

A cause for hope: largely intact coral-reef communities with high reef-fish biomass in a remote Indonesian island group

Gino V. Limmon^{A,B,C}, Halwi Masdar^D, Dominic Muenzel^E, Tanika C. Shalders^F , Cilun Djakiman^A , Maria Beger^{E,G}, Jamaludin Jompa^D and Maarten De Brauwer^{E,H,*} 

For full list of author affiliations and declarations see end of paper

***Correspondence to:**

Maarten De Brauwer
CSIRO Environment, Battery Point, Hobart,
Tas. 7004, Australia
Email: maarten.debrauwer@csiro.au

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ABSTRACT

Context. The health of coral reefs is declining rapidly across the world because of anthropogenic impacts. In the mega-diverse Coral Triangle, the consequences of chronic overfishing and human use are worst near coastal population centres. **Aims.** The remote islands and reefs in the centre of the Banda Sea (Indonesia) remain largely unstudied, but their distance from populated areas could provide protection from fishing. **Methods.** We conducted the first visual census surveys of coral-reef communities at the uninhabited Lucipara group in the Banda Sea. **Key results.** Sites showed medium to high coral cover and fish assemblages with high biomass, including abundant large predatory species. All sites exceeded the fish biomass conservation target of 1150 kg ha⁻¹ proposed by McClanahan *et al.* (2015), by a factor of ~2–10. Benthic cover explained >50% of variance in fish abundance and diversity, with submassive corals, *Dendrophyllia* spp., and bare rock as key predictors. **Conclusions.** Our results suggested that Lucipara's reefs are among the healthiest in Indonesia, likely owing to their remoteness. However, this remoteness might also hamper policing against destructive fishing practices, highlighting a conservation gap. **Implications.** Lucipara's reef communities should be protected in a time of global coral-reef declines.

Keywords: biodiversity, conservation, Coral Triangle, fisheries, Indonesia, Lucipara, oceanic island, visual survey.

Introduction

Indonesia is situated in the heart of the Coral Triangle and the country's coral reefs are ranked as the most biodiverse in the world (Allen 2008; Struebig *et al.* 2022). As with the rest of the world, the condition of Indonesia's coral reefs is rapidly deteriorating because of various anthropogenic stressors (Ferrol-Schulte *et al.* 2015). Although climate change has caused localised bleaching and mortality events in the region (Trialfhianty *et al.* 2020), destructive fishing, coastal development and pollution have caused more damage than have climate-change effects (Ferrol-Schulte *et al.* 2015). Declining reef condition is of particular concern to the Indonesian economy and food security for millions of people (Teh *et al.* 2013; Tranter *et al.* 2022), because over six million people are involved in fisheries and aquaculture, with ~95% of fishery production coming from small-scale fishers (Food and Agriculture Organization of the United Nations 2016).

Indonesia's fisheries are a vital part of its economy, with the commercial value of the industry estimated to be worth close to US\$5 billion per year (Asian Development Bank 2014). Large predatory species such as tuna and groupers are often exported, whereas small pelagic species and fish lower down the food chain are the main source of protein for millions of subsistence fishers in the Coral Triangle (Burke *et al.* 2012; Clifton and Foale 2017). As is the case across the world, stocks of large predatory species have been largely depleted, yet Indonesia remains the world's biggest exporter of shark fins (Yulianto *et al.* 2018; MacNeil *et al.* 2020). The overexploitation of high trophic levels and subsequent fishing down the food chain can cause trophic cascades and result in

severely impoverished fish assemblages or marine ecosystem collapse (Salomon *et al.* 2010). In an island nation where a large proportion of the population depends on marine protein and simultaneously lives close to the coast, rapid access to the marine environment directly contributes to the poor state of coastal coral reefs (Campbell *et al.* 2020).

Remote reefs are often less affected by overfishing because fewer fishers can access sites (Edgar *et al.* 2014; Cinner *et al.* 2018). Fish biomass in remote Pacific reefs can exceed that of mainland reefs by more than 300% (Stevenson *et al.* 2007; Williams *et al.* 2011). Yet, their remoteness can make effective policing more difficult and, as a result, they are more likely to be affected by illegal or destructive fishing (Williams *et al.* 2011; Chapsos *et al.* 2019). Remote reefs around oceanic islands can harbour rich species assemblages that differ distinctly from those on mainland reefs (Hobbs *et al.* 2012). They can be refuges for megafauna and serve as important nesting grounds for turtles, nurseries for sharks, or attract spawning aggregations of commercially important fish species (Letessier *et al.* 2019; Wagner *et al.* 2020). These characteristics make them of interest for fisheries, but also of high value for conservation and tourism (Cinner *et al.* 2016; Friedlander *et al.* 2016).

The Banda Sea in central Indonesia is considered of high marine conservation concern (Huffard *et al.* 2012; Fajariyanto *et al.* 2019; Purwanto *et al.* 2022). Its central location in the Indonesian Throughflow and high diversity in different reef habitats make it a connectivity corridor for coral-reef species in the Coral Triangle (Kool *et al.* 2011). The islands in this deep ocean basin are important breeding grounds for turtles and seabirds, and the area is an important fishing ground for pelagic species such as tuna (Huffard *et al.* 2012). Multiple small, uninhabited islands are found throughout the centre of the Banda Sea, none of the coral reefs around these islands are currently marine protected areas. The reefs around these islands are visited by fishermen and scuba divers, yet little is known about the condition of these remote reefs.

In this study, we surveyed the previously unstudied coral reefs around the Lucipara islands, a remote island group in the central Banda Sea. We specifically aimed to establish baseline understanding of the coral-reef assemblages by investigating (1) the diversity, abundance and biomass of reef fishes across different sites, (2) the diversity and percentage cover of benthic communities across different sites, (3) how differences in the benthic communities are reflected in the abundance and diversity of fish assemblages, and (4) how fish biomass differed between trophic levels.

Materials and methods

Survey location and methods

Surveys were conducted on the coral reefs of the Lucipara islands (5°25'S, 127°38'E) in the Banda Sea, Indonesia,

between 26 and 29 October 2019 (Research permit: FPIK Unpatti – 3051/UN13.1.7/DT/2019). This uninhabited group consists of seven small coral cay islands at more than 10 h of travel time (210 km) south from the closest large population centre, Ambon. Survey sites were representative of the reefs around the island group, consisting of steep walls descending to a depth below 200 m. Two sites (LUC1, LUC2) were surveyed in the Lucipara group, and two sites (LUC3, LUC4) in the Penyu group within the Lucipara islands (Fig. 1). All surveys were conducted at a depth of 8 m, just below the crest of the wall and parallel to the reef contour. Small sections of sloping reef were intermittently present at this depth on all sites. Four replicate underwater visual census (UVC)-belt transects were conducted by scuba diving at each survey site, totalling 16 transects or a combined surface area of 4000 m² (Fig. 1). Following standard UVC methods (Edgar *et al.* 2014; Emslie *et al.* 2015; Cinner *et al.* 2016), two experienced observers identified and counted non-cryptic fishes (see Table S1 in the Supplementary material for full species list) at species level and estimated fish length to the closest centimetre along a belt transect of 50 × 5 m (250 m² per transect, 1000 m² per site). Swimming along the belt transect next to each other, one diver counted small-bodied fish families (e.g. Pomacentridae) and the other diver counted large-bodied fish families (e.g. Acanthuridae), preventing double observations and ensuring data quality. On wall sections, the transect was defined as 2.5 m above and below the transect line and 5 m towards open water. Following the fish observers, two observers identified and counted (number of individuals per transect) macroalgae (2- × 30-m belt transect) and non-cryptic macro-invertebrates (5- × 30-m belt transect), at genus level or species level where possible (see Table S2 of the Supplementary material for full species list). A final diver took 30 pictures of the benthos at 1.5-m intervals overlaid by a 1- × 1-m quadrat across the 50-m transect, to assess the benthic cover.

Data analyses

Fish abundance and total lengths were used to calculate biomass with the weight (W)-length (L) relationship (Eqn 1, Froese *et al.* 2014), on the basis of species-specific length-weight parameters from FishBase (ver. 12/2019, R. Froese and D. Pauly, see <http://www.fishbase.org>).

$$W = a \times L^b \quad (1)$$

When parameters were not available for specific species, parameters of a closely related species in the same genus were used instead. Trophic level, dominant diet, and the maximum length of species were downloaded from FishBase in R (R Foundation for Statistical Computing, Vienna, Austria) by using the package *rfishbase* (ver. 4.0.0, see <https://cran.r-project.org/package=rfishbase>; Boettiger *et al.* 2012). Fish species were then categorised into trophic niches as a

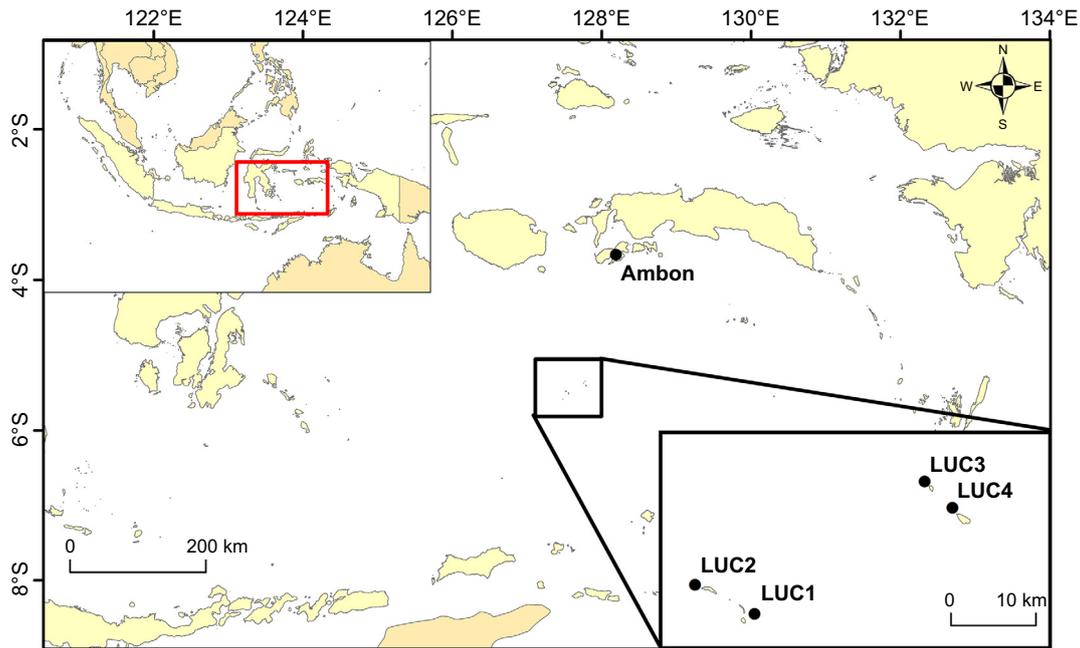


Fig. 1. Map of survey sites in Lucipara, Indonesia.

combination of their maximum size (small, <20 cm; medium, 20–50 cm; large, 50–200 cm; very large, >200 cm) and diet-based feeding strategy (Table 1, species list in Table S4 in the Supplementary material).

Photos of the benthos were analysed using the Coral Point Count with Excel extension (CPCe) software package to estimate benthic cover (ver. 4.1, see <https://hcas.nova.edu/tools-and-resources/cpce/index.html>; Kohler and Gill 2006). Twenty random points were placed over each 1-m² photo quadrat (total of 600 points per transect) and benthic category was defined for each point. Benthos below each

Table 1. Selection criteria for fish feeding strategies based on diet information from FishBase.

Feeding strategy	Diet
Corallivore	Corals
Detritivore	Detritus
Herbivore	Algae and plant matter
Invertivore	Invertebrates
Benthic invertivore	Benthic invertebrates
Omnivore	Plant and animals
Benthic omnivore	Benthic plant and animals
Piscivore	Exclusively targets fishes
Planktivore	Plankton
Opportunistic planktivore	Plankton and other food sources (e.g. benthic taxa)
Predator	Fish and invertebrates
Benthic predator	Benthic fish and invertebrates

point was classified into 17 different benthic categories (see Table S2 in the Supplementary material for full details per category). Because of the low cover of specific categories, the decision was made to combine detailed categories into six more general benthic classifications. Categories with a combined benthic cover lower than 1% for all transects were removed (e.g. molluscs, ascidians, bryozoans). The general benthic categories were classified as ‘abiotic’ (combined cover of rock, sand and rubble), ‘hard coral’ (e.g. branching coral, encrusting coral), ‘other cnidarian’ (e.g. *Millepora* sp., hydroids, seafans), ‘algae’, ‘soft coral’ and ‘sponges’.

Curation and visualisation of univariate data (benthic cover categories, biomass per niche and trophic levels) were conducted in R (ver. 4.0, R Foundation for Statistical Computing) using the *tidyverse* package (ver. 1.3.2, see <https://cran.r-project.org/package=tidyverse>; Wickham *et al.* 2019). Data were first tested for normality and subsequent ANOVA or Kruskal–Wallis (K–W) tests were conducted for normal and non-parametric data respectively. *Post hoc* Tukey tests or Dunn’s tests with Bonferroni correction were conducted for significantly different results. Benthic cover was plotted using the *yarr* package (ver. 0.1.2, see <https://cran.r-project.org/package=yarr>; Phillips 2017).

Multivariate data were analysed using Primer (ver. 7, see <https://www.primer-e.com/>; Clarke and Gorley 2015). Fish assemblage (diversity and abundance) and biomass data were square-root transformed and analysed with PERMANOVA (Bray–Curtis resemblance matrix, 9999 permutations). Subsequent pairwise testing was performed using Monte Carlo corrections. Differences in benthic cover assemblages among sites were compared using ANOSIM (Euclidean

distance resemblance matrix, 9999 permutations) (Anderson et al. 2008). Fish assemblage data (diversity and abundance) were visualised using principal-coordinate analysis and overlaid with correlating fish species (Spearman $R > 0.8$).

To explore the link between benthic cover (from CPCe data) and fish assemblages (total diversity and abundance), we ran distance-based linear models (DistLM) in Primer (ver. 7; Clarke and Gorley 2015). For this analysis, we used the detailed benthic categories (see the ‘Detailed results – PERMANOVA fish’ section in the Supplementary material) rather than the six combined general categories to increase resolution. Prior to analysis, benthic categories with less than 1% cumulative cover combined over all transects were excluded, as well as variables strongly correlated with each other ($r > \pm 0.75$). The categories that were excluded were ‘bryozoans’, ‘foliose coral’, and ‘branching coral’. DistLM models were selected on the basis of the Akaike information criterion corrected to account for the small sample size (AICc) and multiple-predictor variables (Anderson et al. 2008). The fish assemblage was plotted using a distance-based redundancy analysis (dbRDA) and overlaid with benthic predictor variables.

Results

Fish diversity, abundance and biomass

Across the four survey sites, we counted 205 non-cryptic fish species (total $N = 32\,349$). The most abundant fish species were small-bodied planktivorous species *Pseudanthias dispar* ($N = 7250$), *Chromis margaritifer* ($N = 6386$), and *L. tapeinosoma* ($N = 2511$). Total (mean \pm s.e.) fish abundance per 250-m² transect was 2022 ± 236.1 .

Multivariate analyses showed that the fish assemblages (diversity and abundance) were significantly different among sites (pseudo- F , 4.125; d.f., 3; $P < 0.001$; Fig. 2a, PCA abundance). Pairwise analyses indicated that fish assemblages differed significantly between each pair of sites, except for LUC3 and LUC4, which were not significantly different from each other (detailed results in Table S3 in the Supplementary material). The site with the highest fish abundance was LUC2, followed by LUC1, LUC4, and LUC3 (Table 2).

Fish biomass (mean \pm s.e.) per 250-m² transect was 143.1 ± 33.5 kg (5724 kg ha⁻¹), with *Melichthys niger* contributing the highest biomass among all species (289.5 kg summed across all surveys). Multivariate analyses of fish diversity and biomass indicated significant differences among sites (d.f., 3; pseudo- F , 3.438; $P < 0.001$). The site with the highest fish biomass was LUC2, followed by LUC1, LUC3, and LUC4 (Table 2). Pairwise analysis indicated that differences in fish biomass were significant between LUC1 and LUC4 ($P = 0.042$), LUC2 and LUC3 ($P = 0.026$), and LUC2 and LUC4 ($P = 0.008$; Fig. 2b). Only sites LUC3 and LUC4 were not significantly different from each other (Fig. 2b; also see Table S3 the Supplementary material). Principal-coordinate analysis plots illustrated that *Ctenochaetus striatus* was closely associated with LUC1 for both abundance and biomass. *Pseudanthias smithvanizi* was correlated with sites LUC3 and LUC4 for abundance, but not biomass. Fish species with abundance correlated with LUC2 were *L. tapeinosoma* and *Acanthurus pyroferus*. When considering biomass for LUC2, five other species, including *Cephalopholis urodeta*, *Zebbrasoma scopas* and *Balistoides conspicillum*, also showed strong

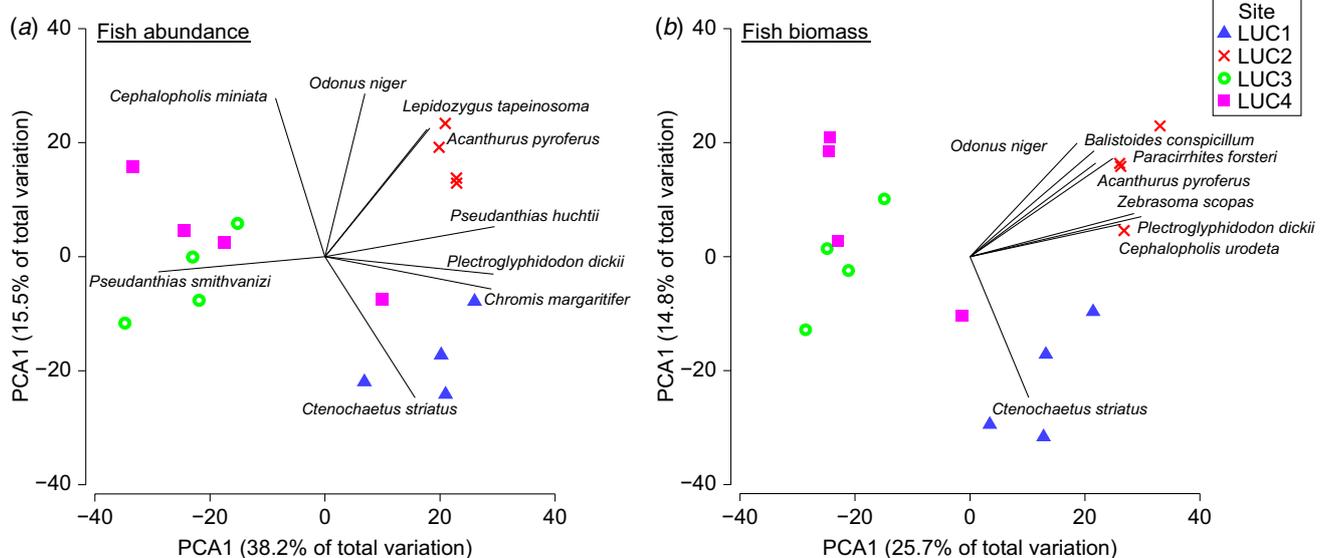


Fig. 2. Principal-coordinate analysis (PCA) plots of fish assemblages (square-root transformed, Bray–Curtis similarity) in Lucipara survey sites: (a) abundance-based assemblages overlaid with correlated fish species ($R > 0.8$); (b) biomass-based assemblages overlaid with correlated fish species ($R > 0.8$).

Table 2. Summary statistics of fish diversity, abundance and biomass at four survey sites in the Lucipara island group, Banda Sea (Indonesia), on the basis of underwater visual census.

Site	Diversity	Total N	N (mean \pm s.e.)	Total biomass (kg)	Biomass (mean \pm s.e.; kg)	Estimated biomass ha ⁻¹ (kg)
LUC1	128	7609	1902.3 \pm 216.0	548.6	137.2 \pm 34.7	5488
LUC2	140	12 113	3028.3 \pm 204.1	1156.9	289.2 \pm 64.3	11 568
LUC3	108	5549	1387.3 \pm 305.2	359.9	90.0 \pm 23.2	3600
LUC4	116	7078	1769.5 \pm 660.0	223.7	55.9 \pm 19.1	2236

Means \pm s.e. are per transect (250 m²), totals for combined transects per site (1000 m²), and estimated biomass per hectare extrapolates mean biomass per hectare (10 000 m²).

correlations. *A. pyroferus* remained strongly correlated with LUC2, suggesting that this species is characteristic of the site.

Diversity and percentage cover of benthic communities

We found 13 algae species, with the most abundant species being *Halimeda opuntia* ($N = 4554$), *Halimeda cylindracea* ($N = 1096$) and *Lobophora* sp. ($N = 182$). Of the 30 invertebrate species that were counted, the most abundant ones included Christmas tree worms, *Spirobranchus* sp. ($N = 208$), and two crinoid species, namely, *Capillaster sentosus* ($N = 138$), and *Comanthus parvicirrus* ($N = 133$).

Hard-coral cover (mean \pm s.e.) across sites was 33.6% \pm 2.0 s.e.. Abiotic cover (combined cover of rock, sand and rubble) was 32.5% \pm 3.4 s.e., soft-coral cover was 12.5% \pm 2.6 s.e., algal cover 7.4% \pm 2.3 s.e., other cnidarian cover 6.4% \pm 2.7 s.e. and sponge cover 6.1% \pm 1.6 s.e. (Fig. 3). The highest percentage cover of specific categories with the 'hard-coral' category were encrusting corals (mean, 15.9% \pm 1.6 s.e.). The abiotic cover consisted mainly of bare rock (mean 28.9% \pm 3.1 s.e.). The category 'other cnidarian' included *Dendrophyllia* sp., hydroids, *Millepora* sp. and sea fans. At LUC4 only, this category was strongly dominated by *Dendrophyllia* sp., with a mean cover of 17.2% \pm 8.0 s.e., compared with a cover of 1.2% \pm 0.8 s.e. at the other three sites.

Multivariate analysis indicated that benthic-cover composition varied significantly across sites ($R = 0.668$; $P < 0.001$), and pairwise multivariate analyses showed that benthic cover differed between all pairs of sites except between LUC2 and LUC3, and LUC3 and LUC4 (see the 'Detailed results – benthic cover' section in the Supplementary material). Pairwise ANOVA tests per benthic category showed that significant differences exist among sites for all benthic categories, except for sponges (Fig. 3, also see the 'Detailed results – benthic cover' section in the Supplementary material). Site LUC1 had the highest mean coral cover (42.3%) compared with 27.5% at site LUC4. Mean abiotic cover ranged from 23.04% at site LUC3 to 52.17% at LUC1. Soft-coral cover was highest at sites LUC2 and LUC3. Algal cover was highest at sites LUC3 and LUC4. The cover of 'other cnidarians' was low at most sites, except for site LUC4, where this category had a mean cover of 18.8%.

Benthic predictors of fish assemblages

The final distance-based linear model explained 50.5% of the variation in fish assemblages (abundance and diversity; AICc, 125.0) and incorporated five benthic categories, including bare rock, *Dendrophyllia*, hydroids, massive corals, and submassive corals (Table 3). The distance-based redundancy-analysis (dbRDA) plot confirmed this model and showed a clear separation of sites, with a strong influence of *Dendrophyllia* on transects at Site LUC4 compared with Site LUC1 (Fig. 4). The dbRDA plot also illustrated the role of hard corals and bare rock in structuring fish assemblages across Sites LUC2 and LUC4, and LUC1 and LUC3 respectively.

Trophic structure

The combined biomass across the Lucipara sites (biomass summed per trophic level (TL) for the surveyed area per site (=1000 m²)) showed a bimodal signal, with the highest biomass in high (TL > 4) and low (TL < 2.5) trophic levels at 656.7 kg (mean per site, 41.0 kg \pm 18.6 s.e.) and 636.3 kg (mean per site, 39.7 kg \pm 9.9 s.e.) respectively (Fig. 5a). The biomass differences between trophic levels were significant (K–W: $\chi^2 = 46.47$, d.f. = 4, $P < 0.001$), with *post hoc* tests showing significant differences among trophic levels: TL < 2.5 v. TL > 4 ($P = 0.002$); TL < 2.5 v. TL 3.01–3.5 ($P < 0.001$); TL 2.51–3.0 v. TL 3.01–3.5 ($P = 0.001$); TL 2.51–3.0 v. TL > 4 ($P = 0.02$); TL 3.01–3.4 v. TL 3.51–4.0 ($P < 0.001$); and between TL 3.51–4.0 v. TL > 4 ($P < 0.001$). The bimodal trend was also apparent when investigating the mean biomass at site level (Fig. 5c). There were significant differences in trophic level mean biomass among sites for all trophic levels except for TL 2.51–3.0 (see Table S5 in the Supplementary material). Contrastingly, Sites LUC3 and LUC4 were not significantly different from each other for any of the trophic levels (see Table S6 section in the Supplementary material).

When considering only feeding strategy and not maximum total length, the summed biomass across survey sites was highest for predatory fishes (736.9 kg), followed by planktivores (426.0 kg) and opportunistic planktivores (326.4 kg).

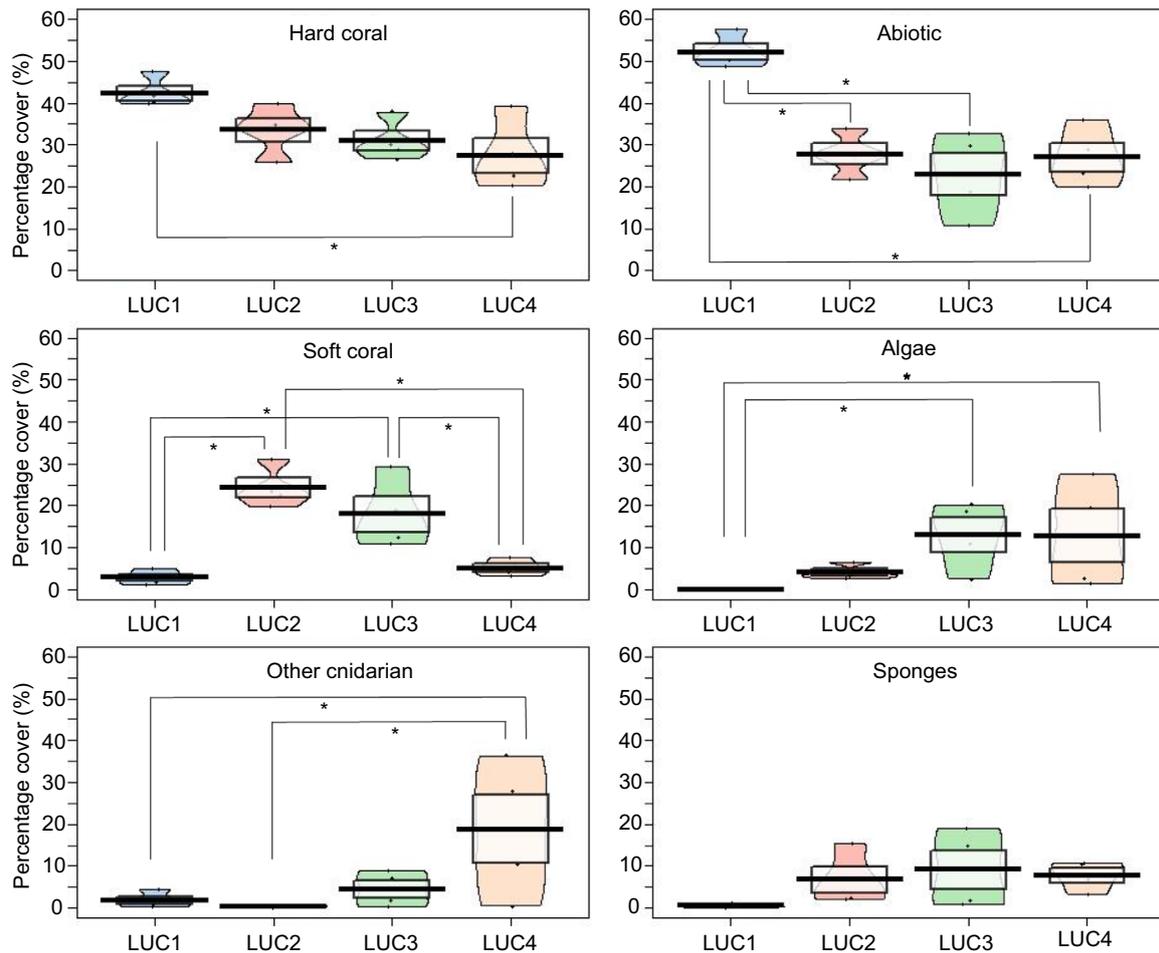


Fig. 3. Plots of benthic cover (%) categories across four survey sites in Lucipara, Indonesia. Abiotic cover is the combined cover of rock, sand, and rubble. Black bar indicates mean, transparent rectangle shows 95% confidence interval, width of coloured sections represents density of data points. Asterisks (*) designate significant differences ($P < 0.05$) between sites.

Invertivores (8.4 kg), benthic omnivores (7.5 kg), and detritivores (6.4 kg) had the lowest biomass.

A more-detailed analysis of trophic niche biomass (=size class + feeding strategy, see Table S5 in the Supplementary material for details) showed that the biomasses of fishes in different niches were significantly different from each other ($K-W: \chi^2 = 207.49$, d.f. = 33, $P < 0.001$). The five niches with the highest fish biomass included three predator categories (very large; large; very large benthic) and two planktivorous categories (large opportunistic; medium; Fig. 5b, d). The trophic niche with the highest mean fish biomass across all sites was the 'very large predator' category (389.5 kg; mean per site, 24.3 kg \pm 15.8 s.e.). The next-heaviest trophic niche was the 'large opportunistic planktivores' category (316.7 kg; mean per site, 19.8 kg \pm 2.8 s.e.), followed by 'large predators' (243.5 kg; mean per site, 15.2 \pm 4.0 s.e.), 'very large benthic predators' (238.1 kg; mean per site, 14.9 kg \pm 8.1 s.e.),

and 'medium planktivores' (178.3 kg; mean per site, 11.1 kg \pm 3.7 s.e.) (Fig. 5b, d). Differences in biomass among these five heaviest niches were significant only for comparisons with the 'large opportunistic planktivore' category. The biomass of 'large opportunistic planktivores' was significantly different from that of 'very large predators' ($P < 0.001$), 'medium planktivores' ($P < 0.001$) and 'large predators' ($P < 0.001$) (full results in Table S5). Looking at each of the five heaviest niches separately, *post hoc* pairwise analyses showed no site-specific differences in biomass for any niche except for the 'large predator' category. The biomass of 'large predators' was significantly different between Site LUC2 and every other site (LUC2–LUC1, $P = 0.01$; LUC2–LUC3, $P = 0.004$; LUC2–LUC4, $P < 0.001$; full results in Table S6). The biomass of 'large predators' and 'very large predators' might have been underestimated for all sites, because there were regular sightings of large sharks and tunas away from the survey transects for all sites.

Table 3. Distance-based linear model results predicting the contribution of benthic variables to fish assemblages (abundance and diversity) on four coral-reef sites in Lucipara, Indonesia.

Variable	SS (trace)	Pseudo-F	P	Proportion
AICc = 125.0, R ² = 0.505, variables = 5				
Algae	1735.4	1.262	0.227	0.083
Bare rock	3434.8	2.740	0.019	0.164
Dendrophyllia	3986.4	3.283	<0.001	0.190
Encrusting coral	2115.4	1.569	0.128	0.101
Hydroid	2770.4	2.129	0.023	0.132
Massive coral	3279.2	2.593	0.019	0.156
Millepora	2183	1.625	0.087	0.104
Rubble	1689.3	1.226	0.250	0.081
Sand	858.32	0.597	0.827	0.041
Sea fan	1926.9	1.415	0.128	0.092
Soft Coral	1679.3	1.218	0.251	0.080
Sponge	2555.9	1.941	0.068	0.122
Submassive coral	3962.6	3.259	0.007	0.189

Variables in bold are those included in the final model.

Discussion

We have presented the first survey of the biodiversity and abundance of the coral-reef faunal communities around a remote island group in the Banda Sea, Indonesia, where we discovered high fish biomass that well exceeds the typically cited ‘conservation target’ or ‘pristine’ biomass (1150 kg ha⁻¹; McClanahan *et al.* 2015; Campbell *et al.* 2020). Fish biomass was higher than in most other known coral reefs in Indonesia and the wider Coral Triangle region

(Campbell *et al.* 2020; Ceccarelli *et al.* 2021). In particular, the biomass of large and predatory fishes, species targeted by fisheries, exceeded the typical biomass reported in Indonesian coral reefs (Welly *et al.* 2012; Wouthuyzen *et al.* 2018; Currier *et al.* 2019; Ceccarelli *et al.* 2021). At 33.6%, hard-coral cover was relatively low compared with other sites in the Banda region, which frequently reaches over 50% hard-coral cover (Currier *et al.* 2019; Ceccarelli *et al.* 2021; Purwanto *et al.* 2022). The fish diversity in the Lucipara coral reefs was in line with previously recorded diversity in the central Indonesian region, given the survey methods and depth (Campbell *et al.* 2020; Ihsan *et al.* 2020). Benthic cover explained more than 50% of the variance in fish abundance and diversity, with *Dendrophyllia* species, submassive corals, and bare rock as key predictors of fish assemblages. Our results indicated that the Lucipara islands coral reefs are among the least affected by human pressures in Indonesia and should be protected in a time of global declines in coral-reef condition.

With just over 200 species, fish species richness was similar or slightly lower than in neighbouring regions in the Coral Triangle (Allen and Werner 2002; Welly *et al.* 2012). Oceanic coral reefs frequently tend to have a lower diversity than do sites closer to the mainland because of their remoteness (Hobbs *et al.* 2012). However, our surveys did not target cryptobenthic fauna and were limited to only one, shallow, depth. Real fish diversity is therefore expected to be higher than we report here, but unlikely to exceed the high diversity found in the nearby diversity hotspot of Raja Ampat (Andradi-Brown *et al.* 2021). Surveys did indicate high fish abundance, particularly for plankton-feeding species such as *P. dispar* and *L. tapeinosoma*. Although hard-coral cover was lower than in Indonesian protected

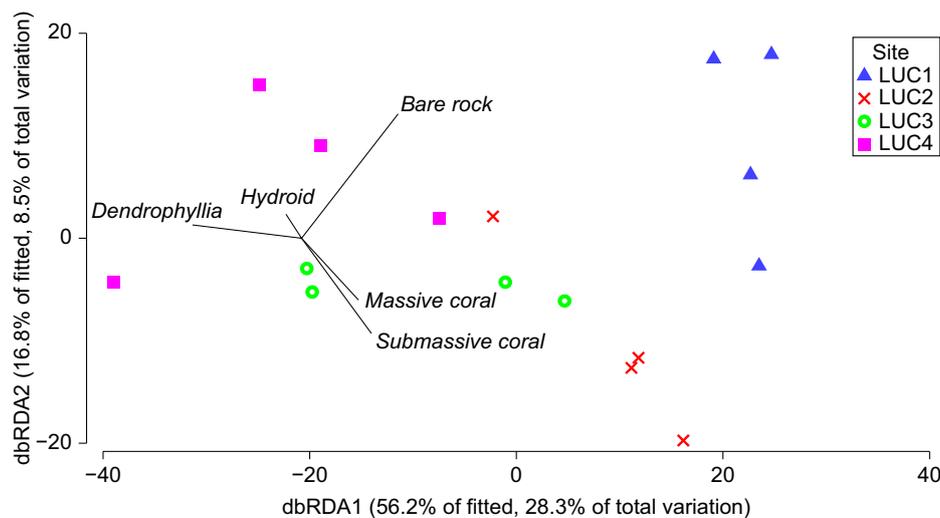


Fig. 4. Distance-based redundancy-analysis plot of fish assemblages (abundance + diversity) in Lucipara, Indonesia, overlaid with benthic variables responsible (from DistLM models) for changes in the assemblages. From Bray–Curtis similarity based on square root-transformed data.

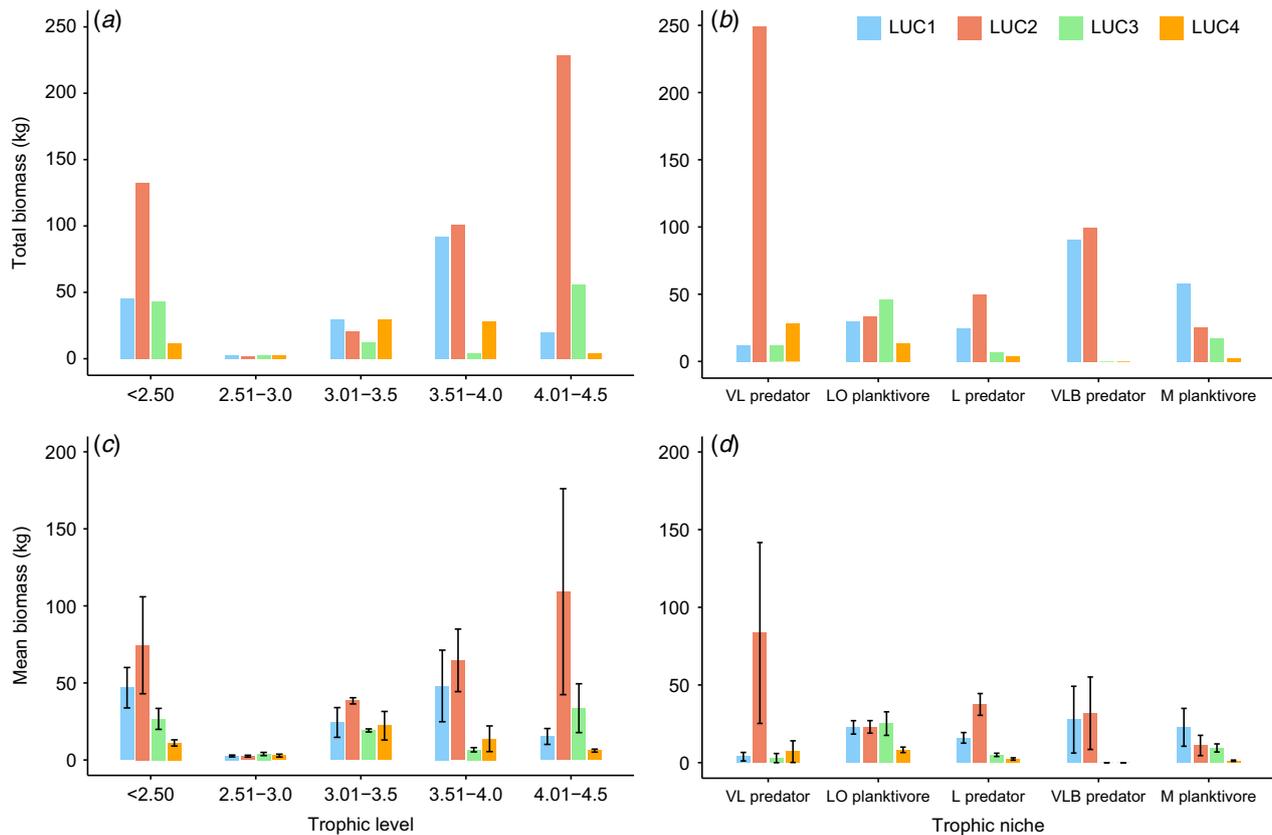


Fig. 5. Trophic structure of fish biomass across four survey sites (1000 m² per site) in Lucipara, Indonesia. (a) Summed fish biomass across sites classified by trophic level. (b) Summed fish biomass of the five trophic niches with the highest fish biomass. (c) Mean fish biomass (\pm s.e.) per site classified by trophic level. (d) Mean fish biomass (\pm s.e.) for all sites classified by the trophic niches with the highest fish biomass. VL, very large (>200 cm); LO, large opportunistic; L, large (50–200 cm); VLB, very large benthic; M, medium (20–50 cm).

areas such as the Wakatobi National Park (>40%, [Ahmadia *et al.* 2018](#)), Ay-Rhun MPA (>50%, [Ihsan *et al.* 2020](#)), or Menjangan island (>59%, [Dustan *et al.* 2013](#)), hard-coral benthic cover was within the expected range for Indonesian coral reefs ([Razak *et al.* 2021](#)). All sites were very steep walls, exposed to seasonal monsoons, which could explain the relatively low hard-coral cover and high soft-coral cover. The typical conditions on near-vertical walls, such as limited light and space availability, are likely to result in less varied microhabitat availability than on sloping reefs. However, the strong currents and surrounding nutrient-rich deep waters provide excellent conditions for planktivorous fishes and associated predators ([Gove *et al.* 2016](#)).

Fish assemblages differed significantly among survey sites, except between the two sites in the Penyau Island group (LUC3 and LUC4). The benthic cover of reefs surveyed in this group had a high macroalgae cover and a notably higher cover of ‘other cnidarians’. This category was dominated by the azooxanthellate *Dendrophyllia* corals, which might indicate a higher proportion of shaded overhangs and caves, because azooxanthellate corals do not need

sunlight to grow ([Marshall and Clode 2004](#)). The higher algae cover found at these sites might also indicate higher nutrient availability ([Adam *et al.* 2021](#)). Benthic variables on the site with the highest biomass, LUC2, did not differ from those on the other sites, so other environmental factors are likely to have played a role in shaping its fish assemblage. LUC2 faces east, whereas the other sites face north-west. This orientation could have provided shelter from the monsoon winds in the Banda Sea, which run along a south-east–north-west axis ([Moore *et al.* 2003](#)). The stronger current during surveys on this site, which had twice the biomass of other sites, also possibly affected the biomass of large predatory fish (e.g. sharks; [Vianna *et al.* 2014](#)).

Overall, the recorded fish biomass for each site exceeded that of published data from most sites in Indonesia. A recent review analysed UVC surveys of 622 coral-reef sites across Indonesia and found that the mean biomass of coral-reef fish per hectare ranged from 309 kg ha⁻¹ in easily accessible sites to 1432 kg ha⁻¹ in remote sites, but reported a maximum recorded biomass >17 000 kg ha⁻¹ ([Campbell *et al.* 2020](#)). Biomass estimates in the Banda Sea in a recent

local report averaged 1099 kg ha⁻¹, with one site exceeding 2000 kg ha⁻¹, but the report did not survey the Lucipara group (Currier *et al.* 2019). The mean biomass in Lucipara is within the higher estimates of this report, although multiple sites exceeded the highest reported biomass in other Banda Sea sites. The widely suggested 'pristine' biomass threshold to indicate a well-functioning coral reef has been estimated to be at least 1150 kg ha⁻¹ (McClanahan *et al.* 2015). This means that reefs around the Lucipara islands can all be considered to have a high fish biomass, with LUC2 exceeding the 'pristine' threshold by a factor of 10.

The trophic structure of Lucipara fish communities showed a bimodal, almost concave, distribution, with the highest biomass being concentrated in high and low trophic levels. Low trophic-level biomass was dominated by planktivorous species such as *Naso vlamingii* and *M. niger*, whereas high trophic-level biomass included species such as sharks, groupers, and snappers. The high biomass of large predatory species and the concave shape of trophic-level distributions indicated that the reefs around the Lucipara group do not experience high fishing pressures (Friedlander and DeMartini 2002; Graham *et al.* 2017). Similar trophic structures are typical for remote Hawaiian coral reefs, where predator biomass made up to 54% of the total fish biomass in sites with limited fishing activity (Friedlander and DeMartini 2002).

In the case of Lucipara, we hypothesise that high predatory biomass is supported by pelagic food subsidies through its abundant planktivorous fishes, which might be driving productivity in this area (Morais *et al.* 2021; Skinner *et al.* 2021). The importance of offshore pelagic subsidies to coral reefs is becoming increasingly clear and is, no doubt, vital to a remote oceanic reef system such as the one studied here (e.g. Morais and Bellwood 2019; Skinner *et al.* 2019; Skinner *et al.* 2021). Planktivorous fishes can dominate trophic pyramids in remote regions and protected areas (Russ *et al.* 2017; Campbell *et al.* 2020); however, to accurately test the trophic structure around Lucipara, both cryptobenthic species and pelagic biomass subsidies would need to be quantified more directly (Goatley *et al.* 2017; Brandl *et al.* 2019; Skinner *et al.* 2019).

Importantly, much of the high biomass on surveyed reefs represented species important for commercial and subsistence fisheries, such as dogtooth tuna (*Gymnosarda unicolor*), Maori wrasse (*Cheilinus undulatus*), milkfish (*Chanos chanos*), and snapper (*Lutjanus monostigma*) (Asian Development Bank 2014). The islands are 210 km away from the nearest large population centre (Ambon) and rough seas during the monsoon make the group inaccessible for more than 6 months of the year. The remote location and strong monsoon system are therefore likely to provide some natural protection and 'passive conservation' from the overfishing that is common in other regions in the Coral Triangle and coastal reefs in the Banda Sea (Cinner *et al.* 2018; Campbell *et al.* 2020; McClanahan 2020). However, the sites are certainly not untouched. Three fishing vessels, one of which was targeting

groupers, were sighted while surveys were being conducted. The large turtle populations in the region have been targeted for food and religious rituals (Moss and Van Der Wal 1998; CITES 2019), yet, despite this, the area has no official protection. The remoteness of the island group seems to form a barrier to intensive fishing impacts, but also hinders effective policing against illegal or destructive fishing. Importantly, remoteness does not offer protection against the impacts of global climate change (Hughes *et al.* 2017).

Our surveys have provided much-needed information on coral reefs in one of Indonesia's most data-poor regions. The Banda Sea is considered an Indonesian Conservation Priority area, on the basis of its high coral diversity, role in connectivity, and as a habitat for megafauna (Huffard *et al.* 2012; Fajariyanto *et al.* 2019). Despite its importance, very little is known about the conservation status of species across central Indonesia (Struebig *et al.* 2022). We have provided extensive data on fish assemblages, but high-resolution data on other taxa remain mostly lacking. Future survey efforts should also include cryptobenthic fishes and smaller invertebrates, but would ideally also cover charismatic megafauna such as turtles and sharks, which were commonly sighted off transects (De Brauwer and Burton 2018; Welly *et al.* 2012). Well established and emerging methods such as environmental DNA, drone surveys, or baited underwater remote video systems could be employed to maximise the outcomes of future data collection in the region (De Brauwer *et al.* 2018; Kelaher *et al.* 2019; Bani *et al.* 2020; Langlois *et al.* 2020).

We described the fish assemblages and benthic cover of a remote group of coral reefs in Indonesia. The Lucipara islands support a coral-reef system with a high fish biomass and high abundance of large predatory fishes. These fish assemblages are likely to be protected by their remoteness, yet this remoteness will offer no protection against future climate-change impacts. Our data indicated that the coral reefs in the Banda Sea are among the healthiest reefs in Indonesia, emphasising the importance of protecting this glimmer of hope in a world of increasingly degraded coral reefs.

Supplementary material

Supplementary material is available [online](#).

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Author affiliations

^AFisheries and Marine Science Faculty, Pattimura University, Jalan Dr Leimena, Kampus Poka, Ambon, Indonesia.

^BMaritime and Marine Science Center of Excellence, Pattimura University, Jalan Dr Leimena, Kampus Poka, Ambon, Indonesia.

^CCentre for Collaborative Research on Aquatic Ecosystem in Eastern Indonesia, Ambon, Indonesia.

^DGraduate School, Hasanuddin University, Makassar, 90245, Indonesia.

^ESchool of Biology, Faculty of Biological Sciences, University of Leeds, Leeds, LS2 9JT, UK.

^FNational Marine Science Centre, Southern Cross University, Faculty of Science and Engineering, Coffs Harbour, NSW, Australia.

^GCentre for Biodiversity and Conservation Science, School of Biological Sciences, University of Queensland, Brisbane, Qld 4072, Australia.

^HCSIRO Environment, Battery Point, Hobart, Tas. 7004, Australia.