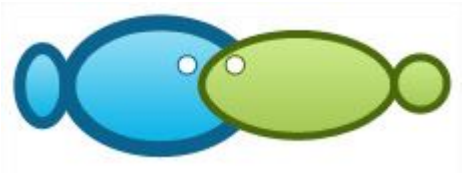

Sharks and rays (Chondrichthyes) around Banggai Island, Banggai MPA, Indonesia: biodiversity data from an environmental DNA pilot study

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Abstract. The Banggai Archipelago is one of six major island groups around Sulawesi Island in Indonesia, within the Wallacea region. Initiated after two district level marine protected areas (MPAs) in the Banggai Archipelago became obsolete under the revised regional autonomy Act (UU 23/2014) before they had become operational, the more extensive provincial level Banggai MPA was formally established under national legislation in 2019. Comprehensive and up-to-date biodiversity data for this MPA are needed; however taxonomic expertise and funding are limited. Furthermore, many taxa are likely to be missed using visual census methods. This study applied molecular biology methods to evaluate biodiversity of the Class Chondrichthyes (sharks and rays) at four sites around Banggai Island, in Banggai Laut District, within the Banggai MPA. Environmental DNA (eDNA) seawater samples were collected in October 2018 (3 replicates per site). The eDNA was extracted at Bionesia in Bali. Metabarcoding (using both standard MiFish 12S primer pairs) and sequence library preparation were conducted at the Barber Lab, University of California Los Angeles (UCLA). High-throughput sequencing was performed on a Nextseq. Generated sequences were processed using the *Anacapa Toolkit*; elasmobranch sequences were analysed by site and aggregated into amplicon sequence variants (ASVs) using the 60% Bayesian confidence score. Across all sites we identified 11 ASVs belonging to 2 Orders, 2 Families, and 7 genera. Nine ASVs were resolved to species level, while over two fifths of sequences were only assigned to genus level. BLAST search of the NCBI GenBank database and phylogenetic analysis of the ASVs in MEGA 10 produced similar results. Taxa identified included endangered species protected under Indonesian law. The results can inform elasmobranch management in the Banggai MPA. They also highlight a need for further efforts to barcode elasmobranchs in Wallacea.

Key Words: elasmobranchs, eDNA, Banggai Archipelago, Wallacea, Anacapa Toolkit, 12S mtDNA.

Introduction. The Banggai Archipelago is one of six major island groups around Sulawesi Island in eastern Indonesia, within the Wallacea Region and Coral Triangle (Ambo-Rappe & Moore 2018). Once part of the Australasian plaque (Hall 2012), the complex geological history is just one of several factors contributing to the rich biodiversity of this region (Stelbrink et al 2012). The seas around and between the many islands to the east of Sulawesi Island in the Gulf of Tolo, Banda, Seram and Molucca Seas provide important habitat for resident and migratory marine megafauna including marine mammals, sea turtles and elasmobranchs (sharks and rays) (Allen & McKenna 2001; Ndobe et al 2005; Dermawan et al 2013; Moore et al 2017).

At national and international levels, the Banggai Archipelago is perhaps most widely known as the home of the Banggai cardinalfish (*Pterapogon kauderni* Koumans,

1933), a marine fish with an unusual life history and exceptionally restricted endemic range (Vagelli 2011; Ndobe et al 2013). Now a partially protected species under regulation of the Minister of Marine Affairs and Fisheries of the Republic of Indonesia (MMAF-RI 2018a), *P. kauderni* was recently declared the national icon for marine ornamentals, with the arwana as the freshwater ornamental icon. Listed as Endangered in the IUCN RED List since 2007 (Allen & Donaldson 2007) and twice proposed for CITES Appendix II listing (Ndobe et al 2018, 2019), concern over the conservation status of *P. kauderni* has been a driving factor for MPA establishment, initially at district level (Moore & Ndobe 2013).

When the revised Regional Autonomy Act UU 23/2014 was passed, jurisdiction over waters from 0-4 NM offshore was transferred from district to provincial level and all district level MPAs automatically became null and void. Working with the district governments and academia, and supported by the MMAF and the World Wild Life Fund for Nature (WWF) Indonesia, Central Sulawesi Province declared a new Banggai MPA under Decree of the Governor of Central Sulawesi Province 523/635A/DIS.KANLUT-GST/2017.856649.13. With a total area of approximately 8,566.5 km^2, this MPA comprises coastal and archipelagic waters in three districts (Banggai, Banggai Laut and Banggai Kepulauan) and has been gazetted at national level under MMAF Ministerial Decree 53/KEPMEN-KP/2019 (MMAF-RI 2019).

The Banggai MPA is important for many resident and migratory species. Surveys in 2014 and 2015 found that 16 out of the 20 priority conservation species or species groups designated by the Indonesian Ministry of Marine Affairs and Fisheries (MMAF) can be found in the area of the Banggai Archipelago now within MPA (Abigail Moore and Samliok Ndobe, unpublished data). These included bony fish: the Banggai cardinalfish (*Pterapogon kauderni*), Napoleon wrasse (*Cheilinus undulatus*), seahorses (genus *Hippocampus*), the sunfish (*Mola mola*), and anguillid eels (genus *Anguilla*); marine turtles (Cheloniidae and Dermochelyidae); marine mammals: whales and dolphins (Cetacea) and dugongs (*Dugong dugon*); invertebrates: tridacnid clams (Tridacnidae), trochus (*Tectus niloticus*), sea cucumbers (Holothuriidae), reef building or hard corals (Scleractinia), and the sea bamboo (*Isis hippuris*); and elasmobranchs: the whale shark (*Rhincodon typus*), hammerhead and requiem sharks (genera *Sphyrna* and *Carcharhinus*), manta and other mobulid rays (Mobulidae).

Sharks and rays, elasmobranchs of the Class Chondrichthyes, are a taxonomic group of concern to marine conservation and fisheries stakeholders alike (White & Cavanagh 2007; Heithaus et al 2014; Momigliano 2016; Jaiteh et al 2017). Globally, elasmobranchs form an increasing proportion of fisheries catch, with new species categories appearing in recent decades (Zeller & Pauly 2007). Many elasmobranch species mature late and produce few offspring (Choat & Bellwood 1991), making them intrinsically vulnerable to over-exploitation (Blaber 2000; Wallace et al 2013; Momigliano 2016). While the fins are generally the main target of fishers (Sembiring et al 2015; Momigliano 2016; Jaiteh et al 2017), many body parts including shark and ray meat and skin, shark liver oil and shark teeth are also traded commercially and/or for subsistence or cultural uses (Burgess 2009; Glaus et al 2015; Lawrence et al 2016; Madduppa et al 2016; Rigby et al 2019a). Elasmobranch body parts are also used in traditional remedies; for example shark flesh, skin, and bile are reported as ingredients in traditional Chinese medicine (Alves & Rosa 2013).

The most recent International Union for Conservation of Nature (IUCN) Red List assessment in 2020 (IUCN 2020) evaluated 1134 chondrichthyan species, of which 37% were classed as Data Deficient (DD). Of the 714 species with sufficient data to classify the conservation status, 6% (43 species) were considered Critically Endangered (CR), a category not present in the 2009 assessment of this group (Camhi et al 2009); 8.7% (62 species) Endangered (EN); 15.7% (112 species) Vulnerable (VU); 16.1% (115 species) Near Threatened (NT); and 53.5% (382 species) Least Concern (LC) (IUCN 2020). Overall, the 2020 assessment (IUCN 2020) shows an increase in both the number of species assessed and the threat levels for several species compared to assessments in 2009 and 2014 (Camhi et al 2009; Dulvy et al 2014).

Fisheries are not the only threat to sharks and rays (Momigliano 2016); however, concerns regarding the sustainability of shark and ray fisheries and trade have led to the listing of a growing number of elasmobranchs in the Appendices to the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES) (FAO 2016). As of August 2020 one elasmobranch family (Pristidae) was listed in CITES Appendix I (species threatened with extinction, no commercial international trade allowed), while another family (Rhinidae), 4 whole genera and 20 named species were listed in CITES Appendix II or III (international trade must be regulated to prevent over-utilisation) (CITES 2020).

In Indonesia, a wide variety of sharks and rays are heavily exploited as target fish and as by-catch (McKenna et al 2001; White & Cavanagh 2007; Blaber et al 2009; Dermawan et al 2013; Sembiring et al 2015; Momigliano 2016; Jaiteh et al 2017; Zainudin et al 2017). Studies on shark fisheries in eastern Indonesia (Jaiteh et al 2017) and southern Indonesia (Blaber et al 2009) found that they tend to be multi-gear and multi-species, data poor, and are unlikely to be sustainable. Furthermore, threatened species and/or juveniles often comprise the majority of the catch (Sembiring et al 2015; Jaiteh et al 2017; Zainudin et al 2017). A study in 2016 found five species of rays for sale on three fish markets in Indonesia (Madduppa et al 2016), while at least 40 shark species are caught for their fins (Sembiring et al 2015) and at least 144 species representing 36 families were recorded in a survey of chondrichthyan landings at 9 fishing ports over four years (White & Cavanagh 2007). In addition, at least six shark species are exported in the ornamental fish trade (Handayani et al 2018). Several shark and ray species are partially protected under national regulations. However there is evidence that the regulations are often poorly understood and/or not implemented effectively (Dermawan et al 2013; Momigliano 2016), at least in part due to a lack of appropriate data (Sembiring et al 2015).

There is a need for comprehensive and up-to-date biodiversity data for the Banggai MPA in general, and in particular for sharks and rays. However, taxonomic expertise and funding are limited. Furthermore, sharks and rays are often migratory or have extensive home ranges, and some species are readily disturbed or cryptic (Portnoy & Heist 2012). These traits make them likely to be missed using visual census methods. This is evidenced by the 1998 Marine RAP survey (Allen & McKenna 2001), where ichthyologist Gerry Allen recorded a total of 661 fish species from 18 sites in the Banggai Archipelago; however no sharks and only two ray species were seen; *Dasyatis kuhlii* was noted as rare, and *Taeniura lymma* as occasional. However, that does not mean that sharks are absent from the Archipelago. There is considerable (albeit largely anecdotal and/or unpublished) evidence that, as has been reported in Fiji (Glaus et al 2015), sharks of all sizes are caught in multigear multispecies artisanal fisheries both as target species and as by-catch, and that the practice of shark finning has long been common in the Banggai Archipelago (Ndobe et al 2005; Abigail Moore and Samliok Ndobe, unpublished data).

The growth of molecular biology methods in recent years offers new ways to evaluate and monitor biodiversity (Lim et al 2016; Goodwin et al 2017; Stat et al 2017; Sard et al 2019). Elasmobranch ecology and population structure are also being investigated using molecular markers (Portnoy & Heist 2012; Chin et al 2013; Gray 2014; Johri et al 2019). DNA barcoding aims to enable species identification using standardised molecular markers (Bucklin et al 2011), typically segments from 12S or COI regions of the mitochondrial DNA (mtDNA) genome (Keyse et al 2014; Gillet et al 2018; Sato et al 2018; Curd et al 2019; Russo et al 2020; Sigsgaard et al 2020). Barcoding has been used to identify elasmobranchs from preserved body parts, especially dried fins, as well as samples from live or fresh specimens (Holmes et al 2009; Prehadi et al 2015; Sembiring et al 2015; Madduppa et al 2016; Abdullah & Rehbein 2017).

In addition to samples collected from whole organisms or body parts, so-called environmental DNA (eDNA) can be obtained from the cells shed by organisms into the surrounding environment (Curd et al 2019; Gold et al 2020). This can enable the identification of species present in an area from samples of soil/sediment or water (Lim et al 2016; Stat et al 2017; Sard et al 2019). The increasing use of eDNA in biodiversity

and conservation programs includes the detection or monitoring of marine megafauna such as marine mammals and elasmobranchs (Civade et al 2016; Goodwin et al 2017; Stat et al 2017; Stewart et al 2017; Baker et al 2018; Gold et al 2020).

Metabarcoding using high throughput sequencing technology involves isolating molecular markers from the DNA present in eDNA samples and reading the nucleotide sequences (Lim et al 2016; Andruszkiewicz et al 2017; Goodwin et al 2017; Curd et al 2019; Sard et al 2019; Gold et al 2020). The sequences are then dereplicated into unique amplicon sequence variants (ASVs), each comprising identical sequence and compared with sequences stored in databases such as the Barcode of Life Database (BOLD) and NCBI GenBank using analysis pipelines such as the *Anacapa Toolkit* (Curd et al 2019; Gold et al 2020). The ASVs are identified to the lowest possible taxonomic level (which may be species, genus, family, or even class). This small-scale pilot study evaluated the shark and ray biodiversity around Banggai Island, in Banggai Laut District, within the Banggai MPA through the application of eDNA metabarcoding approaches.

Material and Method

Sampling site and collection methods. This study applied eDNA metabarcoding approaches to evaluate chondrichthyan biodiversity. The eDNA seawater samples (Table 1) were collected in October 2018 from four sites around Banggai Island, in Banggai Laut District, Central Sulawesi Province, Indonesia (3 replicates per site). Sterile 1 L enteral feeding bags with Sterivex filters attached were used to collect seawater samples while snorkelling in coastal waters. The filled bags were sealed, taken ashore and placed in an ice-filled coolbox. The seawater samples were filtered through the Sterivex filters within a maximum of 3 hours after collection. The bags were hung at a height of approximately 2 m to enable the water to flow through the feeding bag tubes to the filters until they were empty (gravity-induced flow). These filters were then injected with Qiagen ATL buffer solution and sealed with caps and parafilm. The Sterivex filter samples were then maintained at or below 0ºC throughout storage and transport. Kis Thermafreezer icepacks were used when in transport and freezers (at around -18ºC) were available in Banggai and stops in Luwuk and Makassar as well as on arrival at the Bionesia laboratory in Denpasar, Bali.

Table 1

Sampling sites and eDNA samples collected

eDNA collection site				*No. of samples*	*Habitat type*	*Water depth*
Name	*Code*	*Latitude S*	*Longitude E*			
Monsongan	MO	1.832	123.484	3	Semi-exposed reef flat	1-2 m
Bone Baru	BB	1.530	123.491	3	Semi-exposed bay, seagrass, reef flat/crest	1-3 m
Oyama	OY	1.480	123.525	3	Exposed bay, sand and coral bommies	1-3 m
Lokotoy-Popisi	LP	1.497	123.518	3	Sheltered bay, seagrass-dominated with corals	1-2 m

Extraction, ***PCR and sequencing***. Extraction of the eDNA at Bionesia in Denpasar Bali used Qiagen blood and tissue kits with a protocol developed by Bionesia for samples collected using Sterivex filters (Spens et al 2017). The major modification from standard Qiagen protocols was the use of a rotating holder developed by Bionesia to which the Sterivex filters were attached during incubation. The extracted sample eDNA was maintained at or below 0ºC throughout the chain of custody from Bionesia in Denpasar to the Barber Lab at the University of California Los Angeles (UCLA), USA. The same methods as above were used, i.e. Kis Thermafreezer icepacks in a coolbox during transport and freezer storage (at -18^{o}C or lower) during stops in Makassar and Jakarta, and on arrival in Los Angeles. The standard MiFish 12S (Universal and Elasmobranch) primers (Miya et al 2015) were used, and PCR was performed in triplicate for each

sample, a standard practice at the UCLA Barber Lab to maximise the likelihood of successful amplification of the DNA present in each eDNA sample.

PCR product was verified through electrophoresis, after which the product of the three replicates for each sample was pooled and bead cleaned following the methods of Faircloth et al (2014). A second indexing PCR was conducted following the methods of Curd et al (2019) using Illumina Nextera indexes. Indexed libraries were then bead cleaned following the methods above, pooled by equal concentration and then sequenced on an Illumina Nextseq mid-output PE 2 x 150bp at the UCLA Technology Center for Genomics and Bioinformatics.

Data analysis. Sequences generated by the high-throughput sequencing were processed using the *Anacapa Toolkit* (Curd et al 2019) to dereplicate the sequences into ASVs and identify chondrichthyan taxa. The ASVs assigned to the Class Chondrichthyes by the 60% Bayesian confidence score outputs of the *Anacapa Toolkit* (Gao et al 2017) were tabulated in Microsoft Excel 2010 and compared with data from visual surveys and other sources including grey literature and unpublished data collected by two of the authors (Abigail M Moore and Samliok Ndobe) from 2004 to 2019. Graphical analysis at genus and family level was performed using the *ranacapa* R package and Shiny web application (Kandlikar et al 2018) associated with the *Anacapa Toolkit* (Curd et al 2019).

The sequences obtained were further analysed through use of the NCBI BLAST tool (Altschul et al 1990) with default parameters. The ASV sequences were aligned, incorporating representative sequences from the BLAST search (Table 2) and phylogenetic trees for sharks and rays were constructed in MEGA X (Kumar et al 2018). Evolutionary history was inferred using the Maximum Likelihood with Kimura 2-parameter model (Kimura 1980) with default parameters (bootstrap x100). The tree was edited using the interactive Tree of Life (iTOL) on-line tool (Letunic & Bork 2016, 2019).

Table 2

NCBI GenBank accessions used in the shark and ray phylogenetic analyses

No	*Taxon*	*Accession number*	*% Query cover*	*Max % similarity*	*Reference*
		Sharks			
1	*Carcharhinus amboinensis*	KM921745.1	100	97.5	Feutry et al (2014)
2	*Carcharhinus amblyrhynchoides*	KF956523.1	100	100	Feutry et al (2016)
3	*Carcharhinus brachyurus*	AB938094.1	100	97.48	Miya et al (2015)
4	*Carcharhinus brevipinna*	KM244770.1	100	100	Chen et al (2016)
		LC277740.1	100	100	Unpublished 2017
5	*Carcharhinus galapagensis*	LC578887.1	100	100	Unpublished 2020
		LC552343.1	100	100	Unpublished 2020
6	*Carcharhinus leiodon*	MH248226.1	100	100	Unpublished 2018
7	*Carcharhinus limbatus*	AB938095.1	100	100	Miya et al (2015)
		MH248235.1	100	100	Unpublished 2018
		MN883183.1	100	100	Unpublished 2019
8	*Carcharhinus longimanus*	KM434158.1	98	100	Li et al (2016)
9	*Carcharhinus macloti*	LC277739.1	100	100	Unpublished 2017
10	*Carcharhinus melanopterus*	FJ792633	98	98.74	Unpublished 2009
11	*Carcharhinus obscurus*	AB938100.1	100	100	Miya et al (2015)
		KC470543.1	100	100	Blower et al (2013)
12	*Sphyrna mokarran*	AF448022.1	100	100	Unpublished 2001
		KY464952	100	98.78	Ruck et al (2017)
13	*Sphyrna lewini*	AF448021.1	100	100	Unpublished 2001
14	*Triaenodon obesus*	KJ748376.1	100	100	Unpublished 2014
		MN943497.1	100	100	Unpublished 2020

No	Taxon	Accession number	% Query cover	Max % similarity	Reference
		Rays			
1	*Bathytoshia lata*	AB974598.1	100	100	Miya et al (2015)
		AB938121.1	100	99.44	
2	*Dasyatis centroura*	MH377784.1	100	100	Unpublished 2015
3	*Dasyatis kuhlii*	AF447991.1	100	100	Unpublished 2001
4	*Dasyatis thetidis*	AF447993.1	100	99.44	Unpublished 2001
5	*Dasyatis* sp.	LC020857.1	100	100	Unpublished 2015
6	*Himantura gerrardi*	AF447996.1	100	96.3	Unpublished 2001
7	*Himantura imbricata*	MH248229.1	100	95.6	Unpublished 2018
8	*Himantura uarnak*	AB938122.1	100	98.90	Miya et al (2015)
		AF447997.1	100	99.45	Unpublished 2001
		KR019776.1	100	99.45	Shen et al (2016)
9	*Neotrygon kuhlii*	KR019777.1	100	100	Shen et al (2016)
		KC992792.1	100	100	Unpublished 2013
		AF447991.1	100	100	Unpublished 2001
10	*Taeniura lymma*	LC020860.1	100	98.34	Unpublished 2015
		AF448024.1	100	98.34	Unpublished 2001
		KM881715.1	100	99.45	Unpublished 2014

Results

Ranacapa analysis. A total of 4669 chondrichthyan sequences (Class Chondrichthyes, Subclass Elasmobranchii) were recovered out of a total of 308,981 sequence reads. Shark and ray taxa identified from eDNA in this study (Table 3) comprise 2 Orders, 3 Families and 7 genera with 8 named species. ASVs assigned at genus but not at species level (3 ASVs) comprised 43.5% of sequences in the *Anacapa Toolkit* 60% Bayesian confidence score output. The genus level relative abundance of the ASVs (Figure 1) highlight the most abundant taxa and the variability within as well as between the four sites, with no sequences recovered for one replicate at three of the four sites.

Table 3

Shark and Ray (Elasmobranch) ASV's identified from eDNA using the Anacapa Toolkit

No	*Taxonomic identification of ASV (Anacapa toolkit, 60%)*			*Common names*
	Order	*Family*	*Genus/Species*[a]	
1	Carcharhiniformes	Carcharhinidae	*Carcharhinus* sp.	Requiem sharks
2	Carcharhiniformes	Carcharhinidae	*Carcharhinus brevipinna*	Spinner shark
3	Carcharhiniformes	Carcharhinidae	*Carcharhinus obscurus*	Dusky shark
4	Carcharhiniformes	Carcharhinidae	*Triaenodon obesus*	White-tip reef shark
5	Carcharhiniformes	Sphyrnidae	*Sphyrna* sp.	Hammerhead sharks
6	Carcharhiniformes	Sphyrnidae	*Sphyrna mokarran*	Great hammerhead shark
7	Myliobatiformes	Dasyatidae	*Dasyatis centroura* (*Bathytoshia centroura*)	Roughtail stingray
8	Myliobatiformes	Dasyatidae	*Dasyatis* sp. KAUM:I:34129	Stingrays
9	Myliobatiformes	Dasyatidae	*Himantura uarnak* (*Dasyatis uarnak*)	Honeycomb stingray, reticulate whipray
10	Myliobatiformes	Dasyatidae	*Neotrygon kuhlii (Dasyatis kuhlii)*	Bluespotted stingray
11	Myliobatiformes	Dasyatidae	*Taeniura lymma*	Bluespotted ribbontail stingray

[a] Names in parenthesis are synonyms of the species names obtained from the *Anacapa Toolkit* according to FishBase (Froese & Pauly 2020).

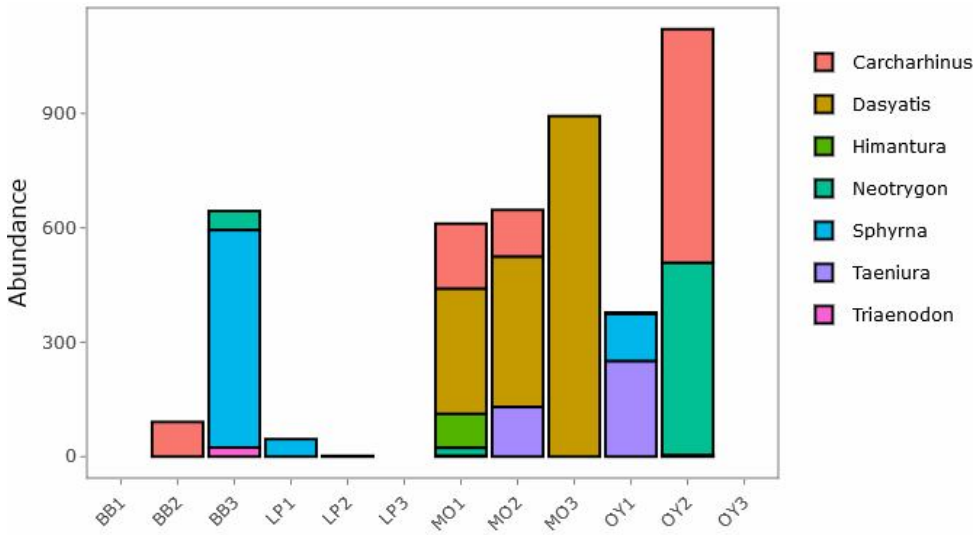

Figure 1. Relative abundance by genus of elasmobranch ASVs identified by sample. Site codes: BB = Bone Baru; LP = Lokotoy-Popisi; MO = Monsongan; OY = Oyama.

Phylogenetic analysis. The BLAST search and combined phylogenetic analysis resulted in two well separated clades representing the sharks and rays. The results are shown in the form of circular trees for sharks (Figure 2) and rays (Figure 3).

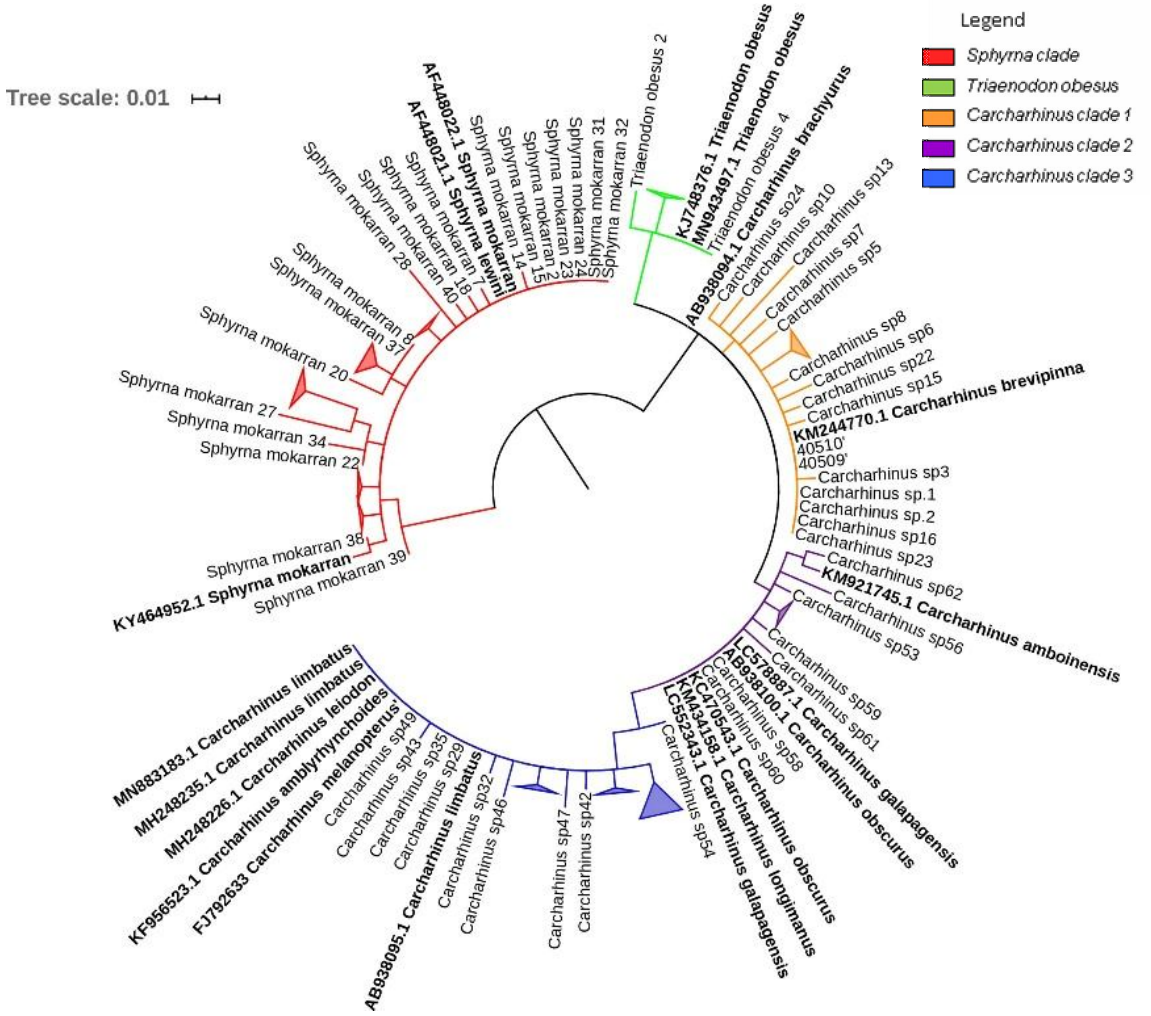

Figure 2. Maximum Likelihood phylogenetic tree of shark ASV sequences combined with GenBank accessions (Table 2) based on a 125 sequence dataset with 160 nucleotide positions. Size of terminal triangles is proportional to the number of sequences in collapsed clades.

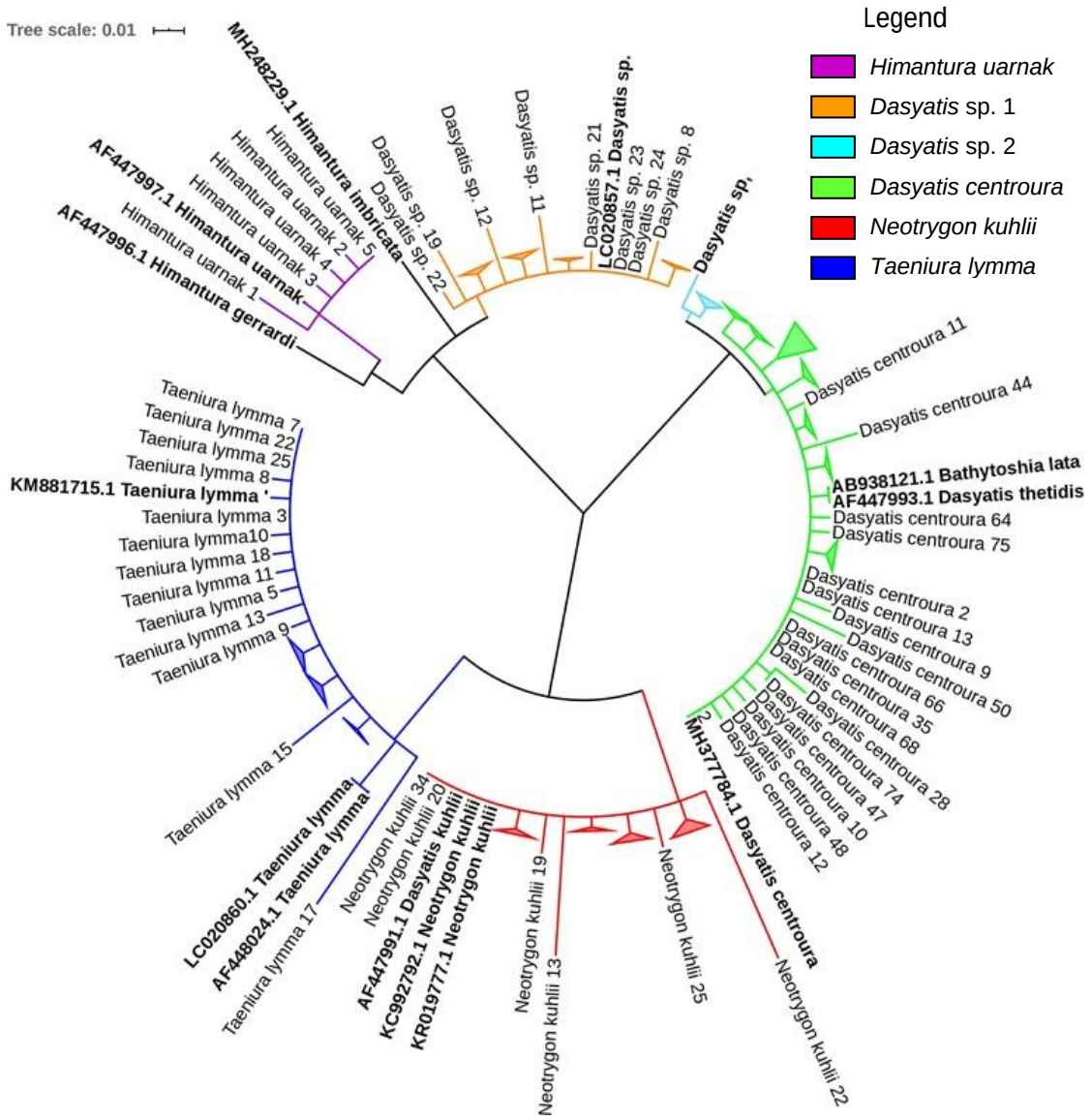

Figure 3. Maximum Likelihood phylogenetic tree of ray (Dasyatidae) ASV sequences combined with GenBank accessions (Table 2) based on a 167 sequence dataset with183 nucleotide positions. Size of terminal triangles is proportional to the number of sequences in collapsed clades.

In addition to the data presented in Table 3 and Figures 1 to 3, the Anacapa toolkit also recovered 235 sequences (4 ASVs) identified as the big skate *Raja binoculata* (Family Rajidae, Order Rajiformes). All these sequences were from the third replicate collected at the Oyama site (sample OY3). The big skate is an Eastern Pacific species which was used as a positive control in the laboratory analysis, and no other chondrichthyan sequences were recovered from this sample.

Discussion

Sampling and analysis methodology. The ASVs identified as *Raja binoculata* (valid name *Beringraja binoculata* in FishBase (Froese & Pauly 2020)) are an artefact of the methods used. This species is only known from the eastern North Pacific region (Ebert & Davis 2007; Froese & Pauly 2020) and was used as a positive control. The presence of this ASV indicates low-level contamination in one sample (OY3) which did not yield any other elasmobranch species. This example highlights the importance of extreme care in the laboratory as well as of maintaining scepticism regarding unexpected findings.

The fact that one sample from each of three out of our four sites did not yield any elasmobranch ASVs reinforces the need for multiple samples to be collected at any given

site, as suggested by Sigsgaard et al (2020). The three samples at each of our sites were collected within minutes of each other a few metres apart, in each case while snorkelling shoreward from the furthest collection point. The differences in taxonomic coverage between samples may have been influenced by spatial or temporal variability in eDNA distribution. Temporal variability, even over very short time-scales is particularly likely at sites with strong currents (e.g. the Oyama site). Spatial variability is likely where there is fine-scale mixing of different water masses; for example at the Bone Baru site where a fine-scale mix of warmer and cooler currents (on the order of metres) were very noticeable while collecting the samples, a phenomenon commonly experienced at this site during surveys since 2004 by two of the authors (AMM and SN). However, it is also likely that random within-sample selection of material for the PCR and sequencing stages played a role in this variability. Overall, these patterns indicate that sampling effort may have been sub-optimal at one or several stages; therefore, the results may not reflect the total elasmobranch diversity at the study sites and/or within the samples collected.

Species identification and taxonomy. The taxonomy of rays, in particular the Myliobatiformes, has undergone numerous revisions over time. The roughtail stingray named as *Dasyatis centroura* in the *Anacapa Toolkit* output is listed with *Bathytoshia centroura* as the valid name in FishBase, with several other synonyms, as is the case for most species currently considered as belonging to the genus *Bathytoshia* (Froese & Pauly 2020). This species has a reported distribution in the eastern Atlantic, while the brown stingray *Bathytoshia lata* (*Dasyatis thetidis* is considered an invalid synonym) and the short-tail stingray *B. brevicaudata* have wide distributions including Indonesia. The phylogenetic tree (Figure 3) indicates there may be more than one species in the genus *Dasyatis* or *Bathytoshia* in the study area. There is considerable structure within this clade, with one sub-clade in particular (*Dasyatis* sp. 2 in Figure 3) which seems likely to be a separate species with no reference sequences.

The now invalid synonyms of *Himantura uarnak* (e.g. *Dasyatis uarnak*) are common in the literature (Iqbal et al 2018) and *Neotrygon kuhlii* (e.g. *Dasyatis kuhlii, Mobula kuhlii*) is now considered as a species complex (Last et al 2016). Two forms of *D. kuhlii* (Javanese and Balinese) were distinguished in a study on chondrichthyan by-catch in Indonesian fisheries (White & Dharmadi 2007). The ASVs assigned to *Dasyatis* sp. by the *Anacapa Toolkit* based on accession LC020857.1 (from Japan) appear to be a sister clade to *Himantura uarnak* and other members of the genus *Himantura* (Figure 3), and may well be in fact another species within this genus, of which several species occur in Indonesian waters according to FishBase (Froese & Pauly 2020). *Himantura imbricata* (accession MH248229.1 from Kuwait) was the closest named species match for the *Dasyatis* sp. 1 clade in Figure 3, and is a species with a wide Indo-West Pacific distribution, from the Persian Gulf and Red Sea to Indonesia. However, the complexity and instability of taxonomy within the Dasyatidae is reflected in the valid names given in FishBase for the sharpnose stingray *Himantura gerrardi* (accession AF447996.1) and the Bengal whipray *H. imbricata* (accession), which are *Maculabatis gerrardi* and *Brevitrygon imbricata*, respectively.

The *Neotrygon/Taeniura* high level clade in Figure 3 resolves into two well-defined clades, nested with accessions of *Taeniura lymma* and *Neotrygon kuhlii*, respectively. While there is considerable structure within these two clades (in particular within the collapsed sub-clades), each appears to be monophyletic. The identification of these two species can be considered to have a very high likelihood of being correct. The ray taxa recovered by the Anacapa Toolkit (Table 3) and the subsequent phylogenetic analysis (Figure 3) which have been observed and identified during underwater surveys at the sampling sites and/or on the Banggai market since 2004 are *Neotrygon kuhlii* and *Taeniura lymma*. Unidentified rays have been seen on several occasions; in particular a school of rays was seen passing by shortly before sample collection at the Oyama site. These rays almost certainly belonged to the Dasyatidae; however, no ASVs from this site were assigned to taxa exhibiting such pelagic migratory schooling behaviour, indicting the data recovered from this eDNA study may be incomplete in terms of elasmobranch taxa present.

Over the period 2004 to 2019, sharks (mostly finned carcasses) and rays (mostly with the tail spines or whole tail removed) have become an increasingly common sight on the fish market in Banggai Town the capital of Banggai Laut District, on Banggai Island. Some of the shark and ray species observed on Banggai market or seen in fisheries catch in the Banggai Archipelago in the past two decades were not included in the *Anacapa Toolkit* output. Plausible explanations include the limited spatial, temporal and habitat sampling (1 time/4 sites, coastal habitats with depth < 3 m) as well as DNA quality, the random subsampling of each sample, as well as the afore-mentioned database incompleteness.

In the case of requiem sharks (genus *Carcharhinus*) it is possible that some species observed on markets or in fisheries catch may have been included in the large number of sequences (over 21% of all elasmobranch sequences) identified to genus level by the *Anacapa Toolkit*. The BLAST and phylogenetic analyses provide support for this view. While the genera *Sphyrna* and *Triaenodon* form well-defined clades in Figure 2 (despite the complexity within the collapsed sub-clades in *Sphyrna*), at least three clades are apparent within the genus *Carcharhinus*. *Carcharhinus* clade 1 in Figure 2 appears to correspond to *C. brevipinna*, and *Carcharhinus* clade 2 to *C. obscurus*, the two species in this genus identified by the *Anacapa Toolkit*. However, *Carcharhinus* clade 3 does not match well with any one species.

The nucleotide sequence segment selected by the MiFish primers and remaining after alignment and trimming in MEGA X appears to be identical between GenBank accessions identified as different species. This seems especially common within the genus *Carcharhinus*. Cases of 100% identity between accessions (and with ASVs from this study) can be seen visually in Figure 2, for example the accessions KM434158.1 (*C. longimanus*), LC578887.1 and LC552343.1 (*C. galapagensis*) and accessions AB938100.1 and KC470543.1 (*C. obscurus*). Both *C. obscurus* and *C. longimanus* are known to be fished in the Banggai Archipelago and surrounding waters. *Carcharhinus* clade 3 contains identical accession sequences for four species: *C. leiodon* (MH248226.1), *C. limbatus* (AB938095.1, MH248235.1, MN883183.1), *C. melanopterus* (FJ792633) and *C. amblyrhynchoides* (KF956523.1). Furthermore, the ASV's in the largest collapsed sub-clade in clade 3 do not have close matches (99-100%) with any GenBank accessions, with closest matches (100% coverage) mostly 96-97%, typically equally close to accessions representing several species. These results point to a possible weakness for identifying species within the genus *Carcharhinus*, and possibly other elasmobranch genera.

Conversely, some accessions purporting to be from the same species show considerable variation. For example, the *Sphyrna mokarran* accession AF448022.1 is closer to *S. lewini* accession AF448021.1 (identical for the sequence segment used in the phylogenic analysis presented in Figure 2) than to the *S. mokarran* accession KY464952. Therefore, the identification of *Sphyrna mokarran* should be considered tentative, although the presence of the genus is strongly supported. The BLAST routine only returned these three accessions for the genus *Sphyrna*, highlighting a need for further 12S barcode data for this genus. A study on *S. lewini* using the COI mtDNA barcode (Hadi et al 2020) showed considerable intra-species variation within Indonesia, although an earlier study reported low intra-species diversity from Lombok (Hadi et al 2019). It is possible that high intra-species diversity within the genus *Sphyrna* may complicate species determination, especially with short molecular markers such as the 12S region used in MiFish metabarcoding.

Intrinsically, eDNA metabarcoding is limited by the scope and quality of sequence data stored in databases such as GenBank and BOLD (Lim et al 2016; Curd et al 2019). DNA barcoding is known to be incomplete for many Indo-Pacific fish taxa (Juhel et al 2020). With respect to the rays (Dasyatidae), it is noteworthy that the majority of GenBank sequences obtained from the BLAST analysis are from Japan (mainly Okinawa) or Taiwan (one each from Australia, Kuwait, China and USA), with no sequences from Indonesia or neighbouring countries in Southeast Asia, reflecting a lack of effort on sampling and submitting reference sequences for rays in this region. Even in Australian waters it is thought that skate and ray species remain to be discovered and that the

taxonomy of this group is in need of revision (Last & Yearsley 2002). DNA barcoding research in western Indonesia identified a ray species (*Dipturus chilensis*) with a known distribution limited to South America (Madduppa et al 2016); this is probably a case of mistaken identity due to the incompleteness of Indo-Pacific elasmobranch barcode records. A similar situation was suspected in a study using eDNA in the Atlantic (Stoeckle et al 2020). New Elasmobranch species are still being discovered and described, especially in eastern Indonesia (Dudgeon et al 2020).

The number of ASVs not conclusively resolved to species level highlights the need for further research (including classical taxonomy and barcoding) on Indo-Pacific elasmobranchs, especially rays (Dasyatidae). Twenty eight species or sub-species of Dasyatidae have been reported as targets or by-catch in Indonesian fisheries based on morphological characters (White & Dharmadi 2007), indicating exceptionally high diversity and/or taxonomic uncertainty within this Family. One possible explanation for some of the unexpected results from the BLAST and phylogenetic analysis is that the taxonomic identification of the specimens from which some deposited GenBank accessions originated may not have been accurate. Another possibility is that there may be similar levels of intra and inter-species variability or similar alleles across species within certain genera for the molecular marker used.

It is possible that some of the ASVs not identified to species level by the *Anacapa Toolkit* in our study could be species that did not have reference voucher sequences. As noted by Portnoy & Heist (2012), "Elasmobranchs are morphologically conserved, and differences between species are often subtle and confounded by variation within species", and species could well be misidentified in underwater or market/catch surveys relying on morphological characters alone. Furthermore, in the case of fisheries catch some identifying features may have been damaged or removed (Prehadi et al 2015), and increased use of molecular markers is leading to the identification of a growing number of cryptic species (Portnoy & Heist 2012). It is possible that elasmobranchs in the study area, including those represented by sequences in this study, may include such cryptic species.

Whatever the explanation regarding the unexpected relationships between the GenBank accessions obtained through the BLAST routine and used in the analysis, the overall structure of the phylogenetic tree for sharks (Figure 2) strongly supports the presence of the three genera identified by the *Anacapa Toolkit*. It also provides support for the presence of the species assigned by the *Anacapa Toolkit*, although the number of species within the genus *Carcharhinus* remains unclear, and there may be more than one species of the genus *Sphyrna* present. Overall, the phylogenetic tree for rays incorporating the results of the BLAST analysis (Figure 3) also corresponds well with the output from the *Anacapa Toolkit*, with the exception of the clade provisionally considered to represent the genus *Dasyatis*, where there is considerable doubt over species and even genus level assignments.

The results of this study, and in particular the high proportion of sequences identified to genus or family level, as well as the likely misidentification of at least one ASV, highlight a need for further collection of elasmobranch specimens in eastern Indonesia in general and the Banggai Archipelago in particular. To build the database, such collection efforts should combine traditional taxonomic identification with molecular methods, at a minimum including the most common barcoding markers (e.g. COI and 12S rRNA). Ideally these specimens should be deposited in reference collections and more advanced molecular analysis should be carried out; for example whole mitochondrial genome sequencing, as recently performed for four shark species in the Indian Ocean (Dunn et al 2020; Johri et al 2020a, b, c), thus enabling the use of multiple molecular markers for future species identification.

Status of sharks and rays in the Banggai MPA. By 2009, out of 64 shark and ray species evaluated under the International Union for Conservation of Nature (IUCN) Red List criteria, 32% were Threatened (6% Endangered (EN) and 26% Vulnerable (VU)), 24% Near Threatened (NT), 25% were considered Data Deficient (DD), and only 19% were assessed as Least Concern (LC) (Camhi et al 2009). Under the most recent

assessment in 2020 (IUCN 2020), 1134 species had been evaluated, of which 37% were classed as DD, indicating insufficient data to estimate the conservation status. Of the 714 species with sufficient data to assess the criteria, 6% (43 species) are considered Critically Endangered (CR), a category not present in the 2009 assessment of this group, with 8.7% EN (62 species), 15.7% VU (112 species), 16.1% NT (115 species) and 53.5% LC (382 species) (IUCN 2020). The 2020 assessment (IUCN 2020) shows an increase in the number of species assessed as well as in threat levels for several species compared to 2009 and 2014 assessments (Camhi et al 2009; Dulvy et al 2014). The status of eight shark and ray species identified in this study (Table 4) shows that none of these species is effectively protected from in-country use, although there is a ban on the export of four shark species under Ministerial Regulation Permen KP No. 5/2018 (MMAF-RI 2018b).

Table 4

Status of eight sharks and rays identified from eDNA around Banggai Island

No	*Species*	*IUCN Red List Category*	*CITES Appendices*	*National Regulations*
1	*Carcharhinus brevipinna*	Near Threatened (NT) (Burgess 2009)	No	None (note: export ban on *C. longimanus*[a])
2	*Carcharhinus obscurus*	Endangered (EN) (Rigby et al 2019a)[b]	No	
3	*Triaenodon obesus*	Near Threatened (NT) (Smale 2009)	No	None
4	*Sphyrna mokarran*	Critically Endangered (CR) (Rigby et al 2019b)	Appendix II	Export ban (genus *Sphyrna*)[a]
5	*Dasyatis centroura*[c]	Least Concern (LC) (Rosa et al 2016)	No	None
6	*Himantura uarnak*	Vulnerable (VU) (Manjaji Matsumoto et al 2016)	No	None
7	*Neotrygon kuhlii*	Data Deficient (DD) (Maskray & Kyne 2018)	No	None
8	*Taeniura lymma*	Near Threatened (NT) (Compagno 2005)	No	None

[a] Permen KP No. 5/2018; [b] Red List status updated in 2019 based on assessment completed in November 2018; on 13 September 2020 still listed as Vulnerable on the Indonesian Ministry of Marine and Fisheries website; [c] Evaluated species of the genus *Bathytoshia* (including *B. lata*, a taxon to which it is likely that a considerable number of ASVs attributed *D. centroura* by the *Anacapa Toolkit* belong) are also listed as LC.

The IUCN Red List assessments for some of the species in Table 4 can be considered out of date and/or based on minimal information. For example, the assessment for *Carcharhinus brevipinna* (Burgess 2009) is dated 2009 and based on data from 2005 with apparently minimal (if any) data from Indonesia. The assessment for *Taeniura lymma* was completed in 2005, and stated that almost no information was available on life history parameters of this widespread species which can be relatively abundant in some areas (Compagno 2005). The Data Deficient *Neotrygon kuhlii* assessment completed in 2017 states that this taxon, once viewed as widespread species, is now thought to be a species complex comprising several species and sub-species. However, despite the genetic differentiation (based on Cytochrome oxidase subunit 1 sequences), the taxa within this complex are very similar morphologically, making species-level identification problematic (Last et al 2016). It therefore remains unclear which member(s) of the *N. kuhlii* complex is/are present in the Banggai Archipelago.

In addition to the species listed in Table 4, several other species with distributions in FishBase (Froese & Pauly 2020) including the study area and accessions recovered from the BLAST analysis are classified in one of the IUCN Red List at risk categories. The oceanic whitetip shark *C. longimanus* is considered Critically Endangered (CR) and listed in CITES Appendix II. Members of the genus *Carcharhinus* listed as Near Threatened (NT) include the graceful shark *C. amblyrhynchoides*, the copper shark *C. brachyurus*, the Galapagos shark *C. galapagensis,* the blacktip shark *C. limbatus*, the hardnose shark *C.*

macloti, and the blacktip reef shark *C. melanopterus* while the pig-eye shark *C. amboinensis* is Data Deficient (DD). Like the dusky shark *C. obscurus*, the smoothtooth blacktip shark *C. leiodon* (closely related to *C. limbatus* and *C. amblyrhynchoides*) is considered Endangered (EN) but has only been reported from the Persian Gulf and Arabian Sea (Moore et al 2011, 2014) and is unlikely to be present in the Banggai Archipelago, or indeed in Indonesia. In the genus *Sphyrna*, the two other species with a global distribution including Indonesia are *S. lewini* (CR) and *S. zygaena* (VU). With respect to rays, only *Dasyatis* (or *Bathytoshia*) *centroura* is considered at low risk of extinction, in the Least Concern (LC) category.

Irrespective of the actual number and identity of the species present in the genera *Carcharhinus*, *Sphyrna* and the family Dasyatidae, it can be concluded that most (possibly all) sharks and rays present in the Banggai Archipelago belong to threatened taxa, even though the majority have no statutory protection to date, the exception being export bans on the species listed in CITES Appendix II.

The paradigm of elasmobranchs (mainly sharks) being increasingly targeted for human consumption as reef fish abundance has diminished in Fiji (Glaus et al 2015) is similar to the changes observed in the Banggai Islands, with the notable difference that rays are the main group targeted specifically as food fish, while shark meat (for consumption or sale) is usually a by-product of shark finning. Most of these sharks and rays are caught by small-scale fishers who operate multi-gear multi-species artisanal fisheries operating in shallow coastal waters. Typically any animal of commercial value will be sold and the remainder used for subsistence, as bait, or as feed for other animals (e.g. fish, lobsters and poultry). For example, in addition to those sold fresh on the market, some finned sharks would be used as bait and/or processed for human consumption. Processing shark meat as jerky (*dedeng*), with thin strips hung up to dry is a practice observed on several occasions in villages across the Banggai Archipelago. Shark teeth and sometimes shark skin are also traded.

Shark and ray ecology in the Banggai MPA. Shallow coastal waters are important nursery habitats and feeding grounds for several elasmobranchs including the bluespotted ribbontail ray, *Taeniura lymma* (Dabruzzi et al 2013), one of the most abundant species in this study based on read numbers (Figure 1). This species is thought to reach sexual maturity at around 20 cm in standard length with a maximum size of around 35 cm in width (Froese & Pauly 2020). The predilection of *Taeniura lymma* for in-faunal bivalves (Maduppa et al 2019) would support the feeding ground hypothesis, as bivalves are commonly gleaned at one of the sampling sites where the species was detected (Monsongan), and likely to be abundant at the other (Oyama). Due to the nearly round body shape (excluding the long spined tail), disc width is a common measurement for this species (Dabruzzi et al 2013). Often seen in large quantities on the Banggai fish market, typically in heaps of de-spined individuals of all sizes (from around 12 cm to 30 cm disc width), *T. lymma* has been seen by the first author at many locations within the Banggai Archipelago, including all four sampling sites.

Most requiem sharks seen on the Banggai market were finned and could not be identified; however, based on their size (typically 50-70 cm in length), information on life history parameters for these sharks (Iqbal et al 2019; Froese & Pauly 2020) indicates the vast majority were juveniles. High proportions of juveniles in shark catches have been reported from other areas in eastern Indonesia, reaching 100% for *Triaenodon obesus* in some fisheries (Jaiteh et al 2017). Tidal waters can also be important as feeding grounds for several species including the blacktip reef shark *Carcharhinus melanopterus* and sicklefin lemon shark *Negaprion acutidens* at some stages of the tidal cycle (Lea et al 2020). Furthermore, FishBase entries mention the use of shallower waters and coastal habitat by juveniles of several members of the genus *Carcharhinus* in Tables 2 and 3, including species such as *C. obscurus* where the adults typically inhabit deeper waters (Froese & Pauly 2020).

The presence of shark eDNA in shallow water habitats combined with direct observations of fisheries catches indicate that the coastal ecosystems around Banggai and other islands in the Archipelago may be important as shark and ray nurseries, as well

as likely feeding grounds. While other methods such as unmanned aerial vehicles (UAVs) can produce important fishery-independent data for elasmobranchs such as reef sharks and whiprays (e.g. *Carcharhinus melanopterus* and *Himantura fai*), particularly in shallow-water habitats (Kiszka et al 2016), this study indicates that eDNA could provide valuable data on shark and ray shallow-water habitat use, including distribution and an indication of relative abundance. In the context of the Banggai MPA, the results reveal a need for basic research on the biology and ecology of elasmobranchs in this region, including some wide-spread species.

Conclusions. This pilot study identified 12 ASVs and 9 named species of sharks and rays around Banggai Island in the Banggai MPA. The pilot eDNA study results indicate higher shark and ray biodiversity in shallow coastal waters compared to previous studies using visual surveys. The taxa identified mostly corresponded with species observed either alive or as fisheries catch, although not all shark and ray species seen on markets were identified from the eDNA samples, possibly due to limited sampling. All but two of the taxa identified to species level are considered at risk of extinction, with one data deficient and one classified as Least Concern in the latest IUCN Red List. However, only one of these species is partially protected under Indonesian law and listed in CITES Appendix II. The high proportion of sequences assigned to genus level and the assignment of an ASV to a species only reported from the Atlantic Ocean also highlight a need for further efforts to barcode elasmobranchs in the Wallacea region. The results can inform elasmobranch management in the Banggai MPA, in particular the need to evaluate the role of coastal ecosystems as shark and ray habitat including potential nursery grounds.

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