance to MPA as predictor variables of LPS richness (Table 3). However, seamount depth was the only variable with a significant effect over LPS richness (Table 3), and the variable with the highest relative importance ($\sum w_i = 0.89$) from all variables examined (Table S3). Although the minimum distance to a MPA was not a significant variable for LPS richness (Table 3), it showed a moderately higher relative importance ($\sum w_i = 0.52$) compared to the other variables ($\sum w_i < 0.3$). Richness of LPS was significantly higher at shallow seamounts relative to deeper ones (Fig. 5A) and increased with increasing distance to nearest MPA in both shallow and deep seamounts (Fig. 5B). Diagnostic plots of standard residuals from the first top ranked model indicated that model fit for LPS richness was appropriate with respect to heteroscedasticity and normality of residuals (Fig. S3).

The Negative binomial GLM with the highest wAICc included seamount depth and minimum distance to a MPA as predictor variables of LPS relative abundance (Table 3). These were the only variables with a significant influence over LPS relative abundance (Table 3) and with the highest relative importance ($\sum w_i = 0.95$) compared to the other predictors (Table S4). Relative abundance of LPS was higher at shallow than deep seamounts and increased with increasing distance from the nearest MPA (either Cocos or Galapagos Islands) (Fig. 6). Diagnostic plots of standard residuals from the first top ranked model indicated that model fit for LPS relative abundance was satisfactory with respect to heteroscedasticity and normality of residuals (Fig. S4).

The models with the lowest residual deviance and within a $\Delta AIC \leq 2$ from the top-ranked model for both LPS richness and LPS relative abundance included time of deployment in addition to seamount depth and minimum distance to MPA (Table 3). Afternoon deployments had higher species richness (Fig. S5) and relative abundance (Fig. S6) compared to morning deployments although the differences were not statistically significant. Time of deployment also presented the highest relative importance value among the non-significant predictor variables for both LPS richness and relative abundance. However, the differences among them were small (Table S4). Other models within a ΔAIC ≤ 2 from the top-ranked model also included camera depth level and chlorophyll-a as predictors for LPS richness and relative abundance, respectively (Table 3).

Table 3. Comparison of optimal generalised linear models (GLM), using a Poisson and a Negative Binomial error distribution, of large pelagic species (LPS) richness and relative abundance (MaxN), respectively.

Richness LPS – Poisson GLM	**RD**	**df**	**LL**	**AICc**	**ΔAICc**	**wAICc**
Richness ~ **seamount depth** + MPA distance, offset = log (soaktime)	15.8	3	-37.35	81.56	0.00	0.13
Richness ~ **seamount depth**, offset = log (soak time)	18	2	-38.97	82.35	0.79	0.09
Richness ~ **seamount depth** + MPA distance + time, offset = log (soak time)	14.9	4	-36.88	83.25	1.69	0.06
Richness ~ **seamount depth** + MPA distance + camera depth, offset = log (soak time)	15.1	4	-36.99	83.47	1.91	0.05
MaxN LPS – Negative Binomial GLM	**RD**	**df**	**LL**	**AICc**	**ΔAICc**	**wAICc**
MaxN ~ **seamount depth** + **MPA distance**, offset = log (soak time)	29.1	4	-82.08	173.64	0.00	0.24
MaxN ~ **seamount depth** + **MPA distance** + time, offset = log (soak time)	28.8	5	-81.41	175.13	1.49	0.11
MaxN ~ **seamount depth** + **MPA distance** + chla, offset = log (soak time)	29.1	5	-81.65	175.61	1.98	0.09

Models presented are those with lowest values of the Akaike Information Criterion corrected for small sample sizes (AICc). Models are ranked by increasing AICc value. Predictors used at each model were: 1) time - time of deployment (morning 6 – 10 am / afternoon 1 – 3 pm); 2) camera depth - camera depth level (shallow 10m / deep 25m; 3) seamount depth - summit depth level (shallow < 400m / deep > 400m); 4) drift – drifting distance of each deployment during the effective recording time (soak time); 5) MPA distance - minimum distance of each seamount to the boundaries of Cocos or Galápagos Islands; 6) temp - mean temperature at the camera depth level and 7) chla - mean chorophyll-a concentration. Log of soak time (hours of effective recording) was used as an offset in the models. Residual deviance (RD), maximum Log Likelihood (LL), degrees of freedom (df), difference of AICc of a given model to the model with best fit (ΔAICc) and relative model probability expressed as AICc weight (wAICc) are shown for each model. Significant predictors are highlighted in bold ($\alpha = 0.05$). Only models with Δ_i values ≤ 2 are presented.

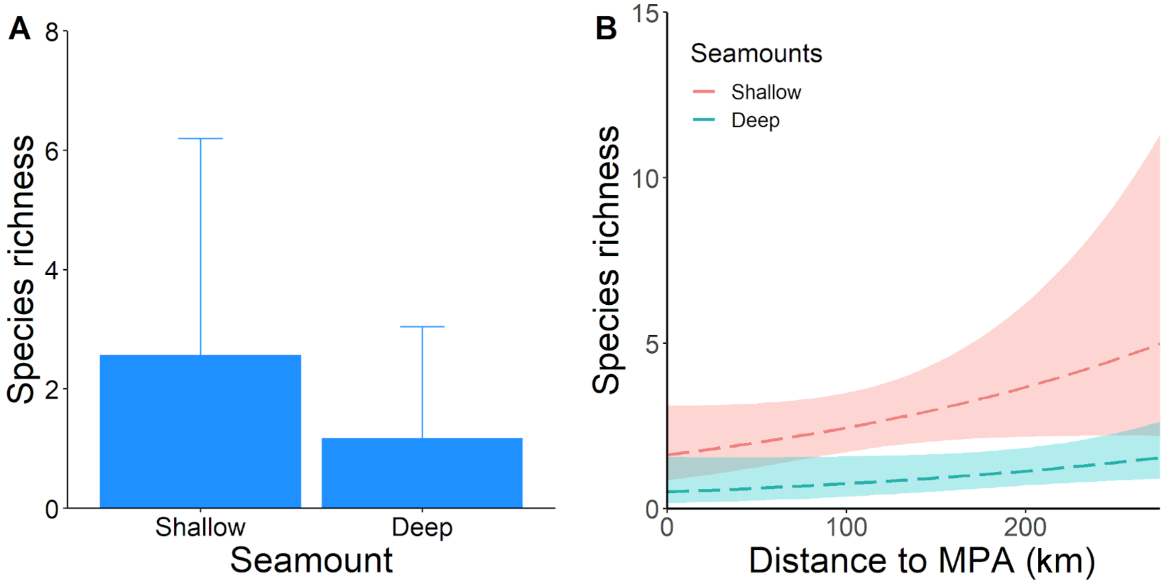

Fig. 5. Graphical results from the two top-ranked AICc generalized linear models for large pelagic species (LPS) richness. A) Estimates of LPS richness (mean ± SD) at shallow (<400 m) and deep (>400 m) seamounts; B) Relationship between richness of LPS and distance to the nearest Marine Protected Area (Cocos or Galapagos Islands) at shallow (<400 m) and deep (>400 m) seamounts.

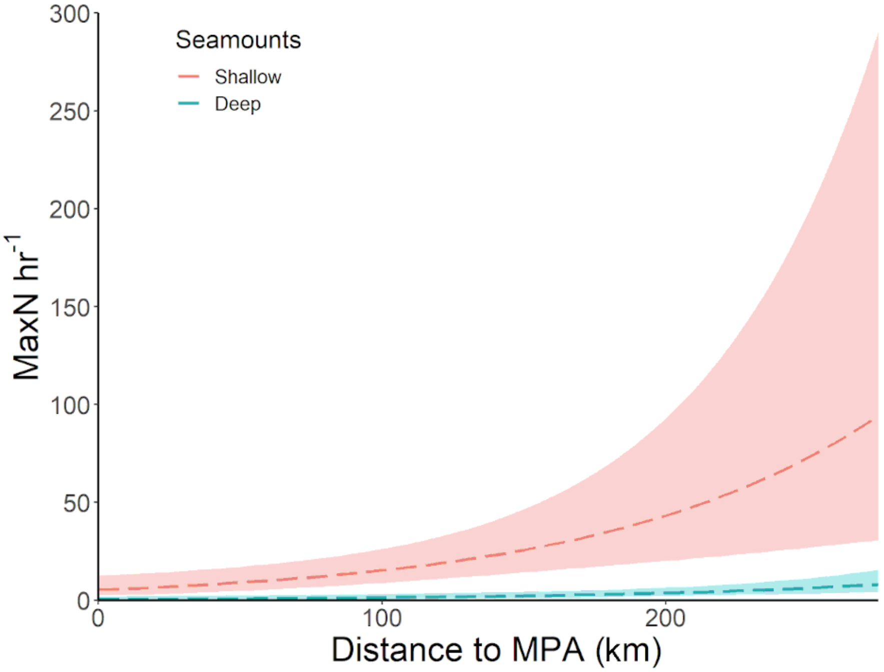

Fig. 6. Graphical results from the top-ranked AICc generalized linear model for large pelagic species (LPS) relative abundance (MaxN hr^{-1}). Representation of the relationship between MaxN hr^{-1} of LPS and distance to nearest MPA (Cocos or Galapagos Islands) at shallow (<400 m) and deep (>400 m) seamounts.

DISCUSSION

Our results suggest that Cocos Ridge seamounts connecting Cocos Island (Costa Rica) and the Galapagos Islands (Ecuador) are important aggregation sites for wide ranging marine species such as elasmobranchs, large teleosts, dolphins and sea turtles. Since these species are suffering severe population declines across the ETP due to fishing pressure (Whoriskey et al. 2011, Dapp et al. 2013, Soler et al. 2014, Peñaherrera-Palma et al. 2015, White et al. 2015), it is critical to identify and protect key habitats in open-oceans (Worm et al. 2003, Morato et al. 2010, Lucifora et al. 2011, McCauley et al. 2015, Letessier et al. 2019). Our study showed that drifting pelagic BRUVS are an effective, accessible and non-extractive technique to monitor LPS in oceanic environments, highlighting its potential to guide management and conservation actions in the ETP.

Large pelagic species at seamounts between Cocos and Galapagos Islands

The evidence of the seamount effect on aggregating pelagic fauna has been demonstrated in a numerous studies and for a wide variety of species including zooplankton (Dower & Mackas 1996, Genin 2004), teleosts (Sala et al. 2003, Morato et al. 2008, Gilman et al. 2012, Fontes et al. 2014, Fontes & Afonso 2017), sharks (Klimley & Nelson 1984, Barnett et al. 2012, Letessier et al. 2019), dolphins (Hastie et al. 2004) and sea birds (Haney et al. 1995). Although we need a higher spatial and temporal replication to elucidate if LPS along Cocos Ridge are positively associated to seamounts presence, our BRUVS recorded LPS (swimming individually or in large schools) in the vicinity of all surveyed seamounts in an open ocean environment where species richness is naturally low (Angel 1993). These results favor the hypothesis that seamounts might serve as important stepping stones where LPS aggregate when moving between oceanic islands of the ETP (Peñaherrera-Palma et al., 2018; Rowden et al., 2010). However, it is important to recognize that our data was taken by the end of La Niña phenomenon, when the thermocline is usually shallower and chlorophyll-a levels are usually higher than normal (Fiedler 2002), potentially increasing species detectability. Moreover, future research should consider deploying drifting-pelagic BRUVS at different distances from seamounts and across different seasons in order to elucidate the aggregation effect of these topographic features on LPS (Morato et al. 2008).

Our models identified the depth of seamount summit as the most significant driver for LPS richness and abundance, which were significantly higher at shallow seamounts (< 400 m) compared to deeper ones (> 400m). The identification of seamount depth as an important driver for LPS is consistent with previous studies, where seamounts shallower than 400 m and 500 m at the Azores Islands (Morato et al. 2010) and the Indo-Pacific region (Letessier et al. 2019), respectively, showed a significant aggregation effect on predator species. Higher fishing catches have been also reported to occur at seamounts shallower than 400 m compared to deeper ones (Genin 2004). The most common explanation given to this pattern is that shallower abrupt topographies accumulate larger zooplankton biomass over the summit (known as the Taylor column generation effect), providing sufficient food to maintain higher trophic levels and commercial fisheries (Genin 2004, Pitcher et al. 2007). There is also the possibility that our BRUVS located at a shallow depth from the surface failed at capturing pelagic life at deeper levels. Future studies deploying drifting-pelagic BRUVS at different depth levels (> 25 m) are necessary to evaluate how pelagic assemblages vary along depth gradients away from the surface (Santana-Garcon et al. 2014c, Bouchet & Meeuwig 2015, Andrzejaczek et al. 2019).

Distance to nearest MPA was also a significant predictor for LPS abundance, which increased at increasing distances from the nearest MPA (Cocos or Galapagos Islands). Although this variable was not a significant predictor for LPS richness, it was present in the first ranked model with the lowest AICc and the highest wAIC. Additionally, this variable presented a high relative importance suggesting some degree of influence over LPS richness. Current literature suggests that MPAs have a beneficial spill-over effect over adjacent areas (Halpern 2003, Lester et al. 2009), and therefore, higher LPS richness and abundance are expected to occur at seamounts closer to Cocos and Galapagos Islands. Since all captured LPS move beyond the protection limits of Cocos and Galapagos Islands, these species are probably not receiving all the benefits from the MPAs, and therefore, their abundance might not be increasing in adjacent areas (Halpern et al. 2009, Starr et al. 2012). Our results may indicate that remote, shallow seamounts in the ETP, in the absence of other nearby topographic structures, represent important aggregation sites of LPS in the open ocean, whereas seamounts closer to MPAs might be sporadically used by LPS that are aggregating inside MPAs where they find more resources and better protection (Hearn et al. 2010, Chávez et al. 2020). Another possible explanation is that greater fishing pressure surrounding the boundaries of MPAs in the ETP is negatively affecting LPS populations at closer seamounts (Alava et al. 2017, Rosero & Rodríguez 2018). However, it is important to recognize that our survey effort at Las Gemelas 1, Las Gemelas 2, and NW Darwin (closest seamounts to Cocos and Galapagos

Islands respectively) was lower (2 deployments) than the rest of seamounts (4 deployments). Therefore, a higher survey effort would allow a better understanding of the effect that MPA proximity has on LPS abundance across seamounts.

Our results suggest that Paramount and West Cocos seamounts may play important roles as aggregation sites for LPS along the Cocos Ridge. Based on the results from our models, it is likely that the higher abundance and richness of LPS at these seamounts was partially explained by a combination of a shallower seamount summit with a high degree of isolation compared to the other seamounts that only met one of the two conditions (Table 1). Large aggregations of *S. lewini* were only found at Paramount and West Cocos and therefore we recommend a special emphasis on both seamounts for future studies and conservation planning in the region.

As a general rule of thumb, models with Δ_i values less than 2 are considered to be essentially as good as the best model (Richards 2005, Symonds & Moussalli 2011). Under this consideration, some of the non-significant predictor variables should be further examined as potential drivers of LPS richness and abundance in future studies. For example, time of deployment was included in the third and second ranked candidate models with Δ_i values ≤ 2 for LPS richness and abundance, respectively. Our data showed a higher richness and abundance of LPS in afternoon deployments, although differences with morning deployments were not significant. Since the bottom trapping mechanism of migrating zooplankton accumulation over the seamounts occurs early in the morning (Pitcher et al. 2007) we would have expected to find a higher LPS richness and abundance in the morning deployments associated with a feeding behavior of LPS close to the surface (Vianna et al. 2013). However, most of our cameras were deployed few hours after dusk (S1 Data), when the trapped zooplankton might have already been consumed or descended to deeper levels (Pitcher et al. 2007). Afternoon deployments instead, remained in the water until dawn when migrating zooplankton begin the ascent towards the surface increasing the probability of detection of larger predators (Andrzejaczek et al. 2019). Since marine predators might use species-specific daily routines depending on prey distribution and environmental changes in order to optimize fitness (Kohin et al. 2005, Vianna et al. 2013, Papastamatiou et al. 2015, Bessudo et al. 2016), a statistical analysis at a group or species level could better explain the observed patterns.

Other non-significant predictor variables included in models with Δ_i values ≤ 2 where camera depth level in the fourth ranked candidate model for LPS richness and chlorophyll-a in the third ranked candidate model for LPS abundance. These parameters are known to influence abundance and distribution patterns of marine megafauna in pelagic environments (Klimley et al. 1988, Smith & Brown 2002, Andrzejaczek et al. 2019, González-Andrés et al. 2020). However, in this study both variables showed low values of relative importance and the models where they were included had the lowest wAICc among the best candidate models. Future studies are needed to better understand the effect of these variables on LPS of the ETP. Dissolved oxygen (Prince & Goodyear 2007), ocean currents (Genin 2004, Heagney et al. 2007), prey availability (Morato et al. 2008), Earth magnetic field (Assael 2016, Keller et al. 2021), and fishing effort (Letessier et al. 2019) may also pose a significant influence on the use of seamounts by LPS, and therefore, should be considered as potential drivers in future studies.

Drifting-pelagic BRUVS to survey pelagic ecosystems in the ETP

Studies where drifting-pelagic BRUVS have been used in fully pelagic ecosystems are scarce (Bouchet & Meeuwig 2015, Letessier et al. 2019). Despite the short-term nature of our study (150 BRUVS or 32 deployments in 9 days of survey), our drifting-pelagic BRUVS showed a high frequency of LPS detection (90.6% of all deployments or 48% of all BRUVS) compared to similar studies in open-water ecosystems of Australia (n = 51 BRUVS) (Bouchet & Meeuwig 2015) and the Indo-Pacific region (n = 1041 BRUVS) (Letessier et al. 2019), where LPS detection was 27% and 34% respectively. These results show a promising potential of the drifting-pelagic BRUVS to survey LPS in pelagic environments of the ETP.

Scientific efforts in the region have already demonstrated that sharks and other LPS move between Cocos and Galapagos Islands (Bessudo et al. 2011, Ketchum et al. 2014b, Acuña-Marrero et al. 2017, Nalesso et al. 2019) suggesting the existence of a marine corridor among both MPAs (Peñaherrera-Palma et al., 2018). However, this is the first fishery-independent study providing valuable insights on the diversity and community structure of LPS outside the protection limits of both MPAs. Fishery-dependent data in the region has provided information on distribution, diversity, effect of environmental drivers and size-structure of many of LPS recorded by our BRUVS (Whoriskey et al. 2011, Martínez-Rincón 2012, Dapp et al. 2013, Martínez-Ortiz et al. 2015). However, sampling effort and location from these studies depend on fishing activities, and therefore, they do not provide specific information from sites of special biological interest such as Cocos Ridge seamounts. Instead, drifting-pelagic BRUVS provide a cost-effective and nondestructive alternative to monitor marine communities *in situ*, and therefore, have the potential to generate novel data at specific sites of interest along unexplored open-water ecosystems. For example, our BRUVS captured the first visual evidence of the schooling behavior of *S. lewini* at open water ecosystems of the ETP, making this critically endangered species even more vulnerable to pelagic-longline and purse-seine fisheries (Dapp et al. 2013, Gallagher et al. 2014, Clarke et al. 2018).

Although baited camera surveys have been positively validated against extractive methods such as trawling and longlines (Cappo et al. 2004, Brooks et al. 2011), the use of BRUVS also have several limitations (Santana-Garcon et al. 2014b, Bouchet et al. 2018). For example, bait plume dispersion is complex and dynamic which makes surveyed area unknown (Heagney et al. 2007). Also, bait responses behaviors may lead to sampling biases towards larger mobile species, yet in this scenario, they were the target group of our study. Since our BRUVS were deployed in offshore clear water (> 15 meters), visibility did not compromise our data. Although our cameras recorded under a wide field of view (220 degrees), there is still a portion of the surrounding area that was not sampled, and therefore counts of relative abundance could be underestimated. This problem can be solved by using 360º cameras that allow a full field of view around each BRUVS, but it will also increase surveying costs, analysis time and limit comparisons with previous studies. Despite the above-mentioned limitations, drifting-pelagic BRUVS generate relevant ecological data of apex predator guilds that are typically cryptic, increasingly exposed to anthropogenic mortality and of high conservation and commercial value without posing a threat to targeted species (Bouchet et al. 2018).

Given the novelty of this study, our results can be used as a first approach to guide future studies using drifting-pelagic BRUVS in the ETP. For example, the species accumulation curves showed that at least 90 min were needed to record a representative sample of apex predators such as elasmobranchs and cetaceans, whereas soak times up to 180 minutes were necessary to increase species detection of teleosts (Fig. S2). These results coincide with those reported by (Santana-Garcon et al. 2014b) where the slope of the curve for pelagic species in Western Australia was reduced after 90 minutes of soak time with a trend still increasing at a reduced rate at 180 minutes. In consideration of the uncertainty associated with bait plume dispersal and sampling area during BRUVS studies (Bouchet et al. 2018), we recommend considering each deployment (with at least three BRUVS units each at a minimum distance of 200 m) as an independent replicate. To reduce potential biases associated with pseudo-replication we recommend leaving at minimum of 1 km as a conservative distance between independent drifting-pelagic BRUVS deployments.

CONCLUSION

Our study represents the first attempt at characterizing the spatial distribution and relative abundance of LPS near seamounts along the Cocos Ridge, providing a first insight on how pelagic communities are structured outside the protection limits of two of the most important oceanic MPAs of the ETP. Our results show that shallow seamounts (<400 m) located at greater distances from MPAs may represent ecologically important refuges and foraging sites for LPS in the ETP, particularly along the Cocos Ridge. Future research is necessary to assess the potential of seamounts as high-priority conservation areas to prevent threatened species from further declines. Our results show a promising potential of the drifting-pelagic BRUVS to survey LPS in pelagic ecosystems of the ETP and elsewhere. This study might serve as an important reference for future studies in the region using this technique.

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SUPPLEMENTARY MATERIAL

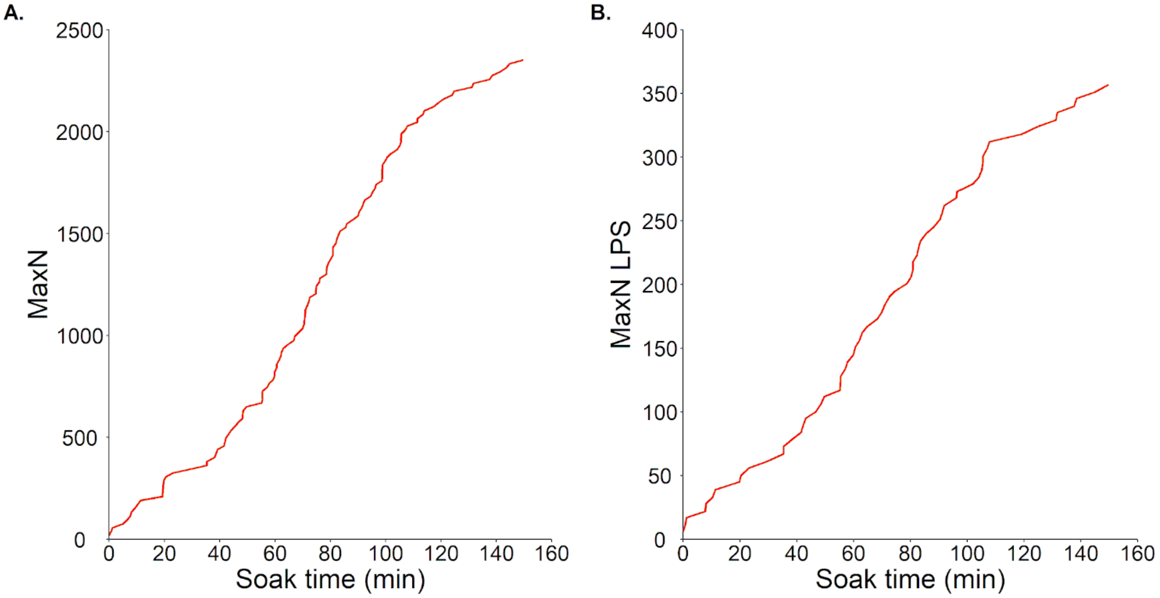

Fig. S1. Relative abundance (MaxN) accumulation curve per soak time of A) all organisms and B) only large pelagic species (LPS). Soak time is defined as the effective recording time of Baited Remote Underwater Video Stations (BRUVS). Each deployment with 5 connected BRUVS is treated as an independent sample.

Table S1. Raw data of environmental and biological information associated to each deployment. Depth 1 (D1) and depth 2 (D2) indicate depth level of the deployment (shallow = 10 m; deep = 25 m) and of the seamount (shallow < 400 m; deep > 400 m). Temperature is shown in ºC, drifting distance in km, and chlorophyll-a in mg m^3. Species are abbreviated based on Table 2.

Deployment	Date	Time	Soaktime	Daytime	D1	D2	Lat	Long	Temp	Drift	Chla	Species	MaxN
NW Darwin_L1	3/4/18	13:06	107.77	afternoon	shallow	deep	1.88147	-92.13954	26.47	4.09	0.2	*N. ductor*	2
NW Darwin_L1	3/4/18	13:06	107.77	afternoon	shallow	deep	1.88147	-92.13954	26.47	4.09	0.2	No id	11
NW Darwin_L2	3/4/18	13:42	119.35	afternoon	deep	deep	1.88717	-92.1436	22.83	3.24	0.2	*C. caballus*	23
NW Darwin_L2	3/4/18	13:42	119.35	afternoon	deep	deep	1.88717	-92.1436	22.83	3.24	0.2	*N. ductor*	2
NW Darwin_L2	3/4/18	13:42	119.35	afternoon	deep	deep	1.88717	-92.1436	22.83	3.24	0.2	*C. hippurus*	1
NW Darwin_L2	3/4/18	13:42	119.35	afternoon	deep	deep	1.88717	-92.1436	22.83	3.24	0.2	No id	7
Paramount_L1	4/4/18	08:45	141.95	morning	deep	shallow	3.32678	-90.79634	27.97	3.77	0.14	*N. ductor*	7
Paramount_L1	4/4/18	08:45	141.95	morning	deep	shallow	3.32678	-90.79634	27.97	3.77	0.14	*C. falciformis*	1
Paramount_L1	4/4/18	08:45	141.95	morning	deep	shallow	3.32678	-90.79634	27.97	3.77	0.14	No id	10
Paramount_L1	4/4/18	08:45	141.95	morning	deep	shallow	3.32678	-90.79634	27.97	3.77	0.14	*S. lewini*	60
Paramount_L2	4/4/18	09:16	146.3	morning	shallow	shallow	3.33215	-90.80167	29.45	3.55	0.13	*N. ductor*	5
Paramount_L2	4/4/18	09:16	146.3	morning	shallow	shallow	3.33215	-90.80167	29.45	3.55	0.13	*C. falciformis*	2
Paramount_L2	4/4/18	09:16	146.3	morning	shallow	shallow	3.33215	-90.80167	29.45	3.55	0.13	No id	5
Paramount_L2	4/4/18	09:16	146.3	morning	shallow	shallow	3.33215	-90.80167	29.45	3.55	0.13	*S. lewini*	11
Paramount_L3	4/4/18	13:53	151.87	afternoon	shallow	shallow	3.33193	-90.77112	29.47	1.87	0.14	*A. pelagicus*	1
Paramount_L3	4/4/18	13:53	151.87	afternoon	shallow	shallow	3.33193	-90.77112	29.47	1.87	0.14	No id	7
Paramount_L3	4/4/18	13:53	151.87	afternoon	shallow	shallow	3.33193	-90.77112	29.47	1.87	0.14	*S. lewini*	1
Paramount_L4	4/4/18	14:39	140.99	afternoon	deep	shallow	3.33329	-90.7885	24.71	1.54	0.14	*A. pelagicus*	1
Paramount_L4	4/4/18	14:39	140.99	afternoon	deep	shallow	3.33329	-90.7885	24.71	1.54	0.14	*C. caballus*	25
Paramount_L4	4/4/18	14:39	140.99	afternoon	deep	shallow	3.33329	-90.7885	24.71	1.54	0.14	*N. ductor*	7
Paramount_L4	4/4/18	14:39	140.99	afternoon	deep	shallow	3.33329	-90.7885	24.71	1.54	0.14	*C. falciformis*	2
Paramount_L4	4/4/18	14:39	140.99	afternoon	deep	shallow	3.33329	-90.7885	24.71	1.54	0.14	*Mobula spp*	2
Paramount_L4	4/4/18	14:39	140.99	afternoon	deep	shallow	3.33329	-90.7885	24.71	1.54	0.14	No id	4

Paramount_L4	4/4/18	14:39	140.99	afternoon	deep	shallow	3.33329	-90.7885	24.71	1.54	0.14	*S. lewini*	8
Medina 1_L1	5/4/18	08:05	142.46	morning	shallow	deep	3.22348	-88.96704	29.25	6.29	0.3	*S. peruana*	2
Medina 1_L1	5/4/18	08:05	142.46	morning	shallow	deep	3.22348	-88.96704	29.25	6.29	0.3	*C. hippurus*	6
Medina 1_L1	5/4/18	08:05	142.46	morning	shallow	deep	3.22348	-88.96704	29.25	6.29	0.3	No id	9
Medina 1_L2	5/4/18	08:41	150.48	morning	deep	deep	3.22408	-88.9873	25.44	5.16	0.3	*C. hippurus*	2
Medina 1_L2	5/4/18	08:41	150.48	morning	deep	deep	3.22408	-88.9873	25.44	5.16	0.3	No id	3
Medina 1_L3	5/4/18	14:18	113.17	afternoon	deep	deep	3.25437	-88.97104	26.23	2.18	0.31	0	0
Medina 1_L3	5/4/18	14:18	113.17	afternoon	deep	deep	3.25437	-88.97104	26.23	2.18	0.31	*N. ductor*	1
Medina 1_L3	5/4/18	14:18	113.17	afternoon	deep	deep	3.25437	-88.97104	26.23	2.18	0.31	*C. hippurus*	7
Medina 1_L3	5/4/18	14:18	113.17	afternoon	deep	deep	3.25437	-88.97104	26.23	2.18	0.31	*K. audax*	1
Medina 1_L3	5/4/18	14:18	113.17	afternoon	deep	deep	3.25437	-88.97104	26.23	2.18	0.31	No id	3
Medina 1_L4	5/4/18	15:03	111.51	afternoon	shallow	deep	3.25758	-88.95382	28.7	3.34	0.31	0	0
Medina 1_L4	5/4/18	15:03	111.51	afternoon	shallow	deep	3.25758	-88.95382	28.7	3.34	0.31	*A. ferox*	1
Medina 1_L4	5/4/18	15:03	111.51	afternoon	shallow	deep	3.25758	-88.95382	28.7	3.34	0.31	*C. hippurus*	28
Medina 1_L4	5/4/18	15:03	111.51	afternoon	shallow	deep	3.25758	-88.95382	28.7	3.34	0.31	No id	7
Medina 2_L1	6/4/18	08:05	152.21	morning	deep	deep	2.79056	-88.17432	25.67	6.38	0.28	*N. ductor*	3
Medina 2_L1	6/4/18	08:05	152.21	morning	deep	deep	2.79056	-88.17432	25.67	6.38	0.28	*C. hippurus*	14
Medina 2_L1	6/4/18	08:05	152.21	morning	deep	deep	2.79056	-88.17432	25.67	6.38	0.28	*P. violacea*	1
Medina 2_L1	6/4/18	08:05	152.21	morning	deep	deep	2.79056	-88.17432	25.67	6.38	0.28	No id	2
Medina 2_L2	6/4/18	08:33	147.37	morning	shallow	deep	2.79195	-88.17379	28.11	8.91	0.28	0	0
Medina 2_L2	6/4/18	08:33	147.37	morning	shallow	deep	2.79195	-88.17379	28.11	8.91	0.28	*C. falciformis*	1
Medina 2_L2	6/4/18	08:33	147.37	morning	shallow	deep	2.79195	-88.17379	28.11	8.91	0.28	*C. hippurus*	3
Medina 2_L2	6/4/18	08:33	147.37	morning	shallow	deep	2.79195	-88.17379	28.11	8.91	0.28	No id	4
Medina 2_L2	6/4/18	08:33	147.37	morning	shallow	deep	2.79195	-88.17379	28.11	8.91	0.28	*T. albacares*	1
Medina 2_L3	6/4/18	14:13	137.5	afternoon	shallow	deep	2.80342	-88.17871	28.22	8.43	0.27	*C. equiselis*	4
Medina 2_L3	6/4/18	14:13	137.5	afternoon	shallow	deep	2.80342	-88.17871	28.22	8.43	0.27	*C. hippurus*	19
Medina 2_L3	6/4/18	14:13	137.5	afternoon	shallow	deep	2.80342	-88.17871	28.22	8.43	0.27	*Mobula spp*	1
Medina 2_L3	6/4/18	14:13	137.5	afternoon	shallow	deep	2.80342	-88.17871	28.22	8.43	0.27	No id	15

Medina 2_L4	6/4/18	14:47	137.52	afternoon	deep	deep	2.80719	-88.18168	25.87	5.78	0.27	*N. ductor*	10
Medina 2_L4	6/4/18	14:47	137.52	afternoon	deep	deep	2.80719	-88.18168	25.87	5.78	0.27	*C. hippurus*	3
Medina 2_L4	6/4/18	14:47	137.52	afternoon	deep	deep	2.80719	-88.18168	25.87	5.78	0.27	No id	1
Medina 3_L1	7/4/18	08:19	150.78	morning	deep	deep	3.31868	-88.26197	27.21	4.64	0.21	*N. ductor*	9
Medina 3_L1	7/4/18	08:19	150.78	morning	deep	deep	3.31868	-88.26197	27.21	4.64	0.21	*S. peruana*	5
Medina 3_L1	7/4/18	08:19	150.78	morning	deep	deep	3.31868	-88.26197	27.21	4.64	0.21	*S. rivoliana*	6
Medina 3_L1	7/4/18	08:19	150.78	morning	deep	deep	3.31868	-88.26197	27.21	4.64	0.21	No id	7
Medina 3_L1	7/4/18	08:19	150.78	morning	deep	deep	3.31868	-88.26197	27.21	4.64	0.21	*S. orientalis*	3
Medina 3_L1	7/4/18	08:19	150.78	morning	deep	deep	3.31868	-88.26197	27.21	4.64	0.21	*S. lewini*	1
Medina 3_L2	7/4/18	08:47	126.86	morning	shallow	deep	3.31522	-88.26329	28.42	5.56	0.21	0	0
Medina 3_L3	7/4/18	14:03	143.96	afternoon	shallow	deep	3.32644	-88.2646	28.91	5.83	0.21	0	0
Medina 3_L3	7/4/18	14:03	143.96	afternoon	shallow	deep	3.32644	-88.2646	28.91	5.83	0.21	*K. audax*	1
Medina 3_L4	7/4/18	14:03	140.03	afternoon	deep	deep	3.31871	-88.2618	27.02	4.31	0.21	0	0
Medina 3_L4	7/4/18	14:03	140.03	afternoon	deep	deep	3.31871	-88.2618	27.02	4.31	0.21	No id	1
West Cocos_L1	8/4/18	08:08	150.7	morning	shallow	shallow	5.47378	-88.53709	29.31	1.11	0.13	*T. truncatus*	6
West Cocos_L1	8/4/18	08:08	150.7	morning	shallow	shallow	5.47378	-88.53709	29.31	1.11	0.13	*I. indica*	1
West Cocos_L1	8/4/18	08:08	150.7	morning	shallow	shallow	5.47378	-88.53709	29.31	1.11	0.13	*A. monoceros*	1
West Cocos_L1	8/4/18	08:08	150.7	morning	shallow	shallow	5.47378	-88.53709	29.31	1.11	0.13	No id	2
West Cocos_L1	8/4/18	08:08	150.7	morning	shallow	shallow	5.47378	-88.53709	29.31	1.11	0.13	*S. lewini*	6
West Cocos_L2	8/4/18	08:39	140.19	morning	deep	shallow	5.4827	-88.55137	28.81	0.76	0.14	*C. falciformis*	1
West Cocos_L2	8/4/18	08:39	140.19	morning	deep	shallow	5.4827	-88.55137	28.81	0.76	0.14	*T. truncatus*	1
West Cocos_L2	8/4/18	08:39	140.19	morning	deep	shallow	5.4827	-88.55137	28.81	0.76	0.14	No id	4
West Cocos_L2	8/4/18	08:39	140.19	morning	deep	shallow	5.4827	-88.55137	28.81	0.76	0.14	*S. lewini*	40
West Cocos_L3	8/4/18	14:04	126.16	afternoon	shallow	shallow	5.47047	-88.53418	29.32	1.48	0.13	*C. caballus*	5
West Cocos_L3	8/4/18	14:04	126.16	afternoon	shallow	shallow	5.47047	-88.53418	29.32	1.48	0.13	*N. ductor*	11
West Cocos_L3	8/4/18	14:04	126.16	afternoon	shallow	shallow	5.47047	-88.53418	29.32	1.48	0.13	*S. peruana*	12
West Cocos_L3	8/4/18	14:04	126.16	afternoon	shallow	shallow	5.47047	-88.53418	29.32	1.48	0.13	*C. hippurus*	10
West Cocos_L3	8/4/18	14:04	126.16	afternoon	shallow	shallow	5.47047	-88.53418	29.32	1.48	0.13	*T. truncatus*	6

West Cocos_L3	8/4/18	14:04	126.16	afternoon	shallow	shallow	5.47047	-88.53418	29.32	1.48	0.13	No id	3
West Cocos_L3	8/4/18	14:04	126.16	afternoon	shallow	shallow	5.47047	-88.53418	29.32	1.48	0.13	*S. lewini*	1
West Cocos_L4	8/4/18	14:27	148.36	afternoon	deep	shallow	5.45254	-88.53546	29.26	1.05	0.14	*C. mydas*	1
West Cocos_L4	8/4/18	14:27	148.36	afternoon	deep	shallow	5.45254	-88.53546	29.26	1.05	0.14	*C. hippurus*	2
West Cocos_L4	8/4/18	14:27	148.36	afternoon	deep	shallow	5.45254	-88.53546	29.26	1.05	0.14	*T. truncatus*	2
West Cocos_L4	8/4/18	14:27	148.36	afternoon	deep	shallow	5.45254	-88.53546	29.26	1.05	0.14	*K. audax*	1
West Cocos_L4	8/4/18	14:27	148.36	afternoon	deep	shallow	5.45254	-88.53546	29.26	1.05	0.14	No id	1
West Cocos_L4	8/4/18	14:27	148.36	afternoon	deep	shallow	5.45254	-88.53546	29.26	1.05	0.14	*T. albacares*	3
West Cocos_L4	8/4/18	14:27	148.36	afternoon	deep	shallow	5.45254	-88.53546	29.26	1.05	0.14	*S. lewini*	30
East Cocos_L1	9/4/18	08:05	150.76	morning	shallow	deep	4.54799	-86.79855	29.7	2.52	0.16	0	0
East Cocos_L1	9/4/18	08:05	150.76	morning	shallow	deep	4.54799	-86.79855	29.7	2.52	0.16	*K. audax*	1
East Cocos_L1	9/4/18	08:05	150.76	morning	shallow	deep	4.54799	-86.79855	29.7	2.52	0.16	*A. monoceros*	3
East Cocos_L1	9/4/18	08:05	150.76	morning	shallow	deep	4.54799	-86.79855	29.7	2.52	0.16	No id	5
East Cocos_L2	9/4/18	08:28	142.1	morning	deep	deep	4.55539	-86.79903	28.46	3.44	0.16	*N. ductor*	5
East Cocos_L2	9/4/18	08:28	142.1	morning	deep	deep	4.55539	-86.79903	28.46	3.44	0.16	*P. violacea*	1
East Cocos_L2	9/4/18	08:28	142.1	morning	deep	deep	4.55539	-86.79903	28.46	3.44	0.16	No id	9
East Cocos_L3	9/4/18	14:04	153.79	afternoon	shallow	deep	4.56418	-86.77961	29.71	2.05	0.16	0	0
East Cocos_L3	9/4/18	14:04	153.79	afternoon	shallow	deep	4.56418	-86.77961	29.71	2.05	0.16	*Decapterus sp*	1
East Cocos_L3	9/4/18	14:04	153.79	afternoon	shallow	deep	4.56418	-86.77961	29.71	2.05	0.16	No id	1
East Cocos_L4	9/4/18	14:37	129.2	afternoon	deep	deep	4.56158	-86.79326	28.53	1.4	0.16	*C. hippurus*	2
East Cocos_L4	9/4/18	14:37	129.2	afternoon	deep	deep	4.56158	-86.79326	28.53	1.4	0.16	*T. truncatus*	2
East Cocos_L4	9/4/18	14:37	129.2	afternoon	deep	deep	4.56158	-86.79326	28.53	1.4	0.16	No id	29
Las Gemelas 1_L1	10/4/18	07:58	143.63	morning	shallow	shallow	4.98193	-87.40864	29.07	2.4	0.23	*T. truncatus*	1
Las Gemelas 1_L1	10/4/18	07:58	143.63	morning	shallow	shallow	4.98193	-87.40864	29.07	2.4	0.23	*K. audax*	1
Las Gemelas 1_L1	10/4/18	07:58	143.63	morning	shallow	shallow	4.98193	-87.40864	29.07	2.4	0.23	No id	7
Las Gemelas 1_L2	10/4/18	08:31	156.63	morning	deep	shallow	4.98379	-87.402	28.04	2.34	0.23	*N. ductor*	1
Las Gemelas 1_L2	10/4/18	08:31	156.63	morning	deep	shallow	4.98379	-87.402	28.04	2.34	0.23	*C. hippurus*	10
Las Gemelas 1_L2	10/4/18	08:31	156.63	morning	deep	shallow	4.98379	-87.402	28.04	2.34	0.23	No id	106

Las Gemelas 1_L3	10/4/18	14:10	120.48	afternoon	shallow	shallow	4.96014	-87.4265	28.96	1.62	0.2	0	0
Las Gemelas 1_L3	10/4/18	14:10	120.48	afternoon	shallow	shallow	4.96014	-87.4265	28.96	1.62	0.2	*N. ductor*	1
Las Gemelas 1_L3	10/4/18	14:10	120.48	afternoon	shallow	shallow	4.96014	-87.4265	28.96	1.62	0.2	*C. hippurus*	27
Las Gemelas 1_L3	10/4/18	14:10	120.48	afternoon	shallow	shallow	4.96014	-87.4265	28.96	1.62	0.2	*T. truncatus*	10
Las Gemelas 1_L3	10/4/18	14:10	120.48	afternoon	shallow	shallow	4.96014	-87.4265	28.96	1.62	0.2	No id	1
Las Gemelas 1_L4	10/4/18	14:42	150.26	afternoon	deep	shallow	4.97366	-87.43927	27.88	1.79	0.2	*A. pelagicus*	1
Las Gemelas 1_L4	10/4/18	14:42	150.26	afternoon	deep	shallow	4.97366	-87.43927	27.88	1.79	0.2	*C. caballus*	500
Las Gemelas 1_L4	10/4/18	14:42	150.26	afternoon	deep	shallow	4.97366	-87.43927	27.88	1.79	0.2	*N. ductor*	37
Las Gemelas 1_L4	10/4/18	14:42	150.26	afternoon	deep	shallow	4.97366	-87.43927	27.88	1.79	0.2	*T. truncatus*	3
Las Gemelas 1_L4	10/4/18	14:42	150.26	afternoon	deep	shallow	4.97366	-87.43927	27.88	1.79	0.2	*I. platypterus*	1
Las Gemelas 1_L4	10/4/18	14:42	150.26	afternoon	deep	shallow	4.97366	-87.43927	27.88	1.79	0.2	No id	1000
Las Gemelas 2_L1	11/4/18	06:30	152.27	morning	shallow	shallow	5.07795	-87.64844	28.15	1.6	0.18	*N. ductor*	3
Las Gemelas 2_L1	11/4/18	06:30	152.27	morning	shallow	shallow	5.07795	-87.64844	28.15	1.6	0.18	No id	25
Las Gemelas 2_L1	11/4/18	06:30	152.27	morning	shallow	shallow	5.07795	-87.64844	28.15	1.6	0.18	*S. lewini*	2
Las Gemelas 2_L2	11/4/18	06:54	147.31	morning	deep	shallow	5.07298	-87.64498	26.81	1.68	0.18	*N. ductor*	1
Las Gemelas 2_L2	11/4/18	06:54	147.31	morning	deep	shallow	5.07298	-87.64498	26.81	1.68	0.18	*T. truncatus*	2
Las Gemelas 2_L2	11/4/18	06:54	147.31	morning	deep	shallow	5.07298	-87.64498	26.81	1.68	0.18	No id	11
Las Gemelas 2_L2	11/4/18	06:54	147.31	morning	deep	shallow	5.07298	-87.64498	26.81	1.68	0.18	*S. lewini*	2

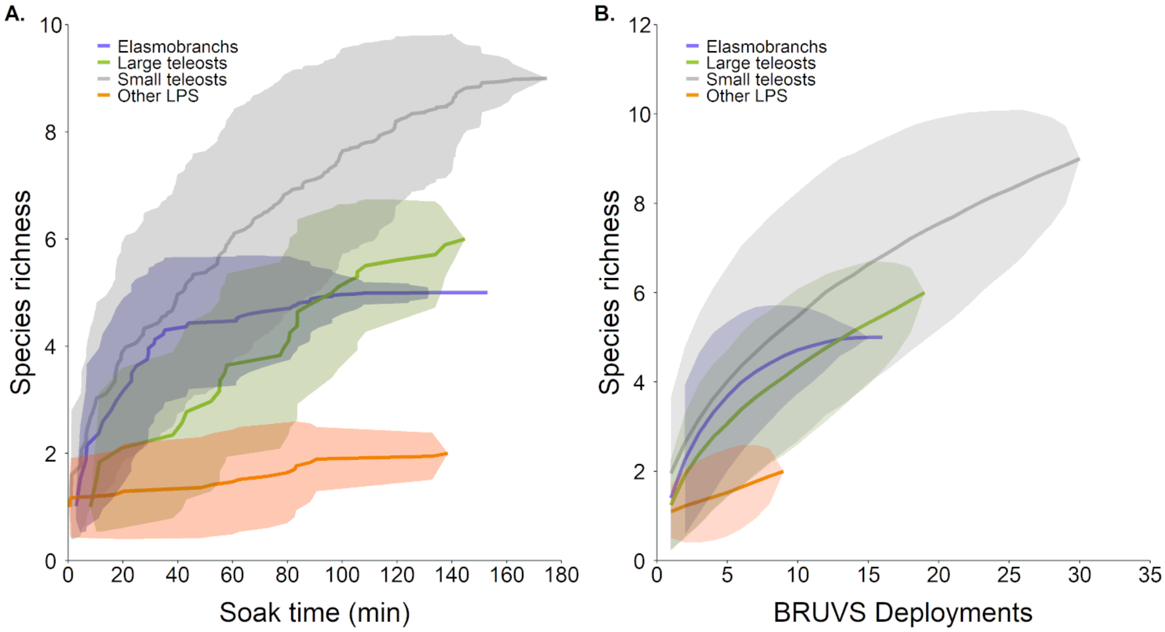

Fig. S2. Species accumulation curves per ecological group. (A) Species richness of each ecological group over cumulative soak time in minutes. Soak time is defined as the effective recording time of Baited Remote Underwater Video Stations (BRUVS). (B) Species richness of each ecological group over the number of BRUVS deployments. Each deployment with five connected BRUVS is treated as an independent sample. Shade colors represent 95% confidence intervals.

Table S2. Relative abundance (MaxN hr^{-1}) and richness of large pelagic species (LPS) by seamount. Relative abundance is expressed as MaxN hr^{-1} (maximum number of individuals of a species recorded on a single deployment standardized by soak time). MaxN hr^{-1} Species are abreviated as: AF) *Alepisaurus ferox*, AP) *Alopias pelagicus*, CF) *Carcharhinus falciformis*, CM) *Chelonia mydas*, CH) *C. hippurus*, II) *Istiompax indica*, IP) *Istiophorus platypterus*, KA) *Kajikia audax*, M) *Mobula* spp., PV) *Pteroplatytrygon violacea*, SL) *Sphyrna lewini*, TA) *Thunnus albacares* and TT) *Trusiops truncatus*. The MaxN hr^{-1} at a group level for the small teleost species (ST) is also presented. The sum and the mean of LPS MaxN hr^{-1} and species richness are also presented per seamount. Seamounts are ordered according to the sum of MaxN hr^{-1}. Shallow seamounts (<400 m) are shown in italics.

Seamounts	**AF**	**AP**	**CF**	**CH**	**CM**	**II**	**IP**	**KA**	**M**	**PV**	**SL**	**TA**	**TT**	**ST**	**MaxN hr^{-1}**		**Richness**	
															sum	**mean±SD**	**sum**	**mean±SD**
West Cocos	0	0	0.4	5.1	0.4	0.4	0	0.4	0	0	34.6	1.1	8.7	16.3	51.1	12.8 ± 6.2	8	3.8 ± 1.5
Paramount	0	0.9	2.3	0	0	0	0	0	0.8	0	32.5	0	0	29.8	36.4	9.1 ± 9.9	4	2.5 ± 1
Las Gemelas 1	0	0.4	0	18.3	0	0	0.4	0.4	0	0	0	0	5.9	15.1	25.4	6.4 ± 8.2	5	2 ± 0.8
Medina 1	0.4	0	0	24.1	0	0	0	0.8	0	0	0	0	0	9.8	25.3	6.3 ± 7.5	3	1.5 ± 0.6
Medina 2	0	0	0.4	15.8	0	0	0	0	0.5	0.4	0	0.4	0	17.8	17.5	4.4 ± 3.2	5	2 ± 0.8
East Cocos	0	0	0	0.8	0	0	0	0.4	0	0.4	0	0	0.8	32.5	2.4	0.6 ± 0.7	4	1 ± 0.8
Las Gemelas 2	0	0	0	0	0	0	0	0	0	0	1.5	0	0.9	680	2.4	1.2 ± 0.6	2	1.5 ± 0.7
Medina 3	0	0	0	0	0	0	0	0.5	0	0	0.4	0	0	12.9	0.9	0.2 ± 0.3	2	0.5 ± 0.6
NW Darwin	0	0	0	0.5	0	0	0	0	0	0	0	0	0	21.9	0.5	0.2 ± 0.4	1	0.5 ± 0.7

Table S3. Model rankings of Poisson GLM for large pelagic species richness in the 95% confidence set of models and the relative importance of each predictor variable. Models are ranked based on minimum Akaike Information Criterion corrected for small sample sizes (AICc). Predictors used at each model were: 1) Time - time of deployment (morning 6 – 10 am / afternoon 1 – 3 pm); 2) D1 - camera depth level (shallow 10m / deep 25m; 3) D2 – seamount summit depth level (shallow < 400m / deep > 400m); 4) Drift – drifting distance of each deployment during the effective recording time (soak time); 5) Dist - minimum distance of each seamount to the boundaries of Cocos or Galápagos Islands; 6) Temp - mean temperature at the camera depth level and 7) Chla - mean chorophyll-a concentration. Log of soak time (hours of effective recording) was used as an offset in the models. Degrees of freedom (df), maximum Log Likelihood (LL), difference of AICc of a given model to the model with best fit (ΔAICc) and relative model probability expressed as AICc weight (wAICc) are shown for each model. The sum of the wAICc was used to calculate the relative importance (RI) of each variable in the 95% confidence set of models (Burnham & Anderson 2002, Zuur et al. 2009a).

Int	Chla	D1	Time	Drift	Dist	Temp	D2	df	LL	AICc	ΔAICc	wAICc
0.49	NA	NA	NA	NA	0.004	NA	+	3	-38.1	88.4	6.9	0.130
0.94	NA	NA	NA	NA	NA	NA	+	2	-38.1	88.5	7.0	0.087
0.37	NA	NA	+	NA	0.004	NA	+	4	-38.3	88.8	7.3	0.056
0.36	NA	+	NA	NA	0.004	NA	+	4	-38.3	88.8	7.3	0.050
0.82	NA	NA	+	NA	NA	NA	+	3	-42.2	88.9	7.3	0.041
0.53	NA	NA	NA	-0.06	0.005	NA	+	4	-41.0	89.0	7.4	0.040
0.81	NA	+	NA	NA	NA	NA	+	3	-36.8	89.0	7.5	0.036
1.07	NA	NA	NA	NA	0.004	-0.02	+	4	-36.9	89.1	7.5	0.036
0.47	0.12	NA	NA	NA	0.004	NA	+	4	-36.9	89.1	7.5	0.035
0.87	NA	NA	NA	0.04	NA	NA	+	3	-38.4	89.1	7.5	0.028
0.82	0.73	NA	NA	NA	NA	NA	+	3	-36.9	89.1	7.5	0.026
1.53	NA	NA	NA	NA	NA	-0.02	+	3	-42.3	89.1	7.5	0.026
0.24	NA	+	+	NA	0.004	NA	+	5	-41.1	89.1	7.6	0.019
0.69	NA	+	+	NA	NA	NA	+	4	-36.9	89.1	7.6	0.015
0.65	NA	NA	+	0.07	NA	NA	+	4	-38.4	89.2	7.6	0.014
0.40	NA	NA	+	-0.03	0.004	NA	+	5	-36.9	89.2	7.6	0.014
0.28	0.58	NA	+	NA	0.004	NA	+	5	-39.9	89.2	7.7	0.014
0.71	NA	NA	+	NA	0.004	-0.01	+	5	-41.2	89.2	7.7	0.014
-1.32	NA	+	NA	NA	0.004	0.06	+	5	-38.5	89.3	7.7	0.013
0.40	NA	+	NA	-0.04	0.004	NA	+	5	-42.5	89.3	7.8	0.013
0.37	-0.06	+	NA	NA	0.004	NA	+	5	-41.2	89.3	7.8	0.012
0.60	1.23	NA	+	NA	NA	NA	+	4	-38.5	89.4	7.8	0.012
0.69	NA	+	NA	0.06	NA	NA	+	4	-41.3	89.4	7.8	0.011
1.15	NA	NA	+	NA	NA	-0.01	+	4	-41.3	89.5	8.0	0.011

-0.46	NA	+	NA	NA	NA	0.04	+	4	-42.6	89.6	8.0	0.010
0.43	0.71	NA	NA	-0.07	0.005	NA	+	5	-41.4	89.6	8.1	0.010
1.07	NA	NA	NA	-0.06	0.005	-0.02	+	5	-38.1	88.4	6.9	0.010
0.72	0.58	+	NA	NA	NA	NA	+	4	-38.1	88.5	7.0	0.010
1.08	-0.04	NA	NA	NA	0.004	-0.02	+	5	-38.3	88.8	7.3	0.009
0.95	NA	NA	NA	-0.11	NA	NA	NA	2	-38.3	88.8	7.3	0.008
1.45	NA	NA	NA	0.04	NA	-0.02	+	4	-42.2	88.9	7.3	0.008
0.83	0.28	NA	NA	0.04	NA	NA	+	4	-41.0	89.0	7.4	0.007
0.72	NA	NA	NA	-0.21	0.003	NA	NA	3	-36.8	89.0	7.5	0.007
0.59	NA	NA	NA	NA	NA	NA	NA	1	-36.9	89.1	7.5	0.007
1.33	0.61	NA	NA	NA	NA	-0.02	+	4	-36.9	89.1	7.5	0.007
1.30	-3.66	NA	NA	NA	NA	NA	NA	2	-38.4	89.1	7.5	0.006
0.45	NA	+	+	0.09	NA	NA	+	5	-36.9	89.1	7.5	0.005
-1.72	NA	+	+	NA	0.004	0.07	+	6	-42.3	89.1	7.5	0.005
0.17	0.40	+	+	NA	0.004	NA	+	6	-41.1	89.1	7.6	0.004
0.24	NA	+	+	0.00	0.004	NA	+	6	-36.9	89.1	7.6	0.004
-0.89	NA	+	+	NA	NA	0.05	+	5	-38.4	89.2	7.6	0.004
0.51	1.08	+	+	NA	NA	NA	+	5	-36.9	89.2	7.6	0.004
0.58	0.47	NA	+	0.07	NA	NA	+	5	-39.9	89.2	7.7	0.003
0.94	NA	NA	+	0.07	NA	-0.01	+	5	-41.2	89.2	7.7	0.003
0.46	NA	+	NA	NA	NA	NA	NA	2	-38.5	89.3	7.7	0.003
1.30	-5.33	NA	NA	NA	0.002	NA	NA	3	-42.5	89.3	7.8	0.003
0.28	0.82	NA	+	-0.03	0.004	NA	+	6	-41.2	89.3	7.8	0.003
0.74	NA	NA	+	-0.03	0.004	-0.01	+	6	-38.5	89.4	7.8	0.003
-1.09	NA	+	NA	-0.04	0.005	0.05	+	6	-41.3	89.4	7.8	0.003
-1.02	NA	+	NA	0.06	NA	0.06	+	5	-41.3	89.5	8.0	0.003
0.55	0.51	NA	+	NA	0.004	-0.01	+	6	-42.6	89.6	8.0	0.003
0.49	NA	NA	+	NA	NA	NA	NA	2	-41.4	89.6	8.1	0.003
0.83	NA	+	NA	-0.11	NA	NA	NA	3	-38.1	88.4	6.9	0.003
-1.47	0.33	+	NA	NA	0.004	0.06	+	6	-38.1	88.5	7.0	0.003
0.75	1.20	NA	+	NA	NA	0.00	+	5	-38.3	88.8	7.3	0.003
0.35	0.36	+	NA	-0.05	0.005	NA	+	6	-38.3	88.8	7.3	0.003
1.05	-2.72	NA	NA	-0.17	0.004	NA	NA	4	-42.2	88.9	7.3	0.003
1.19	-3.76	+	NA	NA	NA	NA	NA	3	-41.0	89.0	7.4	0.003
0.71	-0.15	+	NA	0.06	NA	NA	+	5	-36.8	89.0	7.5	0.003
-0.71	NA	NA	NA	NA	NA	0.05	NA	2	-36.9	89.1	7.5	0.003
1.18	-1.69	NA	NA	-0.08	NA	NA	NA	3	-36.9	89.1	7.5	0.003
-0.88	0.92	+	NA	NA	NA	0.05	+	5	-38.4	89.1	7.5	0.003
0.87	NA	NA	+	-0.11	NA	NA	NA	3	-36.9	89.1	7.5	0.003
0.55	NA	NA	NA	-0.11	NA	0.01	NA	3	-42.3	89.1	7.5	0.002
0.57	NA	NA	NA	NA	0.000	NA	NA	2	-41.1	89.1	7.6	0.002
1.21	-3.60	NA	+	NA	NA	NA	NA	3	-36.9	89.1	7.6	0.002
RI	**0.19**	**0.24**	**0.26**	**0.22**	**0.52**	**0.18**	**0.89**			**Cum wAICc**		**0.95**

Table S4. Model rankings of Negative Binomial GLM for large pelagic species relative abundance in the 95% confidence set of models and the relative importance of each predictor variable. Models are ranked based on minimum Akaike Information Criterion corrected for small sample sizes (AICc). Predictors used at each model were: 1) time - time of deployment (morning 6 – 10 am / afternoon 1 – 3 pm); 2) camera depth - camera depth level (shallow 10m / deep 25m; 3) seamount depth - summit depth level (shallow < 400m / deep > 400m); 4) drift – drifting distance of each deployment during the effective recording time (soak time); 5) MPA distance - minimum distance of each seamount to the boundaries of Cocos or Galápagos Islands; 6) temp - mean temperature at the camera depth level and 7) chla - mean chorophyll-a concentration. Log of soak time (hours of effective recording) was used as an offset in the models. Degrees of freedom (df), maximum Log Likelihood (LL), degrees of freedom (df), difference of AICc of a given model to the model with best fit (ΔAICc) and relative model probability expressed as AICc weight (wAICc) are shown for each model. The sum of the wAICc was used to calculate the relative importance of each variable in the 95% confidence set of models following (Burnham & Anderson 2002, Zuur et al. 2009a).

Int	Cla	D1	Time	Drift	Dist	Temp	D2	df	LL	AICc	ΔAICc	wAICc
1.7	NA	NA	NA	NA	0.01	NA	+	4	-82.08	173.64	0.00	0.24
1.4	NA	NA	+	NA	0.01	NA	+	5	-81.41	175.13	1.49	0.11
1.1	4.3	NA	NA	NA	0.01	NA	+	5	-81.65	175.61	1.98	0.09
-0.7	NA	NA	NA	NA	0.01	0.08	+	5	-81.94	176.18	2.54	0.07
1.7	NA	NA	NA	-0.04	0.01	NA	+	5	-82.01	176.34	2.70	0.06
1.6	NA	+	NA	NA	0.01	NA	+	5	-82.02	176.35	2.72	0.06
0.9	3.6	NA	+	NA	0.01	NA	+	6	-81.10	177.56	3.92	0.03
1.2	NA	+	+	NA	0.01	NA	+	6	-81.16	177.68	4.04	0.03
-0.2	NA	NA	+	NA	0.01	0.06	+	6	-81.34	178.03	4.40	0.03
1.4	NA	NA	+	-0.01	0.01	NA	+	6	-81.41	178.17	4.54	0.02
-2.0	4.8	NA	NA	NA	0.01	0.11	+	6	-81.42	178.20	4.56	0.02
0.8	5.1	+	NA	NA	0.01	NA	+	6	-81.47	178.31	4.67	0.02
1.1	4.7	NA	NA	-0.07	0.01	NA	+	6	-81.52	178.41	4.77	0.02
-3.7	NA	+	NA	NA	0.01	0.18	+	6	-81.60	178.55	4.92	0.02
-0.5	NA	NA	NA	-0.04	0.01	0.08	+	6	-81.89	179.14	5.51	0.02
1.6	NA	+	NA	-0.04	0.01	NA	+	6	-81.98	179.32	5.68	0.01
-8.0	7.5	+	NA	NA	0.01	0.29	+	7	-80.45	179.57	5.93	0.01
-4.8	NA	+	+	NA	0.01	0.20	+	7	-80.63	179.92	6.29	0.01
0.5	4.5	+	+	NA	0.01	NA	+	7	-80.70	180.06	6.42	0.01
1.2	11.4	NA	NA	NA	NA	NA	+	4	-85.40	180.28	6.65	0.01
-1.5	4.1	NA	+	NA	0.01	0.08	+	7	-80.95	180.57	6.93	0.01
0.9	3.9	NA	+	-0.03	0.01	NA	+	7	-81.07	180.80	7.17	0.01
1.2	NA	+	+	0.02	0.01	NA	+	7	-81.15	180.97	7.33	0.01
-9.2	7.2	+	+	NA	0.01	0.32	+	8	-79.52	181.29	7.66	0.01
-1.9	5.1	NA	NA	-0.06	0.01	0.10	+	7	-81.32	181.30	7.66	0.01

-0.2	NA	NA	+	0.00	0.01	0.06	+	7	-81.34	181.34	7.70	0.01
0.8	5.3	+	NA	-0.05	0.01	NA	+	7	-81.39	181.45	7.81	0.00
RI	**0.25**	**0.20**	**0.28**	**0.17**	**0.95**	**0.20**	**0.95**			**Cum wAICc**		**0.95**

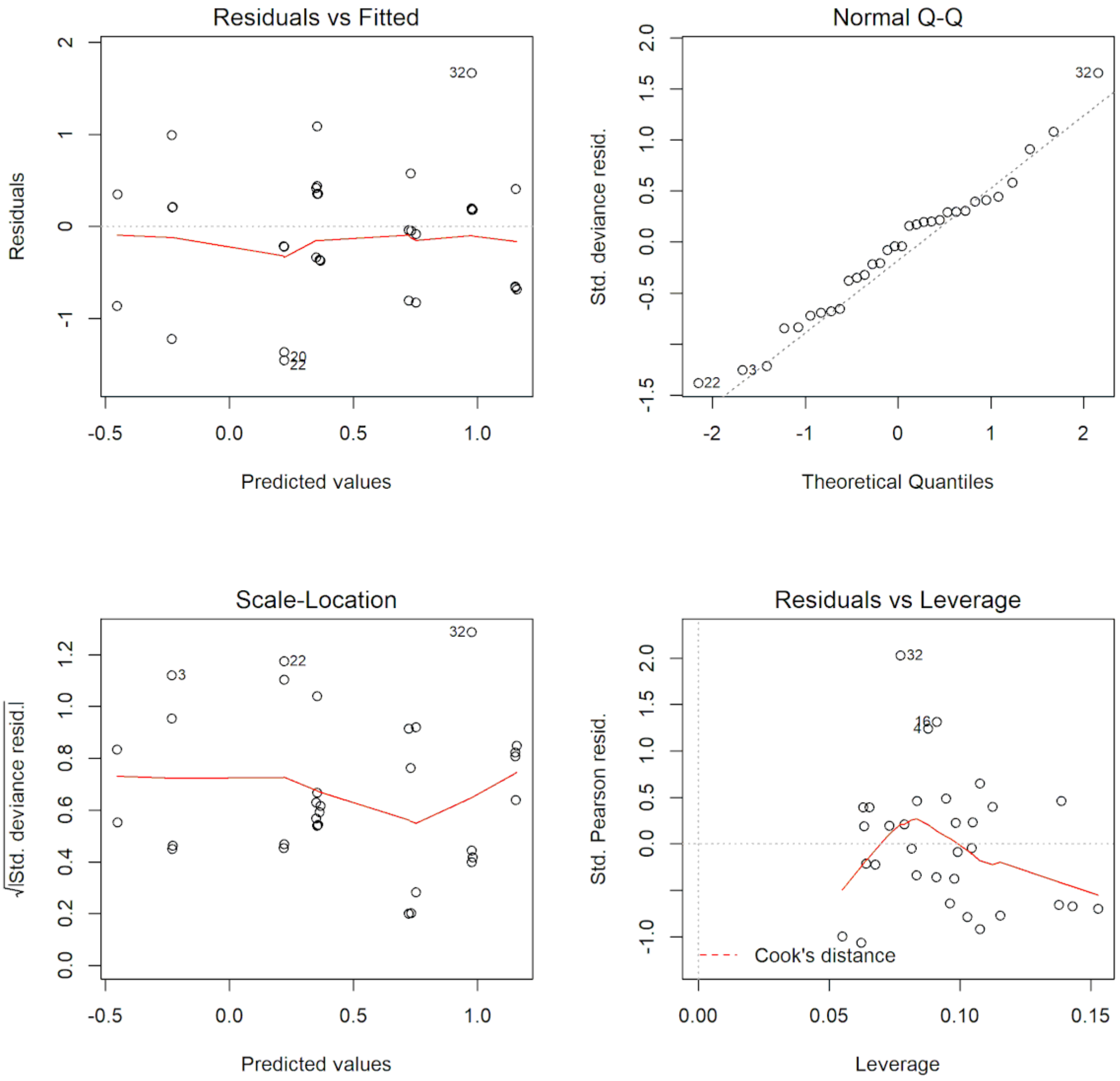

Fig. S3. Diagnostic plots of standard residuals from the first top ranked Poisson GLM for large pelagic species richness. The model is presented in Table 3.

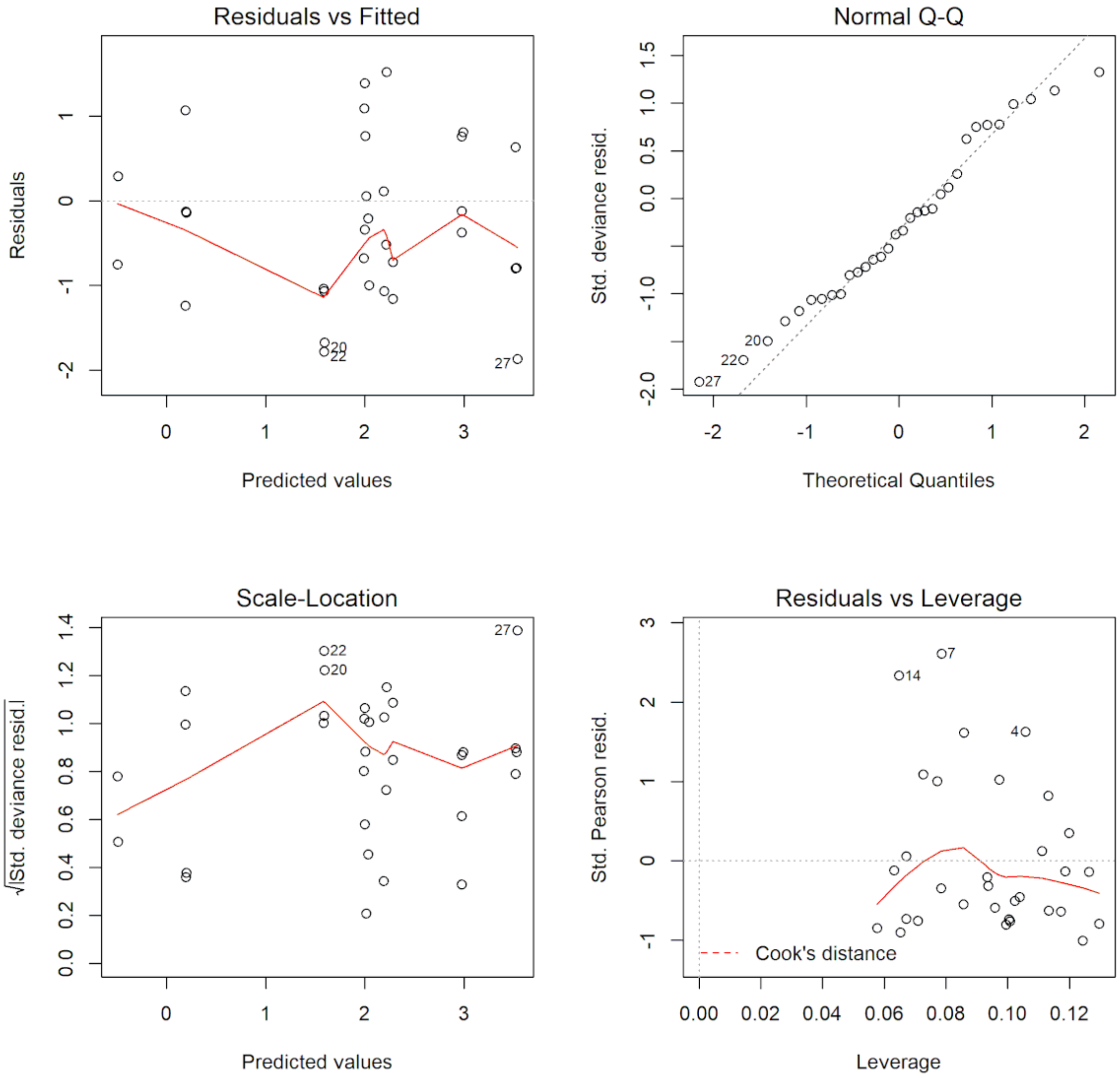

Fig. S4. Diagnostic plots of standard residuals from the first top ranked Negative Binomial GLM for large pelagic species relative abundance. The model is presented in Table 3.

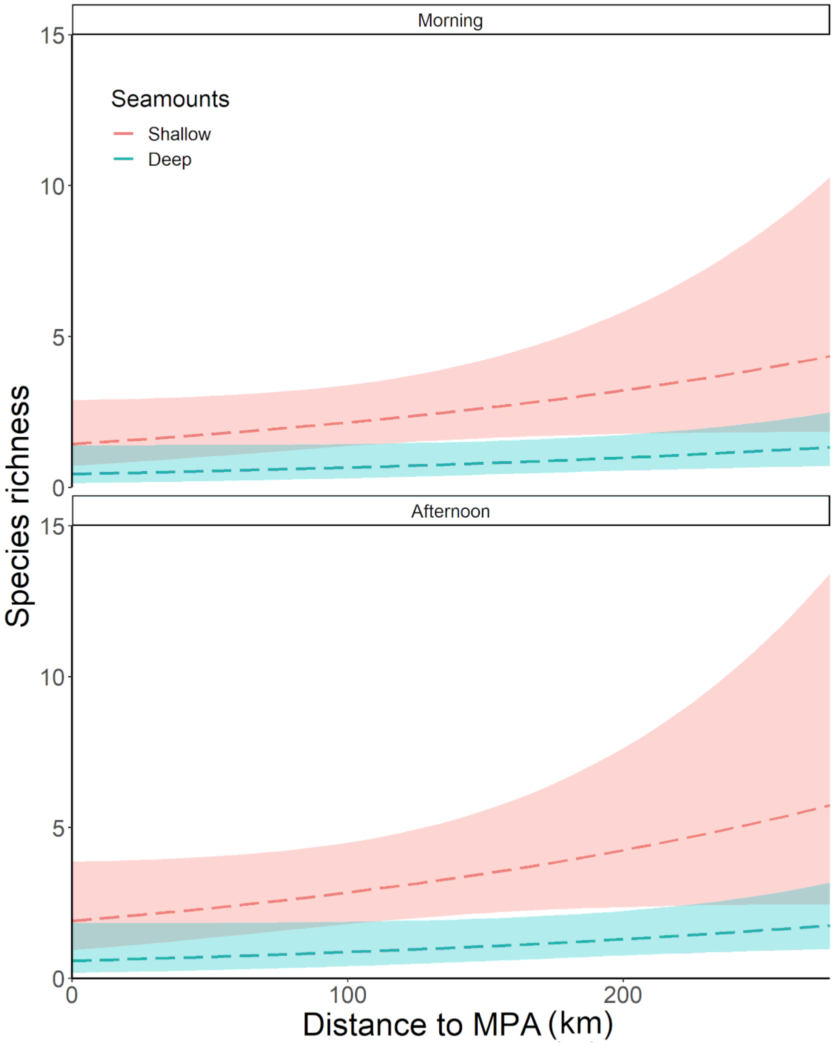

Fig. **S5.** Graphical results from the third ranked Poisson generalized linear model for large pelagic species (LPS) richness. Representation of the relationship between richness of LPS and distance to nearest MPA (Cocos or Galapagos Islands) at shallow (<400 m) and deep (>400 m) seamounts during morning and afternoon deployments.

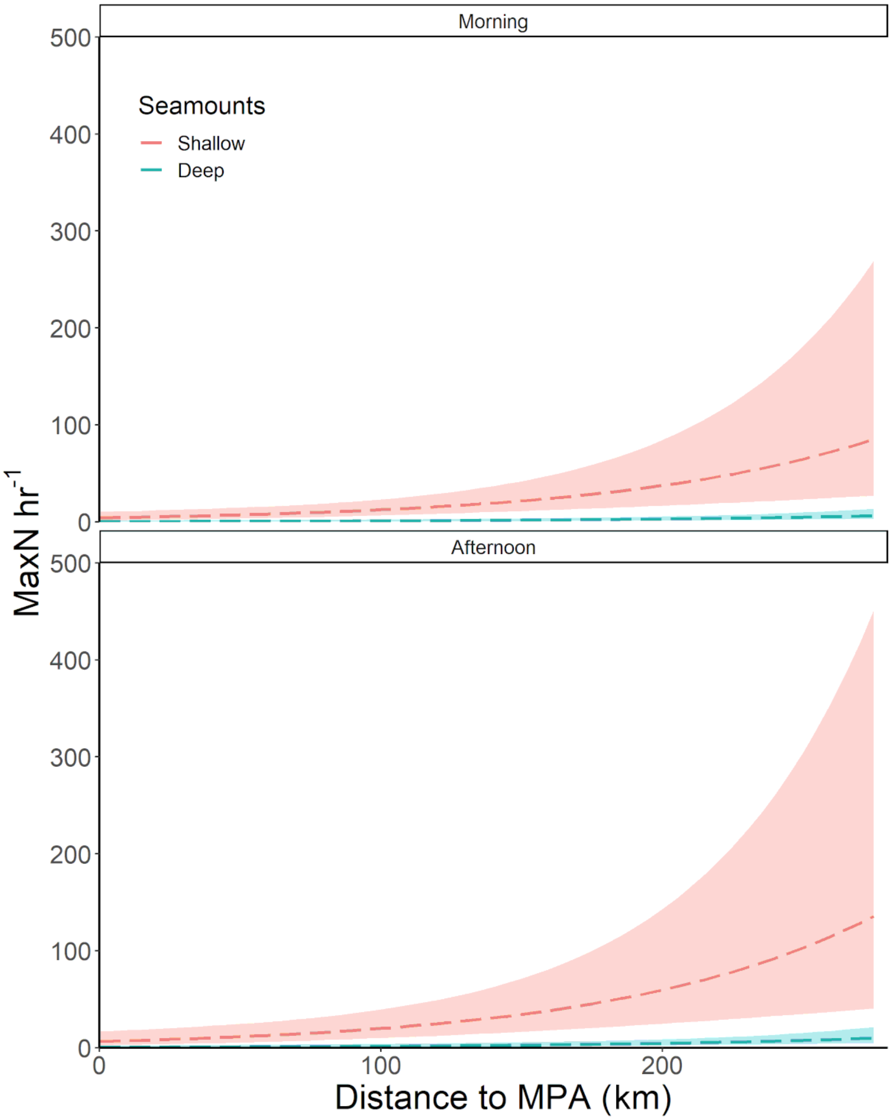

Fig. S6. Graphical results from the second ranked Negative Binomial generalized linear model for large pelagic species (LPS) relative abundance. Representation of the relationship between relative abundance of LPS and distance to nearest MPA (Cocos or Galapagos Islands) at shallow (<400 m) and deep (>400 m) seamounts during morning and afternoon deployments.

CAPÍTULO 3

First record of a potential neonate tiger shark (*Galeocerdo cuvier*) at a remote oceanic island in the Eastern Tropical Pacific

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ABSTRACT

Tiger sharks (*Galeocerdo cuvier*) play an important ecological role as top predators, yet knowledge of their reproductive ecology is scarce. Here, we report the first observation of a potential neonate *G. cuvier* at Cocos Island, a predator-dominated oceanic island in the Eastern Tropical Pacific. The individual was captured using baited remote underwater video stations (BRUVS). Our cameras also captured female individuals potentially pregnant, suggesting that parturition may take place at or near the island. However, it is still unclear if the presence of a single neonate is an isolated event or evidence that the species is using the island for reproduction.

Key words: Apex predator, Cocos Island, Costa Rica, pupping area, Baited-Remote-Underwater-Video-Stations

Identifying critical habitats of marine species, particularly those areas that are associated with reproduction (e.g., mating, spawning, gestation or parturition), is central to conservation planning (Beck et al. 2001, Nagelkerken 2009). This is especially important for heavily exploited and/or threatened species such as sharks, some of which play key ecological roles in the structure and functioning of marine ecosystems (Branstetter 1990, Walker 2005, Curtis et al. 2013, Heupel et al. 2014). However, for wide-ranging sharks, this information is often lacking due to the challenges of identifying species-specific behaviors or habitats associated with reproduction (Cortés 2000, Chapman et al. 2015).

The tiger shark, *Galeocerdo cuvier* (Péron & Lesueur 1822), is a large, iconic predator with a circumglobal distribution in warm-temperate and tropical marine waters (Compagno 1984). Despite its wide distribution and apex predator role in some tropical reef ecosystems (Hilting et al. 2013, Heithaus et al. 2014, Ferreira et al. 2017, Fourriére et al. 2019), the identification of mating, pupping, and nursery areas for *G. cuvier* is still lacking (Holland et al. 2019). Contrary to many other carcharhinids, *G. cuvier* has not been generally observed using specific locations as nursery areas (Whitney & Crow 2007, Driggers et al. 2008, Holmes 2015, Holland et al. 2019). As a result, parturition in this species is thought to be dispersed throughout their range (Whitney & Crow 2007, Driggers et al. 2008, Holmes 2015). However, at some oceanic islands such as Hawaii and Bahamas, there is some evidence that *G. cuvier* might be using specific pupping habitats (Papastamatiou et al. 2013, Sulikowski et al. 2016). A better understanding of the reproductive ecology of *G. cuvier* may help guide management strategies towards the conservation of the species (Whitney & Crow 2007, Sulikowski et al. 2016) and, in some cases, inform strategies for human safety (Meyer et al. 2018).

Here, we report the first observation of a potential neonate of *G. cuvier* at Cocos Island National Park, a remote oceanic island (>500 km from Costa Rica mainland) from the Eastern Tropical Pacific Ocean (ETP). This individual was detected at Yglesias Bay (5º30'33.52"N, 87º3'42.98"W) on the morning of 16 October 2020 by one of our baited remote underwater video stations (BRUVS) (Fig. 1a). The potential neonate was recorded swimming above a sandy seafloor near the bait container of the BRUVS at a depth of 26 m (Fig. 1b-c).

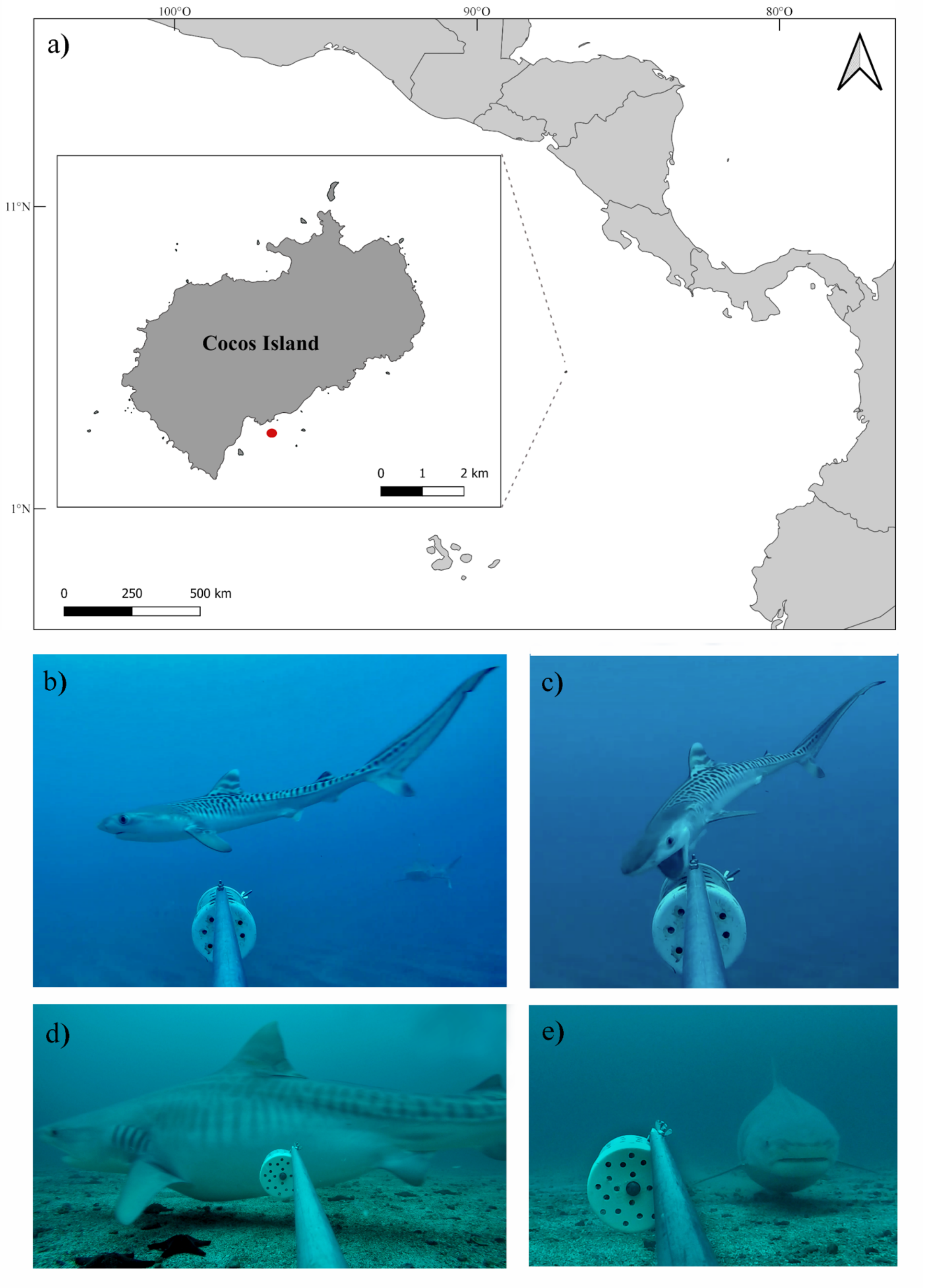
a)
100°O
90°O
80°O
11°N
1°N
Cocos Island
0
1
2 km
0
250
500 km
b)
c)
d)
e)

Fig. 1. Neonate tiger shark *(Galeocerdo cuvier)* sighting at Cocos Island in the Eastern Tropical Pacific Ocean. Panel (a) indicates the location where a neonate tiger shark was detected (red mark) within Yglesias Bay; panels (b, c) show still images from a neonate tiger shark; panels (d,e) show still images from apotentially pregnant tiger shark. Images were extracted from baited remote underwater video stations (BRUVS) deployed around Cocos Island as part of an ongoing shark monitoring study (Espinoza et al. 2020).

The reported size at birth of *G. cuvier* can range from 45 cm (Bigelow and Schroeder 1948) to 90 cm total length (Simpfendorfer 1992, Whitney & Crow 2007, Holmes 2015). Although we did not use stereo-BRUVS to estimate shark length, the size and position of the bait holder (11.5 cm at 80 cm from the camera) relative to the shark lateral position in multiple frames provided a reliable approach to estimate its furcal length (from the anterior-most part of the head to the deepest point of the notch in the upper lobe of the caudal fin), which was estimated to be 55 ± 5 cm (Fig. 1b-c). Furthermore, the specimen exhibited body features previously reported in neonates of this species such as a conical head and a slender body form, with a disproportionate caudal fin with the upper lobe substantially larger than the lower lobe and a low thrust angle (Fu et al., 2016; Randall, 1992). Similarly sized individuals of this species (<80 cm total length) have been caught on bottom longlines at similar depths and benthic habitats off the windward-side of Oahu, Hawaii (C. Lowe, Pers. Obser.).

Long-term sighting data from dive guides at Cocos Island (>25 years) indicate that the first records of *G. cuvier* at Cocos Island occurred in 2008 (White et al. 2015). Since then, the probability of occurrence of this species has increased steadily over time (White et al. 2015) and currently, the species is commonly observed by divers year-round (M. Cambra, Pers. Comm.). Despite these observations, to date there is no evidence in support of this species using Cocos Island as a parturition site. In over 400 BRUVS deployments made around the Cocos Island across a range of habitats since 2016 (Espinoza et al. 2020), this is the first sighting of a potential neonate of *G. cuvier*. Given the remoteness of Cocos Island and the low probability of neonates traveling long distances after parturition (Driggers et al. 2008), the observation reported herein suggests that a pregnant female could have given birth at or near Cocos Island.

During our BRUVS surveys we have observed, on multiple occasions and at different times of the year, female individuals displaying abdominal distension (Fig. 1d-e), indicative of pregnant females. Although we cannot discount the possibility that abdominal distension in these females was the result of recently consumed large meals, it is likely that these individuals correspond to pregnant females, supporting our hypothesis that at least some individuals of this species may be using Cocos Island as a parturition site rather than undertaking long-distance migrations to coastal areas. Newborn *G. cuvier* and pregnant females have also been reported at other predator-dominated remote (> 500 km) oceanic islands such as Hawaii (Whitney & Crow 2007) and Galápagos Islands (Acuña-Marrero et al. 2017), where individuals of this species are considered resident. In Hawaii, *G. cuvier* are thought to exhibit higher residency because all primary resources (food, conspecifics and suitable pupping areas) are available throughout the archipelago (Meyer et al. 2018). High levels of isolation, particularly in large productive reefs, might also result in an increase of residency of sharks (Heupel & Simpfendorfer 2014). Although Cocos Island is a relatively small island (23 km^2), it may offer sufficient food supply and a variety of habitats that this species requires for reproduction and long-term survival. An alternative hypothesis to explain the presence of a potential neonate of *G. cuvier* at Cocos Island is that a pregnant female captured near Cocos Island may have aborted her pups while hooked (Whitney & Crow 2007), as fishing is still considered the main threat affecting this remote island (Arias et al. 2016, López-Garro et al. 2016b). Therefore, there is a possibility that the observation of a single neonate *G. cuvier* at Cocos Island represents an isolated event.

Considering the high biomass of apex predators at this near pristine ecosystem (Edgar et al. 2011, Friedlander et al. 2012) and the relatively small size of neonate sharks at birth, mortality of this individuals due to predation could be high (Branstetter 1990, Heupel & Simpfendorfer 2002). Wafer and Chatham Bays (north side of Cocos Island; Fig. 1a) have been identified as important refugees for several juvenile and young-of-the-year (YOY) shark species (López-Garro et al. 2012, Zanella et al. 2012, 2016a b). However, the site where the neonate *G. cuvier* was recorded (Yglesias Bay), is located on the south side of the island, which has more exposure to wave action and stronger currents compared to the larger and more protected bays of the north (Lizano 2008a, Cortés 2016b) (Fig. 1a). Additionally, coral reef formations at Yglesias Bay are less extensive, complex and diverse than in Wafer and Chatham Bays (Alvarado et al. 2016). Notably, one factor that all these bays have in common is the freshwater influx from rivers and waterfalls that increase suspended sediments and water turbidity, especially during the rainy season (July – November) (Zanella et al. 2016b). Since water turbidity offers some degree of protection from visual predators in shark nurseries (Yates et al. 2015, Heupel et al. 2019), the presence of turbid waters at Yglesias

Bay could explain why a neonate of *G. cuvier* was found at this less complex habitat. Another hypothesis is that large litter sizes and a fast growth of YOY of this species (Branstetter *et al*. 1987) in an environment with abundant prey resources such as Cocos Island (Edgar et al. 2011, Friedlander et al. 2012, Fourriére et al. 2019) may compensate the need for protection from sheltered areas (Driggers et al. 2008). Finally, there is also the possibility that this neonate dispersed from its original parturition site at or near Cocos Island and moved to Yglesias Bay afterwards where it was detected by our BRUVS.

Even though Cocos Island is a remote and isolated no-take marine reserve, identifying a nursery for this wide-ranging, near threatened species, particularly in an area of the ETP with a high intensity of fishing effort (Whoriskey et al. 2011, Dapp et al. 2013, Arias et al. 2016) would have important implications for its management and conservation. Furthermore, providing evidence that this species may use other remote and isolated islands for parturition may be important for reducing regional population declines (Jaquemet et al. 2012). To better understand the reproductive ecology of *G. cuvier* at Cocos Island, combining our long-term shark monitoring program with other non-lethal tools such as acoustic/satellite telemetry, the use of portable ultrasound equipment or blood chemistry (Sulikowski et al. 2016) would allow us quantify their reproductive cycles (migratory routes, parturition sites, home range, etc.). Using stereo-BRUVS in the future (two cameras instead of one per station) will allow for more precise length measurements of shark species. Such research efforts are expected to guide more effective management and conservation approaches for *G. cuvier* in the region.

ACKNOWLEDGEMENTS

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CONCLUSIONES

Este trabajo de investigación cumplió con los objetivos inicialmente propuestos generando información relevante y previamente desconocida sobre la distribución de grandes depredadores en ambientes remotos del PTO. En el primer capítulo representa el eje central de esta tesis y donde se concentró la mayor parte del esfuerzo de monitoreo y de análisis. En este capítulo se cuantificó el efecto de factores ambientales y espaciales en la distribución y estructura comunitaria de elasmobranquios en ambientes bentónicos y pelágicos del PNIC. Dada la escasez global de sitios remotos mínimamente perturbados con una alta diversidad y abundancia de elasmobranquios, este estudio representa una contribución relevante sobre la relación que existe entre variables naturales y especies altamente amenazadas por actividades antropogénicas. Estos resultados pueden ser utilizados como una línea base a partir de la cual evaluar cambios en la estructura comunitaria y los patrones de abundancia y distribución de elasmobranquios tras la reciente expansión del Área de Conservación Marina Cocos.

Adicionalmente, en el capítulo 2 se presentó la primera caracterización del ensamblaje de grandes depredadores en montes submarinos ubicados fuera de los límites de protección del PNIC, así como otras Áreas Marinas Protegidas (AMP) del PTO. A raíz del éxito de esta primera expedición a montes submarinos, se desarrollaron otras expediciones en distintas zonas del PTO, que en conjunto brindan información fundamental para el manejo y protección de especies migratorias en estado de amenaza. Esta información es especialmente importante ante la reciente expansión de varias AMP en ambientes pelágicos del PTO incluyendo el PNIC, el Área Marina de Manejo del Bicentenario, la Reserva Marina Galápagos (Ecuador) y el Santuario de Flora y Fauna Malpelo (Colombia). La identificación de montes submarinos como sitios de agregación de especies amenazadas permite focalizar los esfuerzos de monitoreo y protección en sitios ecológicamente relevantes dentro de estas AMP.

En el capítulo 3 se demostró como el uso de BRUVS puede proporcionar información relevante más allá de la abundancia y distribución de especies, sino también evidencias del uso del hábitat para realizar actividades biológicamente importantes, tales como la reproducción de especies de depredadores, como lo es el tiburón tigre.

Los capítulos 2 y 3 de esta tesis ya fueron revisados por revisores externos los cuales aprobaron su publicación en revistas científicas de renombre como Plos One (capítulo 2) y Journal of Fish

Biology (capítulo 3). Los esfuerzos derivados del capítulo 1 y 3 de este proyecto se realizaron bajo un convenio entre el Centro de Investigación en Ciencias del Mar y Limnología de la Universidad de Costa Rica y el Área de Conservación Marina Cocos, el cual ha permitido el desarrollo y actual continuación de este estudio como un proyecto de monitoreo a largo plazo. Los estudios a largo plazo en este tipo de ambientes son cruciales dado que representan una de las pocas referencias disponibles para entender el funcionamiento natural de los arrecifes coralinos saludables en ausencia de impactos humanos.