



# Fishing patterns shaped by history, place, and access leave lasting ecological signatures on coral reef fish assemblages

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## ARTICLE INFO

### Keywords:

Small-scale fisheries  
Reef fish communities  
Fisheries management  
Resource use  
Subsistence fisheries  
Spatial fix

## ABSTRACT

As global demand for seafood increases, reef fisheries expand with increasing mobility and market integration. Yet, many remain small-scale and informally regulated, where place-based knowledge shapes how fishing is distributed across space and between diverse resource users. These social geographies impact reef fish assemblages, with consequences for ecosystem function. However, this is challenging to document in data-poor fisheries. We used a mixed-methods approach with i. interview surveys to characterise perceptions of catch availability, spatial patterns and intensity of reef fishing and ii. in-water surveys to quantify the impact of fishing on fish communities, in the Lakshadweep archipelago (Indian Ocean). We found that although the fishery is nominally open access, subsistence fishing was limited to a distinct 'home resource catchment'; confined to reefs proximate to inhabited islands. The recently emerged commercial reef fishery maintains profitability by focusing on distant, uninhabited atolls that have not experienced historical pressure and are perceived as richer fishing grounds. This represents a 'spatial fix', where problems of overaccumulation are solved by expanding or restructuring geographical space. Historically fished, proximate reefs are associated with significantly lower biomass (up to 69.8 %) and abundance (up to 97.14 %) of target predator species than reefs of distant, uninhabited atolls. The densely populated capital atoll shows the strongest fishing impacts with significant differences in size structure and community composition as well. Our approach reveals nuances in how subsistence and commercial fishers navigate shared resources and highlights a critical need for careful understanding of the social geographies of reef use.

## 1. Introduction

Understanding how fishing is distributed across the seascape is essential to assessing its ecological impacts on coral reef fish assemblages. Spatial patterns of extraction reflect more than convenience or resource availability; they often emerge from a complex interplay of social relations, historical contingencies, cultural norms, and local ecological knowledge (Aswani, 1998; Berkes et al., 2000). While over six million fishers participate in coral reef fisheries globally—most in small-scale or artisanal operations (L. S. L. Teh et al., 2013)—these fisheries increasingly intersect with global markets, intensifying extraction and raising concerns about declining reef fish populations and the breaching of ecological thresholds (Cinner and McClanahan, 2006). Recent estimates show that more than 50 % of fished reefs have fish biomass below

levels deemed sustainable (Zamborain-Mason et al., 2023), with catch having reduced dramatically despite increasing efforts (Eddy et al., 2021). Ensuring the sustainability of reef fisheries remains a central challenge for resource management of tropical reefs. Where state-led or customary institutions exist, they play a critical role in regulating access and limiting overharvest through mechanisms of monitoring, sanctioning, and norm-setting (Johannes, 1978, 2002; Ulate et al., 2018). These instruments typically result in an explicit spatial partitioning of resource extraction, as different areas are designated for use, protection, or exclusion based on social or ecological criteria (Cinner and Aswani, 2007; Cinner, 2007). Yet even in the absence of codified institutional arrangements, fishers may follow tacit norms and regularised behaviours that influence how marine spaces are used. These unwritten codes result in socially meaningful geographies of extraction—embedded

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<https://doi.org/10.1016/j.biocon.2025.111675>

Received 25 July 2025; Received in revised form 1 December 2025; Accepted 12 December 2025

Available online 2 January 2026

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spatial practices shaped by societal relations, perceptions of familiarity, safety, and historical usage (Beitl, 2014; Islam and Berkes, 2016). For example, fishers often concentrate effort on fishing grounds near their home island or coast, where ecological knowledge is greatest and travel costs are lowest (Stuart-Smith et al., 2008; L. C. L. Teh et al., 2012). Thus, even in nominally open-access systems, fishers must navigate a reefscape that is both socially and ecologically constructed, resulting in a heterogeneous distribution of effort. Accurately characterising the intensity, scale and diversity of this effort, and evaluating its impact on ecological systems requires engaging with the social, historical and ecological factors that together influence the fishery.

The social geography of fishing can leave distinct ecological signatures on fish biomass, abundance and community composition. Yet, detecting these impacts is far from straightforward. Unfortunately, very few tropical reef fisheries are equipped with the resources and institutions required to maintain historical records of resource use and catch harvested (Johannes, 1998; Purcell and Pomeroy, 2015). Furthermore, declines in reef fish are not apparent in even the best-monitored fisheries due to the phenomenon of hyperstability wherein catch per unit effort (CPUE) remains high despite declines in wild populations. This occurs both due to the aggregating behaviours of fish as well as the adaptive skill of fishers, who are able to track and extract stable volumes of fish irrespective of changes in resource availability (Sadovy and Domeier, 2005). As a result, unless monitored by methods other than catch records, change in actively fished populations may not be detected until it is too late and the population is nearing collapse (Hamilton et al., 2016; Ward et al., 2013). In data-poor fisheries, it is possible to rely on fishers' perceptions and memories to reconstruct patterns of fishing. Key community informants can help accurately map how resource extraction is distributed in space, and how current patterns of resource use link to perceptions of fish availability and decline (Karnad et al., 2024). Local knowledge can also throw light on subtle trends in fishing practices, including community norms and conventions that standard fisheries surveys would normally overlook (de la Barra, Iribarne and Narvarte, 2019; Karnad et al., 2020; Stuart-Smith et al., 2008).

Eventually, these spatial-temporal trends will be reflected in reef fish community structure, shaped by how targeted and intense the fishing is, as well as by the relative ability of species to cope with fishing pressure. Predators such as sharks, rays, groupers, snappers, emperors and jacks as well as large-bodied herbivores including parrotfish and surgeonfish are all highly prized fishery targets. Their large body size, slow-growing, late-maturing and long-lived life history characteristics make their populations especially vulnerable to fishing impacts (Sadovy, 2005). Targeted extraction of species, and within species, of large individuals, can radically alter community composition and size-structure of the fish assemblage (Graham et al., 2005; Trenkel and Rochet, 2003). Reef fish communities are essential to mediating several critical ecosystem processes such as predation, herbivory, bioerosion and nutrient cycling (Brandl et al., 2019). While evidence of the existence of trophic cascades in coral reefs is equivocal (Casey et al., 2017; Frisch et al., 2016), alteration of reef fish communities can have lasting impacts on ecosystem function. In the Western Indian Ocean, a reduction in numbers of the predatory red-lined triggerfish (*Balistapus undulatus*) led to an exponential increase in urchin abundances on Kenyan reefs which led to a decline in ecosystem condition with an erosion of reef substratum (McClanahan, 1995). Similarly, outbreaks of Crown-of-thorns starfish (*Acanthaster planci*) in the Great Barrier reef, responsible for high coral mortality, have been linked to depletion of its predators due to overfishing (Babcock et al., 2016).

The degradation of community structure in historically overfished reef systems is also reflected in the shifting baselines of fisher perception, as seen for instance in Mauritius, where younger fishers lack the ecological knowledge and memories of fish abundance reported by older generations (Bunce et al., 2008); as well as in extraction patterns, as fishers in parts of East Africa and South-East Asia resort to dynamite

fishing and drag-netting to maintain a fishery in an increasingly resource-scarce environment (Chou et al., 2002). While more distant oceanic systems in the Indian Ocean like Maldives, Chagos and Lakshadweep archipelagos, do not yet face these high-intensity pressures (Sattar et al., 2012), there is evidence to suggest that fishing-related declines have occurred even on some of the most remote reefs such as in the Chagos archipelago (Graham et al., 2013).

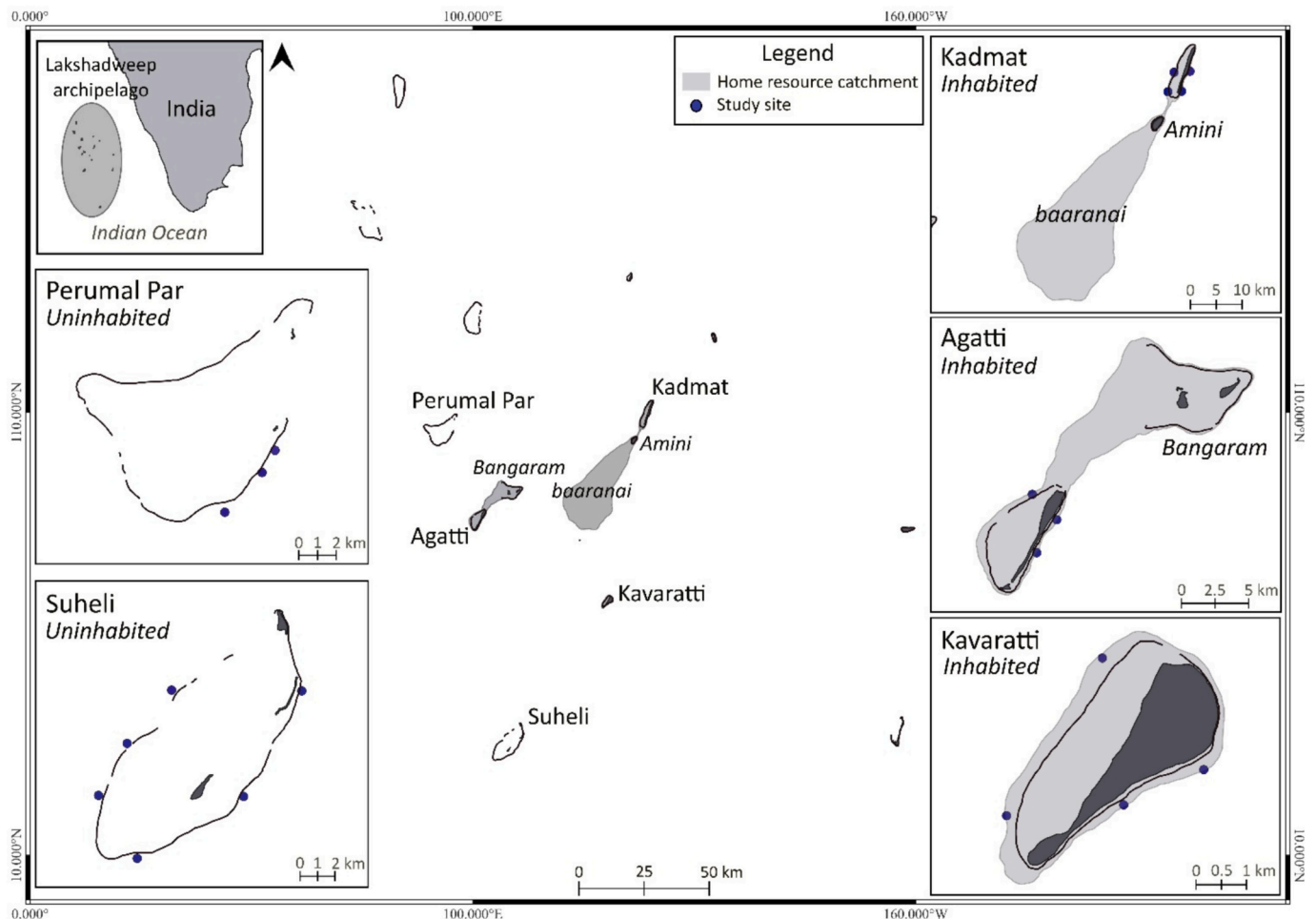
Here, we examine how fishing patterns emerge from the interplay between social arrangements, ecology and history to impact fish community composition across inhabited and uninhabited reefs in the Lakshadweep Archipelago, Indian Ocean. Since the 1960s, the commercial fishery in Lakshadweep has been dominated by pole-and-line fishing of pelagic tuna and reef fishing has historically been for subsistence rather than trade (Jaini et al., 2018). However, the last decade has seen the growth of commercial reef fishing, with the influx of mainland 'collector boats' that enable export of fresh reef fish (U.T Administration of Lakshadweep, 2025). In the absence of annual fish landing data or other fisheries records, we draw on fisher perception and ecological data to: i. characterise spatial and temporal patterns of fishing and ii. quantify the impact of fishing on fish community biomass, abundance, size-structure and composition.

## 2. Methods

### 2.1. Study site

The study was conducted in two phases; with the first between February and May 2022 and the second between January and April 2024, across 5 atolls in the Lakshadweep archipelago (8°N-12°N, and 71°E74°E) (Arthur et al., 2006). There are 10 inhabited islands, with 64,429 residents, making it one of the most densely populated island groups in the region (Census of India, 2011) with a decennial growth rate of 6.3 % (Administration of the Union Territory of Lakshadweep, 2023). The northern group of islands (formerly *Amindivi* and *Laccadive* groups) operates as a single socio-cultural unit, with a shared history and ethnolinguistic similarities with the southern Indian state of Kerala (Khan, 2024; Mustak et al., 2019). The southernmost island of Minicoy; however, is socio-culturally and historically distinct, having once been part of the sultanate of Maldives and joining the Indian state in 1956 (Ahmad, 2020). We focused our study across 3 inhabited atolls of Kavaratti, Agatti, and Kadmat, and 2 uninhabited atolls of Perumal Par and Suheli (Fig.1), all located in the northern group of islands. The inhabited atolls form a gradient of human population density, with Kadmat having the smallest population and Kavaratti, the capital island, having the largest and fastest growing population (Census of India, 2011; U.T Administration of Lakshadweep, 2025).

Uninhabited atolls in the archipelago are characterised by large, deep lagoons and often, a collection of multiple small islands. They are used by local communities for various purposes; mainly fish and coconut processing, and agriculture, but are too constrained in area and too water-scarce to support permanent settlements. Lakshadweep's oldest protected area is Pitti Bird Sanctuary, established in 1995 and covering an area of 0.01 km<sup>2</sup>. In 2020, 3 more protected areas spread over 645 km<sup>2</sup>, across the uninhabited atoll of Cheriyanpani and the submerged reef between the islands of Amini and Pitti, were created. However, these are designated primarily for the protection of marine birds and sea cucumbers (Rizvi et al., 2024), and do not prohibit fishing. Officially, Lakshadweep fishers have exclusive access to the territorial waters of Lakshadweep (within 12 nautical miles), and no fishery restrictions exist for reefs and pelagic areas (Department of Fisheries UTL, 2014). While the southernmost atoll of Minicoy has systems of customary tenure to manage bait fish resources (Abraham et al., 2025), the northern group of atolls have no documented form of traditional fishery management.



**Fig. 1.** Map depicting sampled atolls in the Lakshadweep archipelago. Boundaries of de facto 'home resource catchments' are depicted in patch of grey surrounding the inhabited atolls of Kadmat, Agatti and Kavaratti (panels on the right, arranged from top to bottom in order of increasing fishing pressure). Sites sampled at each atoll are marked in blue. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

## 2.2. Characterising patterns of reef fishing

### 2.2.1. Questionnaire surveys and key informant interviews:

In the first phase of the study a mix of short questionnaire surveys ( $n = 11$ ) on Kavaratti and semi-structured key informant surveys ( $n = 22$ ) across the 3 inhabited atolls (Kadmat, Agatti and Kavaratti) were conducted with members of the local fishing community to characterise patterns of reef fishing. Short, questionnaire surveys were conducted in February 2022 by convenience sampling of fishers along the beach and at important junctions on the islands where fish is usually sold. The questionnaire consisted of questions on (1) species commonly fished (2) bait used (3) location of fishing grounds (4) date and duration of most recent trip (5) frequency of trips in a month (6) size and type of boat used (7) market price. Information from these surveys helped form the basis for key informant interviews. Details on locations of fishing grounds used and additional information on preferences for fishing grounds and perceptions of catch that arose opportunistically during quantitative surveys were also utilised for the analysis and interpretation of responses from key informant surveys.

Key informant interviews were carried out between mid-March to mid-May 2022. A mix of sampling strategies were used for the key informant surveys. A snowball sampling strategy was used to identify individuals within the fishing community with experience and knowledge of historical and current fishing practices across the archipelago. Alongside this, certain key informants were encountered opportunistically, either at locations where fish were being sold or along the islands'

lagoon roads, which are commonly used by fishers for rest and recreation. Participants were interviewed at their convenience after gaining consent. When participants did not consent to being audio-recorded, interviews were recorded through notes. All interviews were conducted by the lead author in Malayalam, one of the region's official languages. Notes made during and after key informant surveys, as well as annotations made by respondents on maps, were used in later analyses. Some interviews ( $n = 4$ ) involved more than one participant, as fishers nearby sometimes joined the interview midway. Differing responses, if expressed, were recorded accordingly, although the interview was treated as a single entity for the purpose of analysis.

Key informant interviews were semi-structured and explored practices, norms or behaviours associated with the fishery, preferred fishing grounds, market opportunities, personal experiences and perceptions of fish catch. Some quantitative data on fish commonly targeted, gear used, crew and boat size and frequency and duration of fishing trips was also collected from each informant to better characterise effort. We also used blank maps of Lakshadweep to mark preferred fishing locations, and to focus our discussions on how fishing effort was distributed between fishing types (commercial and artisanal) and across atolls. Catchment areas associated with each inhabited island were delineated using this information (see Fig. 1).

All key informants were male, as women in the Lakshadweep do not participate in the harvest and sale of catch, nor in the maintenance of commercial fishery operations. Instead, they fish for subsistence in the lagoon areas close to shore (Hoon, 2003). We interviewed a mix of

commercial and subsistence fishers spanning an age range of 20 to 60 years, in order to capture a variety of practices and perspectives, both historical and current. All interview surveys were conducted in accordance with the ethical standards of the Institutional Human Ethics Committee, National Centre for Biological Sciences, India.

### 2.2.2. Analysis of key informant interviews

A total of 16 of the 22 key informant surveys were voice-recorded, translated and transcribed verbatim. Along with notes and impressions, data was analysed through inductive coding to draw out broad themes and categories that emerged from participants' responses (Fereday and Muir-Cochrane, 2006). Each theme was further analysed and condensed into key ideas, perceptions and narratives that informed the interpretation of themes that form the focus of this study. A descriptive, rather than quantitative or theoretical approach was taken to understand and present interview results.

### 2.2.3. Characterising fishing pressure:

Due to a lack of spatially-explicit secondary data on fisheries operations, a combination of results from interview surveys, official records on registered fishing boats (Department of Fisheries UTL, 2014), and human population data (Census of India, 2011) were used to characterise fishing pressure at reefs on each island.

### 2.2.4. Characterising coral reef ecological communities

Reef fish communities are structured by benthic habitat condition, structural complexity and depth, amongst other environmental variables (Chong-Seng et al., 2012; Graham and Nash, 2013) which may confound our ability to detect fishing impacts. In-water surveys were used to characterise the reef fish community (through underwater visual census), benthic habitat (through photoquadrats) and structural complexity (through canopy height measures) to more accurately characterise the impacts of reef fishing.

## 2.3. Underwater visual census

### 2.3.1. Reef fish community:

A total of 20 locations across 5 atolls were sampled at deep (14–16 m) and shallow (7–9 m) depth classes using SCUBA ( $n = 40$  sites). We sampled between 3 and 4 belt transects of  $5 \times 50$  m at each depth class ( $n = 132$ ) to characterise the reef fish community. All diurnally active, non-cryptic reef fish 10 cm and larger were recorded on the transect. Individual fish were identified to the level of the species and total lengths estimated to the nearest centimetre. A total of 3 experienced observers collected fish data over the course of the study.

### 2.3.2. Benthic habitat:

Additional observers collected 6,  $1 \times 1$  m benthic photoquadrats at 10 m intervals along the same transect. The photoquadrats collected were used to quantify cover of 5 benthic habitat categories (planar area cover of live coral, algae, sand, rubble and reef framework). The software ImageJ (Schneider et al., 2012) was used to lay  $10 \times 10$  cm grids over the quadrat. Following this, the number of grid cells covered by each benthic habitat category was estimated.

Along each belt transect, canopy height (the maximum height of the total standing structure) was measured at 2 m intervals. Average canopy height was chosen to be used as a measure of reef structural complexity as it correlates well with other indices (Bayley et al., 2019). All in-water surveys were conducted in the second phase of the study between the months of January and April 2024.

## 2.4. Data analysis

### 2.4.1. Size-spectra slopes:

Individual fish at each sampled location were categorised to 5 cm bins of size classes ranging from 11 to 65 cm. Size-spectra slopes for each

location were calculated by regressing  $\log_{10}(x + 1)$  of number of individuals in each size class against the  $\log_{10}$  mid-point of each size class (Graham et al., 2005). The slope of this line is an important metric of fishing impacts (Trenkel and Rochet, 2003). 'Island' served as a proxy for fishing pressure that encompasses differences seen across islands in terms of historical and current fishing pressure (refer Table 1). We used ANOVA to examine differences in size-spectra slopes and Tukey's HSD Test was conducted on ANOVA outputs to identify significant pairwise differences in slope.

### Modelling impact of fishing on biomass and abundance:

In order to disentangle the effects of habitat variables on fish biomass and count from that of fishing pressure, mixed-effects regression models were used. Species recorded on each transect were grouped into three functional groups based on their trophic level as listed on FishBase (Froese and Pauly, 2000) (i) tertiary consumers (such as *Epinephelus fuscoguttatus*, *Carangoides ferdau*), with a trophic level of 4 or higher, (ii) secondary consumers, which consisted of macro and microinvertebrates (such as *Cheilinus fasciatus*, *Chaetodon trifasciatus*; trophic level between 3 and 4) and (iii) primary consumers composed of herbivores and detritivores (Acanthurids and Scarids; trophic level between 2 and 3). Mid-water planktivores such as Caesionids were not modelled as their presence is governed by currents and upwellings not accounted for in this study (Hamner et al., 1988).

Model structure included (i) island (ii) canopy height (iii) depth class (iv) coral cover and (v) algal cover as fixed effects and 'Site' (location sampled) as random effect. The categorical variable of 'Island' served as proxy for fishing pressure as explained in the section above (refer Table 1) and also encompassed other oceanographic factors associated with island. Preliminary analysis showed that Suheli was associated with the highest biomass and abundance of target fish (tertiary consumers) and was thus modelled as the intercept for the categorical variable of 'Island', relative to which estimates of other islands were calculated. Reef structural complexity is known to significantly impact fish biomass and abundance (Syms and Jones, 2000) and was included as a fixed effect through the proxy variable of  $\log_{10}$  transformed 'Canopy height'. Fish assemblages change with depth, with larger bodied species preferring to occupy deeper sites, and a categorical 'depth class' fixed effect was included. Percent 'coral cover' and 'algal cover' for the site as characterised through benthic image analysis were also included as habitat variables that potentially predict fish biomass (Chong-Seng et al., 2012). Both variables were scaled and centred around zero for modelling.

Biomass of fish recorded on transects was calculated using species-specific allometric length-weight relationships as listed on FishBase (Froese and Pauly, 2000). No correction was applied to sizes as estimated by observers. Biomass data pooled into trophic groups was  $\log_{10}(x + 1)$  transformed to fit the assumptions of normality and 3 linear mixed effects models (one for each trophic group) were fitted with the model structure detailed above.

Fish count was similarly pooled into the three trophic groups described above. A generalised linear mixed model (GLMM) with a negative binomial error structure was used to model count data for each trophic group with the structure described above. All models were fitted based on the distribution of data as revealed during preliminary analyses. The Shapiro-Wilk test for normality was conducted on datasets where normality could not be visually assessed. Exploratory analyses revealed no correlation between explanatory variables. Model fit was visually assessed using diagnostic plots. GLMMs were assessed for overdispersion, model convergence and collinearity of predictors using the package 'performance' and by calculating the ratio of residual deviance to residual degrees of freedom. The models were then used to estimate marginal means associated with the variable 'Island' by predicting mean biomass and abundance associated with each island for each consumer group by maintaining all other parameters (i.e., canopy height, coral cover, algal cover and depth) at their mean values, thus helping visualise the sole effect of 'Island', used as proxy for cumulative

**Table 1**

Fishing pressure as experienced by each island with supporting information from secondary sources.

Variable	Island				
	Suheli	Perumal par	Kadmat	Agatti	Kavaratti
Human population <sup>1</sup>	0	0	5389	7560	11,221
No. of registered boats <sup>2</sup>	0	0	126	281	349
de facto resource catchment	None (open to all)	None (open to all)	Kadmat + baaranai	Agatti + Bangaram	Kavaratti
Area of de facto resource catchment (km <sup>2</sup> )	–	–	86	59	4
Human population/km <sup>2</sup> of resource catchment	0	0	62.54	129.11	3214.17
Subsistence Fishing pressure (Historical <sup>3</sup> )	Very low	Very low	Low-intermediate	Low-intermediate	High
Commercial fishing pressure (Recent <sup>4</sup> )	High	High	Low	Intermediate	Very low
Cumulative fishing pressure	Very low	Very low	Low	Intermediate	High

fishing pressure, on biomass and count.

#### 2.4.2. Community composition through ordination:

A community matrix using species abundances for each site was constructed. Due to heterogeneity of variances causing overdispersion in the dataset, as result of aggregating behaviour of certain species such as *Lutjanus gibbus*, count data was  $\log(x + 1)$  transformed and Bray-Curtis distance indices were calculated for pair-wise comparison between sites (Legendre and Gallagher, 2001). To explore if community composition differed significantly between islands, a PERMANOVA was performed on the distance matrix. The matrix was then visualised with a Principal Coordinates Analysis and the plot was overlaid with Weighted Averages of Species scores to visualise correlations between site scores and species relative abundances.

R Statistical Software (v4.3.3; R Core Team 2024) was used for all statistical analyses. Packages ‘tidyverse’ (Wickham et al., 2019) and ‘vegan’ (Oksanen et al., 2025) were used for data cleaning, plotting and for ordinations. Packages ‘lme4’ (Bates et al., 2015) and ‘MASS’ (Venables and Ripley, 2002) were used for running LMEs and negative binomial GLMMs, respectively. Package ‘performance’ (Lüdecke et al., 2021) was used to assess model fit and model utility functions from ‘MuMin’ (Bartoń, n.d) were used to extract values from fitted model objects.

### 3. Results

#### 3.1. Patterns of reef fishing:

Fishers irrespective of their home island, tended to view the entire northern Lakshadweep (excluding Minicoy) as a single large resource catchment over which they retained exclusive extractive rights. This exclusivity is monitored by the government Fisheries Department that prohibits fishers from other Indian states from fishing in the nearshore waters of Lakshadweep’s atolls. However, interview responses revealed nuances as fishers from different islands made clear choices in their fishing grounds within the archipelago. Which atoll they preferred to fish depended on: (i) scale of extraction undertaken, (ii) perception of catch, (iii) proximity to home island.

#### 3.2. Uninhabited (distant) versus inhabited (home) atolls:

All respondents reported using the lagoons and reefs of their home atolls for subsistence and recreational fishing. However, for commercial extraction, fishers across the islands overwhelmingly preferred the waters around uninhabited atolls (Fig. 1). Catch on uninhabited distant atolls was perceived to be greater than inhabited ones. It was stated, repeatedly, that “for (commercial) reef fishing, nobody goes to inhabited islands” (KV05).

The higher abundance and sizes of fish in uninhabited atolls was attributed by informants to the fact that uninhabited atolls often had large and deep lagoons. In addition, the inherent inaccessibility of distant atolls was also cited as a key reason for better catch. According to fishers, their remoteness protected them from (i) disturbance due to boat

traffic and (ii) fishing, anthropogenic stressors that on inhabited reefs were seen to have depleted fish populations.

In contrast, subsistence fishing on each atoll was restricted to nearby reefs. However, the area over which it took place, a *de facto* resource catchment (hereby referred to as ‘home resource catchment’), differed for fishers of different islands. Kavaratti fishers were restricted to the reefs of their own atoll (Fig. 1). The residents of Agatti on the other hand, had access to a much larger home resource catchment, actively fishing off both Agatti and nearby Bangaram (Fig. 1). Bangaram is located approximately 14 km from Agatti and can be accessed by smaller motorised boats as well. Respondents from other atolls also viewed Bangaram as an extension of Agatti’s fishing grounds. The reefs of Kadmat, while used by locals, were described as being narrow with a steep drop off, making it unideal for fishing. Their preferred fishing grounds were reefs of the ‘baaranai’, an easily accessible shallow submerged ridge sprawled over an area spanning 49 km in length and upto 18 km at its widest (Fig. 1).

#### 3.3. Perceptions of resource availability across islands:

Resource availability on uninhabited atolls was unanimously reported to be higher than that of inhabited atolls. In contrast the responses relating to resource availability and use on home reefs were more nuanced. The heterogeneity of responses mirrored the gradient of urbanisation and population density that the sampled inhabited islands represent.

#### 3.4. Kavaratti:

Fishers across the sampled atolls spoke of insufficient availability of catch for commercial purposes on the reefs of Kavaratti, the capital, and most densely populated, island. As Informant KV01 reported: “[Commercial reef fishing in Kavaratti] is a waste of time. You get only a little bit of fish - we go to other places” (KV01).

Kavaratti’s fishers described visiting distant atolls such as Suheli and Bitra right from the onset of the commercial fishery, dated by respondents to have started around 2013–14. Even subsistence fishing, in recent years, was described as requiring more time and effort (See Supplementary 1.4, Quote. 1). Many fishers cited Kavaratti’s small lagoon and by extension, smaller available reef area, as the reason behind low resource availability. Some participants, however, attributed this to fishing impacts and stated clearly that the depletion was a more recent phenomenon and that they remembered catch in Kavaratti being plentiful 2–3 decades ago and fishers did not need to venture out to other atolls (Supplementary 1.4, Quote 2).

Another participant spoke of Kavaratti being unlike other islands in the magnitude of pressure its reefs received. As he described it, being a densely populated capital island with a large expatriate population in addition to the local community, meant that its reefs did not get any respite from fishing, even during the rough monsoon season when more large-scale extraction for commercial purposes was halted (Supplementary 1.4, Quote. 3). Regardless of the underlying reason attributed to it, participants across atolls agreed that Kavaratti’s reefs were no

longer suitable for large-scale harvest.

### 3.5. *Agatti*:

A similar narrative emerged in Agatti, where several informants stated that fishing-related decline in Agatti reefs drove them to seek out remote atolls for commercial harvest. As with fishers from Kavaratti, some Agatti informants linked their preference for uninhabited atolls to the larger lagoons and greater reef area of submerged banks like Perumal Par.

However, responses were not as homogenous as on Kavaratti. Of the 8 key informants interviewed, three reported fishing exclusively within their home resource catchment and being able to remain profitable. Here again, the volume of extraction played a role. These participants operated on smaller boats with 3–4 crew members and could not travel to distant atolls. Participants that operated larger boats with crews of 10–12 men needed to harvest larger volumes to make a profit; these informants reported experiencing catch depletion within Agatti's resource catchment, and preferred to travel to distant atolls.

### 3.6. *Kadmat*:

Fishers from Kadmat also reported visiting uninhabited atolls for commercial reef fishing. However, they still used part of their home resource catchment, the '*baaranai*', for commercial fishing as it was rich in 'large, deep water reef fish' such as groupers and snappers (Supplementary 1.4, Quote. 4). Narratives of decline at the home reef were not strong amongst Kadmat key informants. While three participants did report having experienced a decline in catch, only one attributed it to anthropogenic impact, while the others cited seasonality as the cause. Most informants in Kadmat did not have the same perception of the depletion of home reefs expressed in Kavaratti and (to a lesser extent) Agatti.

### 3.7. *Resource partitioning across home and distant atolls*:

The spatial patterns of commercial fishing indicated subtle separations in resource access by the different islanders. While most islanders agreed that Kavaratti was not currently suitable for commercial reef fishing, fishers across all islands reported occasionally visiting Agatti and Bangaram to fish commercially, although they were not preferred as highly as uninhabited atolls. Commercial fishers from other atolls did not visit Kadmat waters to fish, although some participants from Agatti did report fishing at the '*baaranai*' near Kadmat'. Amongst the available uninhabited atolls, fishers chose atolls based on proximity to the home island, with Kavaratti fishers showing an overwhelming preference for Suheli, while Agatti fishers largely preferred Perumal Par, perceived as being relatively close and taking approximately 'two and a half hours' to reach. Kadmat fishers' responses were mixed, with Cheryapani, Valiyapani and Bitra, being mentioned most frequently as distant water reefs they preferred to visit for commercial fishing. While the island of Bitra has a small population (~60 households), the atoll has a large lagoon known to host high numbers of groupers and key informants confirmed that it was visited frequently by fishers from other islands.

Although primarily driven by resource availability, fishers' movements were also informed by the perception that while uninhabited atolls were 'open' to commercial fishers of all islands, reefs of inhabited atolls were to be avoided not just because of lower resource availability, but also because they 'belonged' to the local community that used it for subsistence fishing. As one informant from Agatti put it:

'That's *their* place (referring to people of other inhabited islands), which they use to fish and sell locally. There is no need for us to fish there. What you get here, you get there as well. But if we want a lot of fish, we don't go there. We don't visit inhabited islands when we want to catch a lot of fish. (AG03)'

This spatial separation, however, was governed by regularised

patterns of behaviour rather than formal norms or restrictions. When asked questions about fishers' decision-making specifically with regard to the location of fishing grounds, key informants insisted that there was no exclusivity or restrictions in accessing specific atolls.

### 3.8. *Interplay with tuna fisheries*:

Commercial fishers have, since the 1960s to present day, fished primarily for tuna. All responses on fishing effort, preference for fishing grounds and profitability were thus framed in comparison to tuna fishing. While most fishers agreed that reef fishing was indeed 'profitable' as it had a lower cost of operation, some stated that it only 'seemed' profitable as it was carried out at times when tuna fishing was no longer profitable; i.e., when either catch for skipjack tuna or market demand for tuna was low.

As a fisher from Kavaratti stated: "We fish reef fish when we are unable to catch anything else, that's why it feels like it is profitable" (KV05).

Several fishers across the three islands spoke of the decline in profitability of tuna fishing as a result of reduced market value and rise in operation costs (Supplementary 1.4, Quote. 5). Despite the apparent net benefit associated with it, expansion of commercial reef fishing was reported to be limited by storage facilities and more importantly by reef fish themselves. As our informants explained, pelagic tuna, unlike most reef fish, occur in large schools numbering in the thousands. A single skipjack tuna weighs about 2–3 kg on average. Thus, once encountered, the effort required to harvest large volumes of tuna is much less than the effort required to harvest the same amount of reef fish. Additionally, skipjack tuna are a fast-growing species that range over thousands of kilometres. Targeted reef fish, such as groupers, occur in relatively low densities and are caught using hooks-and-lines (see Supplementary Table 1.3). Accordingly, they were viewed as being a resource unsuitable to large-scale harvest (Supplementary 1.4, Quote. 6). As a result, none of the commercial fishers interviewed for the study fished exclusively for reef fish. A common response was that they fished for 'whatever was available' and whatever was 'in demand' at the market.

### 3.9. *Gradient of fishing pressure*:

Collating results from key informant interviews (including details of de facto home resource catchments and fishing practices) together with population sizes and registered fishing boats, we identified fishing pressure experienced by reefs on each island based on historical and present-day, subsistence and commercial fishing across all five sampled atolls (see Fig. 2, Table 1). The distant uninhabited atolls of Suheli and Perumal Par had the lowest amount of subsistence fishing, but operated as 'open access' locations that were periodically used for commercial fishing. In contrast, the home reefs, Kadmat, Agatti and Kavaratti represented a strong gradient of increasing fishing pressure, largely as a function of the size of their de facto resource catchment and the number of fishers at each atoll. Fishing at these inhabited atolls was largely to meet subsistence needs, except for Agatti where some fishers used it for commercial catch as well (Table 1). (See Fig. 3.)

## 4. *Coral reef ecological communities*

### 4.1. *Size-spectra slope across islands*:

The slopes of fish size spectra decreased broadly across the fishing pressure gradient (See Table 1) (except for the reefs of Agatti) and differed significantly between islands (F-values = 6.56, p-value <0.05); however, Tukey's test revealed that not all slopes were significantly different: (i) the mean slope of Kavaratti differed significantly from that of Agatti and Suheli and (ii) Agatti differed significantly from Kavaratti, Kadmat and Suheli.

*Fish biomass and abundance of different trophic groups across islands:*

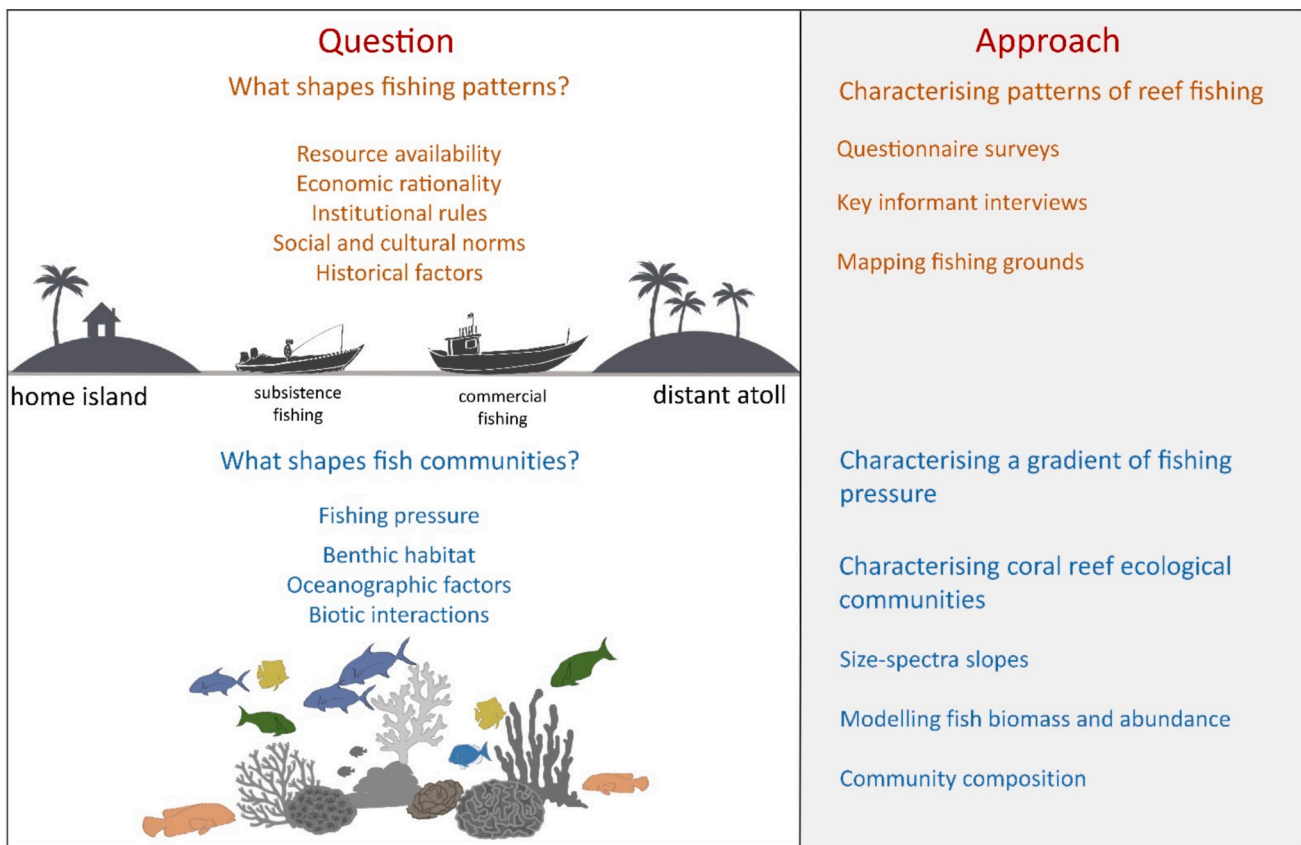


Fig. 2. Conceptual map of study system and research approach.

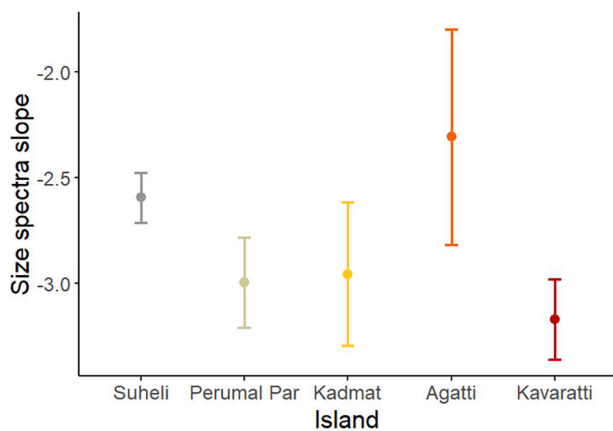


Fig. 3. Mean size-spectra slopes for islands ( $\pm 95\%$  CI). Islands arranged in order of increasing cumulative fishing pressure (See Table 1).

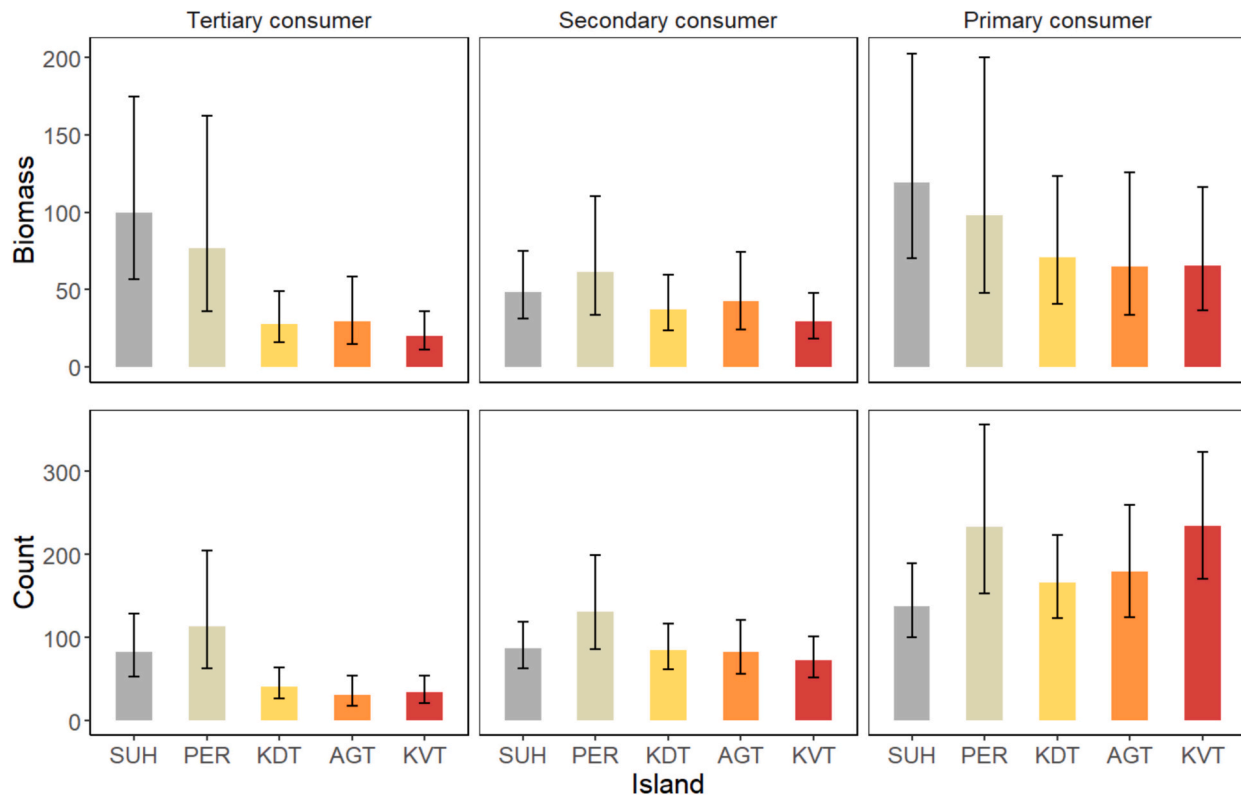
Reefs of inhabited islands were associated with significantly lower biomass of tertiary consumers. Kavaratti was associated with the lowest biomass (log scale estimate =  $-0.7; \pm 0.17$  SE), followed by Kadmat ( $-0.55; \pm 0.16$  SE) and Agatti ( $-0.53; \pm 0.19$  SE) (Table 3.1.3 Supplementary). The abundances of tertiary consumers were also significantly lower for inhabited atolls than for uninhabited atolls (Fig. 4). Here, Agatti was associated with the lowest abundances ( $-0.97; \pm 0.35$  SE) compared to Suheli (intercept; log scale estimate =  $3.11; \pm 0.87$  SE), followed by Kavaratti ( $-0.89; \pm 0.31$  SE) and Kadmat ( $-0.71; \pm 0.31$  SE). Perumal Par did not differ significantly from Suheli in terms of both tertiary consumer biomass and abundance (Fig. 4; Table 3.4.3 Supplementary). (See Fig. 5.)

The effect of 'island' on the biomass and abundance of secondary

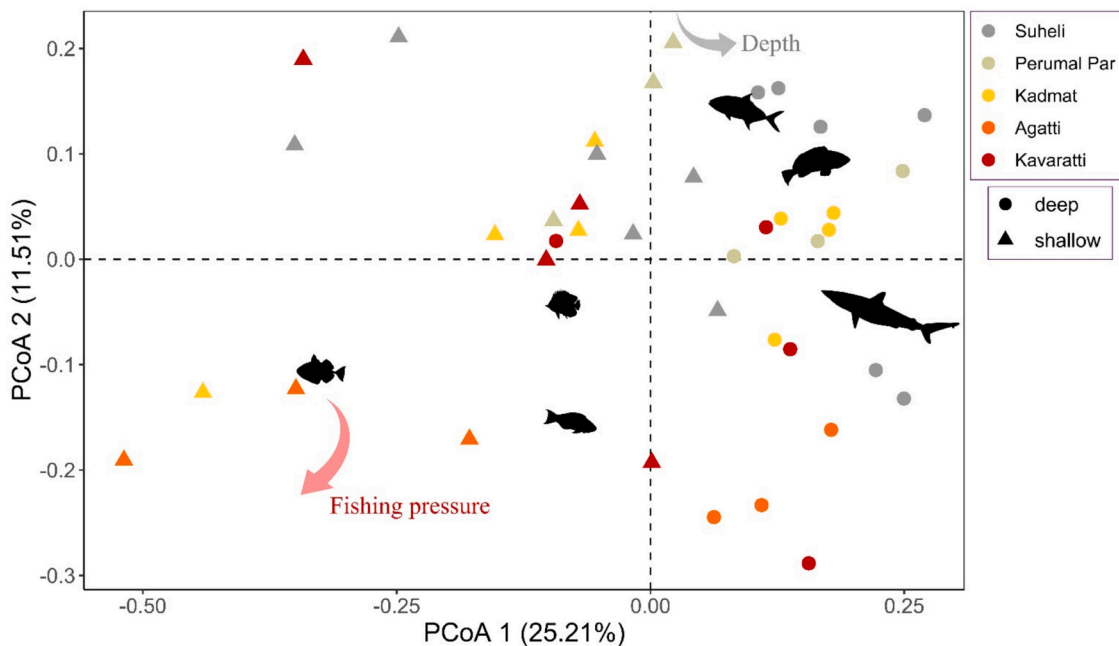
consumers was not statistically significant (Fig. 4, Table 3.2 Supplementary). Similarly, the effect of 'island' on the biomass of primary consumers was non-significant (Fig. 4, Table 3.3 Supplementary). However, abundance data showed a different pattern. Perumal Par was associated with significantly higher primary consumer abundances than the intercept (log scale estimate =  $+0.53; \pm 0.24$  SE;  $p$ -value = 0.03) and the same was seen for Kavaratti ( $+0.54; \pm 0.22$  SE;  $p$ -value = 0.01). 'Site' or sampled location, modelled as a random effect, showed very low variance across groups, for biomass as well as abundance regression models.

As expected across the three trophic groups, biomass showed a strong positive, significant correlation with structural complexity. Primary consumer biomass showed the strongest association (log scale estimate =  $1.44; \pm 0.35$  SE;  $p$ -value  $< 0.01$ ) followed by tertiary consumer biomass ( $0.96; \pm 0.21$  SE;  $p$ -value  $< 0.01$ ) and secondary consumer biomass ( $0.59; \pm 0.13$  SE;  $p$ -value  $< 0.01$ ). Structural complexity was also strongly associated with primary consumer abundances (log scale estimate =  $1.44; \pm 0.35$  SE;  $p$ -value  $< 0.05$ ) and, to a lesser extent, with tertiary consumer abundances ( $0.8; \pm 0.45$  SE,  $p$ -value = 0.08). Tertiary consumer biomass was also found to be significantly correlated with depth, with shallower sites being associated with lower biomass (log scale estimate =  $-0.32; \pm 0.09$  SE;  $p$ -value  $< 0.01$ ). Effect of depth on biomass of other consumer groups was not statistically significant (Table 3.2, 3.3 Supplementary). Abundances of all three groups showed a significant association with depth; deeper sites were associated with higher tertiary consumer abundances (log scale estimate =  $0.63; \pm 0.19$  SE;  $p$ -value  $< 0.01$ ). The effect was reversed for the other two groups; shallow sites were associated with an increase in secondary consumer ( $0.21; \pm 0.12$  SE) and primary consumer ( $0.34; \pm 0.14$  SE) abundances (Table 3.5, 3.6 Supplementary).

Coral and algal cover showed a non-significant and weak correlation with biomass across most consumer groups. However, tertiary



**Fig. 4.** Plots depicting the estimated marginal means associated with ‘Island’ on biomass (first row) and count (second) of the three consumer groups. The first row of plots depicts mean biomass (g m<sup>-2</sup>) across atolls, for each consumer group, as predicted by the linear mixed effects model fit to the dataset. The second row of plots similarly depicts mean count (per 250 m<sup>2</sup>) as predicted by the generalised linear mixed effects models fit to the dataset. Error bars depict 95 % CIs. Islands are arranged on the x axis in increasing order of cumulative fishing pressure (SUH = Suheli, PER = Perumal Par, KDT = Kadmat, AGT = Agatti, KVT = Kavaratti).



**Fig. 5.** Result of Principal Coordinate Analysis depicting 20 deep (represented by circles) and 20 shallow (triangles) sites spread across the ordination space. Points are coloured by island, with the gradient of colour (grey to red) representing the gradient of cumulative fishing pressure across islands (Suheli < Perumal Par < Kadmat < Agatti < Kavaratti). Reef fish icons depict weighted average score for the represented species (refer Supplementary table 4.2.2 for values). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

consumers showed a significant, positive correlation with live coral cover, with a slope of 0.24 (±0.09 SE), while primary consumers

decreased by 0.13 (±0.07 SE) with 1 SD increase in coral cover. Algal cover was associated with a significant positive correlation only with

tertiary consumer abundances (0.21;  $\pm 0.09$  SE) (Table 3.4 Supplementary).

#### 4.2. Community composition across islands:

PERMANOVA results showed significant differences in community composition between atolls (F-value = 1.872; p-value <0.01). The principal coordinates analysis shows deep and shallow sites separating along the first principal coordinate axis, with deeper sites being strongly correlated with the first axis and less fished sites being largely correlated with the second principal coordinate axis and separating along the vertical axis. Species weighted average scores indicate a largely positive correlation of predator species (tertiary consumers, trophic level  $\geq 4$ ) with the second principal coordinate axis (Supplementary Fig. 2). Long-lived predators most vulnerable to fishing impacts such as white-tip reef sharks (*Triaenodon obesus*), giant reef rays (*Taeniura melanospilos*) and large groupers and snappers such as the brown-marbled grouper (*Epinephelus fuscoguttatus*) and red snapper (*Lutjanus bohar*) show strong positive correlation with the second axis (refer Supplementary table 4.2.2 for species-specific values). A single shallow site from the heavily-fished atoll of Kavaratti is correlated with the second axis and with a species of moray eel (*Gymnothorax favagineus*), a predator that is not considered palatable and experiences minimal fishing pressure (Refer Supplementary Fig. 2 and table 4.2.2).

### 5. Discussion

Even without formal zoning mechanisms or territorial use rights, fishers may still engage in practices that spatially structure the fishery, and influence the way ecological impacts are distributed across the reefscape. These tacit arrangements are negotiated as much by social and historical factors as by resource availability and profitability. In the Lakshadweep Archipelago, our work shows that fishers partition reef areas between 'home' (proximate) and 'distant' fishing grounds, corresponding to subsistence and commercial fishing patterns, respectively. Our in-water ecological surveys reinforce perceptions reported by our key informants in Lakshadweep that inhabited atolls have already experienced a significant depletion in reef predator populations, and amongst them, reefs of the densely-populated, capital island of Kavaratti show the strongest signature of fishing pressure with significant differences in size-structure, as well as community composition of the fish assemblage. While metrics of fishing pressure, such as human gravity (Cinner et al., 2018) or measures of human density per unit area of reef (Hawkins and Roberts, 2004), may accurately predict fishing impacts, they tell us little about what drives fishers' choice of fishing grounds along this gradient of intensity.

#### 5.1. Patterns of reef fishing and the 'spatial fix'

Unlike islander communities in other parts of the Indo-Pacific (Aswani and Hamilton, 2004; Cinner, 2007; Johannes, 2002) including the archipelago's southernmost island of Minicoy (Abraham et al., 2025), our key informant interviews show there are no customary institutions that regulate fishing, either to formally partition resources for different kinds of resource users, or for the purposes of long-term sustainability of the fishery. The *de facto* resource catchments of fishers in Lakshadweep emerge out of regularised patterns of behaviour (sensu Leach et al., 1999) rather than through restrictions imposed by state-led or traditional institutions of management. Key informants consistently reported that the reefs of the archipelago were accessible to all Lakshadweep fishers. In practice however, fishing for subsistence was limited to the home resource catchment. In contrast, while it has been only a decade since a commercial reef fishery began in Lakshadweep, fishers found home reefs unprofitable right from the start, and have had to travel to more distant reefs. This practice varies between fishers from different islands – and is most pronounced for fishers from Kavaratti,

which has the smallest 'home resource catchment'. This indicates that long before commercial fishery began, low-grade subsistence fishing had already depleted many Lakshadweep reefs. Fishers' use of the landscape is thus adaptive and seeks to maximise catch from the most 'optimal' fishing grounds (Aswani, 1998). Interestingly though, the frequency with which commercial fishers engaged with reef fishing was as much about pelagic tuna as it was about reef fish. Commercial fishers in Lakshadweep appear to keep their options open while navigating an uncertain market – between the profitability of processed pelagic tuna (a product called *maas*) and the presence of collector boats for reef fish. Fishers' decisions thus hint at the interplay of economic, sociocultural, historical and individual constraints that studies across disciplines have found operate in fisheries (Béné and Tewfik, 2001; Salas and Gaertner, 2004). These factors together influence the spatiality of fishing impact, even without formal rules of access.

In many ways, the adaptive behaviours of Lakshadweep fishers track what David Harvey refers to as a 'spatial fix'. While the original theory critically examines how capitalist economies attempt to resolve crises by the 'production of space' and 'fixing' of overaccumulated capital into new infrastructure and geographies (Harvey, 1981; Schoenberger, 2004), a 'socio-ecological fix' can be understood as a reconfiguration of human-ecological relationships and landscapes. The goal of the 'fix' is always to maintain production or renew 'conditions of profitability' without addressing the inherent unsustainability of extractive capitalist economies (Ekers and Prudham, 2015). In Lakshadweep, the dynamic use of the pelagic seascape for fishing wide-ranging and seasonal skipjack tuna contrasts with the current use of the region's reefs for commercial fisheries production, revealing how the introduction of export markets has made fishers look beyond home reefs to the 'fix' of distant, uninhabited atolls for profitable resource extraction.

#### 5.2. Impacts on reef fish communities

The ecological context within which the spatial fix operates is clear. Results of in-water surveys show significant depletion in biomass and abundance of groups most heavily targeted by fishing; i.e., predators of trophic level 4 or higher, comprising commercially valued species such as squaretail groupers (*Plectropomus areolatus*), bluefin trevallies (*Caranx melampygus*), paddletail snappers (*Lutjanus gibbus*) and red snappers (*Lutjanus bohar*), on historically fished, inhabited atolls (Kadmat, Agatti and Kavaratti). This is in keeping with declines that have been documented on fished reefs across the tropics (Goetze, Langlois, Egli and Harvey, 2011; Hawkins and Roberts, 2004; Lokrantz et al., 2009). While biomass values for secondary consumers (largely invertivores) and primary consumers (herbivores and detritivores) do not show significant differences across the fishing gradient, primary consumer abundances appear to be highest in the reefs of Perumal Par, a relatively less-fished uninhabited atoll, and Kavaratti, the atoll most heavily fished historically. This contrasting trend in biomass and abundance, taken with the steepening of Kavaratti's size-spectra slope, suggests that the assemblage is depleted of large-bodied predators and has a large number of smaller-bodied herbivores instead. While Perumal Par also has a large number of herbivores, it still has a significant large-bodied predator community, adding up to a total biomass that is higher than that of fished, inhabited atolls. Heavily fished inhabited atolls also show significant differences in community composition as visualised by the PCoA, having very low numbers of highly vulnerable species that are the first to decline due to fishing, such as white-tip reef sharks (*Triaenodon obesus*) and rays, with some functionally important species such as bumphead parrotfish (*Bulbometopon muricatum*) seemingly absent from inhabited atolls. Given that Agatti also shows a significant depletion in tertiary consumer biomass and count, its size-spectra slope results from lower frequencies of individuals at both ends of the spectrum; i.e., lower numbers of smaller as well as larger-bodied fish.

Reef fish communities are structured by benthic habitat as well (Almany, 2004). Lakshadweep's reefs had experienced three ENSO mass

bleaching events since 1998 until the time of data collection for this study that have profoundly restructured its benthic communities (Yadav et al., 2018). This could have attendant consequences for reef fish. In order to disentangle the confounding effects of a benthic habitat affected by repeated disturbance events from that of fishing, fish communities were modelled using environmental covariates. Structural complexity was the strongest predictor of fish biomass across trophic groups (except for secondary consumers, or invertivores), in keeping with studies on its role in maintaining fish populations, such as in the survival of benthically-associated, ‘ambush’ predators belonging to the commercially-valued family Serranidae (Syms and Jones, 2000; Karkarey et al., 2014; Darling et al., 2017). Structural complexity has been found to operate somewhat independently of live hard coral cover on disturbed or recovering reefs, as mass coral mortality does not immediately lead to a complete loss of topographic complexity. Structure is instead maintained by the persistence of coral skeletons as well as underlying geomorphological features (Pratchett et al., 2014; Wilson et al., 2010). Our dataset is consistent with this, as structural complexity was weakly correlated with coral cover. Our results show a clear separation of the effect of structure from that of fishing on fish communities and thus address gaps highlighted in similar studies (Ashworth and Ormond, 2005). Our modelling results; however, point to potentially interesting patterns in primary consumer biomass and abundance. The effect of reef fisheries on large-bodied herbivores across the tropics is well-documented as is the associated loss of herbivory and its consequent effects on coral recruitment and growth, such as on Caribbean reefs (Edwards et al., 2014; Hughes, 1994). In Lakshadweep; however, herbivores are fished much less frequently and patterns in herbivore community and size-structure cannot be readily ascribed to fishing impacts without a deeper investigation into the effect of algal resource availability (Russ, 2003; Tootell and Steele, 2016).

Our findings thus highlight the unique vulnerability of reef fish to the cumulative impacts of subsistence exploitation and corroborate evidence of fishing effects from other regions (Campbell and Pardede, 2006; Hawkins and Roberts, 2004; Mangi and Roberts, 2006; Lokrantz et al., 2009). Despite the decline of higher trophic groups on fished, inhabited atolls, Lakshadweep may still compare well to other locations in the Indian Ocean with long histories of intensive, commercial harvest. For instance, at the highest extreme of historical fishing pressure, Kavaratti’s reefs possess a mean biomass of  $156.88 \text{ g m}^{-2}$  ( $\pm 6.95 \text{ SE}$ ; refer Table 2), which is higher than the mean biomass of  $80.4\text{--}93.1 \text{ g m}^{-2}$  (95 % CI) reported for ‘old and large’ marine protected areas off the coast of East Africa and Madagascar (McClanahan et al., 2021). These benchmarks need to be evaluated with caution however. More than 60 % of Kavaratti’s total fish biomass is contributed to by primary consumers, with tertiary consumers contributing less than 20 %. Taken together with the alteration in assemblage size-structure, this represents a fundamental change in the functional potential of the community (indirectly inferring ecological processes by looking at functional groups or traits, rather than rates of processes; sensu Hadj-Hammou et al., 2021), with implications for prey populations and behaviour, nutrient cycling and potentially cascading effects on benthic communities (Bruno and O’Connor, 2005; Madin et al., 2010; Schmitz et al., 2010). Given the increasing threat of climate-change induced disturbance events affecting reefs globally (Virgen-Urcelay and Donner, 2023), reef resilience and recovery is contingent on effective fisheries management that maintains fish populations and the ecological processes they mediate (Hughes,

1994).

### 5.3. Social geographies shape coral reef ecosystems

Reef fishing, alongside reef and inter-tidal gleaning, is fundamental to food security and fulfils a large part of islanders’ nutritional requirements, especially in times of economic hardship and limited livelihood opportunities (Garcia and Rosenberg, 2010; Hoon, 2003). Studies in the region that have examined subsistence fishing report pressure on reef resources long before mainland ‘collector boats’ became a regular part of the region’s fisheries (Tamelander and Hoon, 2008). We find that a nuanced characterisation of the spatial distribution of fishing effort provides important insights into an open access fishery that may not be otherwise apparent. Without formal harvesting rules, the spatial distribution of effort might be expected to reflect solely how individual fishers balance resource harvest gains against operational costs. Yet, in practice, spatial patterns of use and impact often emerge — structured not by formal rules, but by history, social ties, and ecological memory. Our findings also challenge simplified narratives about the relative impacts of ‘traditional’ or subsistence fishing and commercial harvest, as we find that the duration of exploitation, whether subsistence or market-driven may be as important as its intensity in shaping ecological outcomes. While our study reports broad trends that indicate as yet ‘intact’ predator assemblages on commercially-fished distant atolls, other studies in the region have found nuanced behavioural and potential reproductive impacts amongst vulnerable species manifesting in those same reefs (Karkarey et al., 2024). Commercial fisheries can evolve rapidly, with an influx of private players offering significant economic incentives, which, in the absence of proactive management, can severely deplete populations, degrade ecosystem functioning and jeopardise local livelihoods (Cinner et al., 2007; Johannes, 1978; Muallil et al., 2014; Ludwig et al., 1993). The lens of the ‘spatial fix’ demands an urgent need to rethink capitalist modes of production that transfer the problem of depleted fisheries resources from old fishing grounds to new ones. Instead, strengthening local institutions to more carefully manage patterns of use within the bounds of the socioecological system in which they operate, is essential to sustain both local livelihoods as well as the ecological resilience of already embattled coral reefs.

### 5.4. Biosketch

The lead author is a research assistant with Nature Conservation Foundation. This work originated as part of her Masters thesis with the Wildlife Biology and Conservation Programme at the National Centre for Biological Sciences, Bangalore, and was continued during her time with the Nature Conservation Foundation as part of the Oceans and Coasts Programme. Her current research priorities are on studying ecology and the dynamics of reef fish communities, and how they are shaped by humans and climate change-induced disturbances.

### CRedit authorship contribution statement

**Radhika Nair:** Writing – review & editing, Writing – original draft, Visualization, Validation, Software, Project administration, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualization. **Siddhi Jaishankar:** Writing – review & editing, Methodology, Investigation, Data curation. **Mayukh Dey:** Writing –

**Table 2**  
Summary statistics of total reef fish biomass across islands (n = 132).

Variable	Uninhabited islands		Inhabited islands		
	Suheli	Perumal Par	Kadmat	Agatti	Kavaratti
Median biomass ( $\text{g/m}^2$ )	341.88	325.56	133.68	129.94	127.34
Mean biomass ( $\text{g/m}^2 \pm \text{SE}$ )	492.49 $\pm$ 23.94	321.05 $\pm$ 19.08	173.61 $\pm$ 8.54	132.55 $\pm$ 8.62	156.88 $\pm$ 6.95
95 % CI ( $\text{g/m}^2$ )	445.57–539.42	283.65–358.45	156.87–190.36	115.65–149.46	143.26–170.50

review & editing, Validation, Methodology, Investigation, Data curation, Conceptualization. **Wenzel Pinto:** Writing – review & editing, Methodology, Investigation, Data curation. **B.T. Rajeswari Bhai:** Methodology, Investigation, Data curation. **Teresa Alcoverro:** Writing – review & editing, Writing – original draft, Visualization, Validation, Supervision, Project administration, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualization. **Rohan Arthur:** Writing – review & editing, Writing – original draft, Visualization, Validation, Supervision, Resources, Project administration, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualization.

### Compliance with ethical standard

All interview surveys were conducted in accordance with the ethical standards of the Institutional Human Ethics Committee, National Centre for Biological Sciences, India (Ref: NCBS/IEC-29/03). Informed consent was given by all participants in the study and their responses were presented anonymously.

1. Census, 2011; Administration of the Union Territory of Lakshadweep, 2023.
2. Department of Fisheries UTL, 2014.
3. 'Historical' refers to pre-commercialisation of reef fishing, i.e., before 2013.
4. 'Recent' refers to the time leading up to the study period, i.e., post-commercialisation of reef fishing up to 2022.

### Funding statement

This work was funded by National Centre for Biological Sciences (NCBS), The Rufford Foundation, Shri A.M.M. Murugappa Chettiar Research Centre, Rohini Nilekani Philanthropies, Cholamandalam Investment and Finance Company Limited, The Ashraya Hashta Trust, and Arvind Dattar. The Spanish National Research Council supported T. Alcoverro through the Memorandum of Understanding between Centre D'Estudis Avançats de Blanes (CEAB, CSIC) and Nature Conservation Foundation (NCF).

### Declaration of competing interest

The authors declare no conflicts of interest.

### Acknowledgments

We thank the Department of Science and Technology (DST), and the Ministry of Environment, Forest and Climate Change, Lakshadweep, for their constant support and help in obtaining permits. This work would not have been possible without the support and guidance of the Wildlife Office, National Centre for Biological Sciences. We would also like to thank Anver Hussain, Aman, Jaffar, Sabu, Shajahan and numerous other people who helped us out with logistics and guided us in our time on the islands.

### Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.biocon.2025.111675>.

### Data availability

Data will be made available on request.

### References

- Abraham, A.J., Deepak, D., Khot, I., Namboothri, N., 2025. Traditional systems and contemporary transitions on an Oceanic island: insights for participatory fisheries management from Minicoy Island, India. *Marit. Stud.* 24 (1), 18.
- Administration of the Union Territory of Lakshadweep, 2023. Directorate of Planning, Statistics and Taxation, Kavaratti: Statistical Handbook. <https://lakshadweep.gov.in/document-category/reports/>.
- Ahmad, M.N., 2020. Expressing the Unexpressed: The Minicoy Islanders of Lakshadweep. In: *Tribal Studies in India: Perspectives of History, Archaeology and Culture*, pp. 279–292.
- Almany, G.R., 2004. Differential effects of habitat complexity, predators and competitors on abundance of juvenile and adult coral reef fishes. *Oecologia* 141, 105–113.
- Arthur, R., Done, T.J., Marsh, H., Harriott, V., 2006. Local processes strongly influence post-bleaching benthic recovery in the Lakshadweep Islands. *Coral Reefs* 25, 427–440.
- Ashworth, J.S., Ormond, R.F.G., 2005. Effects of fishing pressure and trophic group on abundance and spillover across boundaries of a no-take zone. *Biol. Conserv.* 121 (3), 333–344.
- Aswani, S., 1998. Patterns of marine harvest effort in southwestern New Georgia, Solomon Islands: resource management or optimal foraging? *Ocean Coast. Manag.* 40 (2–3), 207–235.
- Aswani, S., Hamilton, R.J., 2004. Integrating indigenous ecological knowledge and customary sea tenure with marine and social science for conservation of bumphead parrotfish (*Bolbometopon muricatum*) in the Roviana Lagoon, Solomon Islands. *Environ. Conserv.* 31 (1), 69–83.
- Babcock, R.C., Dambacher, J.M., Morello, E.B., Plagányi, É.E., Hayes, K.R., Sweatman, H. P., Pratchett, M.S., 2016. Assessing different causes of crown-of-thorns starfish outbreaks and appropriate responses for management on the Great Barrier Reef. *PLoS One* 11 (12), e0169048.
- Bartoň, K. MuMIn: Multi-Model Inference. R package version 1.48.11. <https://CRAN.R-project.org/package=MuMIn>.
- Bates, D., Mächler, M., Bolker, B., Walker, S., 2015. Fitting linear mixed-effects models using lme4. *J. Stat. Softw.* 67 (1), 1–48. <https://doi.org/10.18637/jss.v067.i01>.
- Bayley, D.T., Mogg, A.O., Koldewey, H., Purvis, A., 2019. Capturing complexity: field-testing the use of 'structure from motion' derived virtual models to replicate standard measures of reef physical structure. *PeerJ* 7, e6540.
- Beitl, C.M., 2014. Navigating over space and time: fishing effort allocation and the development of customary norms in an open-access mangrove estuary in Ecuador. *Hum. Ecol.* 42, 395–411.
- Béné, C., Tewfik, A., 2001. Fishing effort allocation and fishermen's decision making process in a multi-species small-scale fishery: Analysis of the conch and lobster fishery in Turks and Caicos Islands. *Hum. Ecol.* 29, 157–186.
- Berkes, F., Colding, J., Folke, C., 2000. Rediscovery of traditional ecological knowledge as adaptive management. *Ecol. Appl.* 10 (5), 1251–1262.
- Brandl, S.J., Rasher, D.B., Côté, I.M., Casey, J.M., Darling, E.S., Lefcheck, J.S., Duffy, J.E., 2019. Coral reef ecosystem functioning: eight core processes and the role of biodiversity. *Front. Ecol. Environ.* 17 (8), 445–454.
- Bruno, J.F., O'Connor, M.I., 2005. Cascading effects of predator diversity and omnivory in a marine food web. *Ecol. Lett.* 8 (10), 1048–1056.
- Bunce, M., Rodwell, L.D., Gibb, R., Mee, L., 2008. Shifting baselines in fishers' perceptions of island reef fishery degradation. *Ocean Coast. Manag.* 51 (4), 285–302.
- Campbell, S.J., Pardede, S.T., 2006. Reef fish structure and cascading effects in response to artisanal fishing pressure. *Fish. Res.* 79 (1–2), 75–83.
- Casey, J.M., Baird, A.H., Brandl, S.J., Hoogenboom, M.O., Rizzari, J.R., Frisich, A.J., Connolly, S.R., 2017. A test of trophic cascade theory: fish and benthic assemblages across a predator density gradient on coral reefs. *Oecologia* 183, 161–175.
- Census, 2011. Primary Census Abstracts, Registrar General of India, Ministry of Home Affairs, Government of India. Available at: <http://www.censusindia.gov>.
- Chong-Seng, K.M., Mannering, T.D., Pratchett, M.S., Bellwood, D.R., Graham, N.A., 2012. The influence of coral reef benthic condition on associated fish assemblages. *PLoS One* 7 (8), e42167. <https://doi.org/10.1371/journal.pone.0042167>.
- Chou, L.M., Tuan, V.S., Philreefs, Y.T., Cabanban, A., Suharsono, K.I., 2002. Status of Southeast Asia coral reefs. *Status of coral reefs of the world. Australian Institute of Marine Science Townsville*, 123–153.
- Cinner, J., McClanahan, T.R., 2006. Socioeconomic factors that lead to overfishing in small-scale coral reef fisheries of Papua New Guinea. *Environ. Conserv.* 33 (1), 73–80.
- Cinner, J.E., 2007. Designing marine reserves to reflect local socioeconomic conditions: lessons from long-enduring customary management systems. *Coral Reefs* 26 (4), 1035–1045.
- Cinner, J.E., Aswani, S., 2007. Integrating customary management into marine conservation. *Biol. Conserv.* 140 (3–4), 201–216.
- Cinner, J.E., Maire, E., Huchery, C., MacNeil, M.A., Graham, N.A., Mora, C., Mouillot, D., 2018. Gravity of human impacts mediates coral reef conservation gains. *Proc. Natl. Acad. Sci.* 115 (27), E6116–E6125.
- Cinner, J.E., Sutton, S.G., Bond, T.G., 2007. Socioeconomic thresholds that affect use of customary fisheries management tools. *Conserv. Biol.* 21 (6), 1603–1611.
- Darling, E.S., Graham, N.A., Januchowski-Hartley, F.A., Nash, K.L., Pratchett, M.S., Wilson, S.K., 2017. Relationships between structural complexity, coral traits, and reef fish assemblages. *Coral Reefs* 36, 561–575.
- de la Barra, P., Iribarne, O., Narvarte, M., 2019. Combining fishers' perceptions, landings and an independent survey to evaluate trends in a swimming crab data-poor artisanal fishery. *Ocean Coast. Manag.* 173, 26–35.

- Department of Fisheries UTL, 2014. Development activities: I. Supply of mechanised boats. <https://fisheries.utl.gov.in/FisheriesPortal/Developments>. (Accessed April 2024).
- Eddy, T.D., Lam, V.W., Reygondeau, G., Cisneros-Montemayor, A.M., Greer, K., Palomares, M.L.D., Cheung, W.W., 2021. Global decline in capacity of coral reefs to provide ecosystem services. *One Earth* 4 (9), 1278–1285.
- Edwards, C.B., Friedlander, A.M., Green, A.G., Hardt, M.J., Sala, E., Sweatman, H.P., Smith, J.E., 2014. Global assessment of the status of coral reef herbivorous fishes: evidence for fishing effects. *Proc. R. Soc. B Biol. Sci.* 281 (1774), 20131835.
- Ekers, M., Prudham, S., 2015. Towards the socio-ecological fix. *Environ. Plan. A* 47 (12), 2438–2445.
- Fereday, J., Muir-Cochrane, E., 2006. Demonstrating rigor using thematic analysis: A hybrid approach of inductive and deductive coding and theme development. *Int J Qual Methods* 5 (1), 80–92.
- Frisch, A.J., Ireland, M., Rizzari, J.R., Lönnstedt, O.M., Magnenat, K.A., Mirbach, C.E., Hobbs, J.P.A., 2016. Reassessing the trophic role of reef sharks as apex predators on coral reefs. *Coral Reefs* 35, 459–472.
- Froese, R., Pauly, D. (Eds.), 2000. *FishBase 2000: Concepts, Design and Data Sources*. ICLARM, Los Baños, Laguna, Philippines, p. 344.
- García, S.M., Rosenberg, A.A., 2010. Food security and marine capture fisheries: characteristics, trends, drivers and future perspectives. *Philos. Trans. R. Soc. B* 365 (1554), 2869–2880.
- Goetze, J.S., Langlois, T.J., Egli, D.P., Harvey, E.S., 2011. Evidence of artisanal fishing impacts and depth refuge in assemblages of Fijian reef fish. *Coral Reefs* 30 (2), 507–517. <https://doi.org/10.1007/s00338-011-0732-8>.
- Graham, N.A., Nash, K.L., 2013. The importance of structural complexity in coral reef ecosystems. *Coral Reefs* 32, 315–326.
- Graham, N.A., Pratchett, M.S., McClanahan, T.R., Wilson, S.K., 2013. The status of coral reef fish assemblages in the Chagos Archipelago, with implications for protected area management and climate change. In: *Coral reefs of the United Kingdom overseas territories*, pp. 253–270.
- Graham, N.A.J., Dulvy, N.K., Jennings, S., Polunin, N.V.C., 2005. Size-spectra as indicators of the effects of fishing on coral reef fish assemblages. *Coral Reefs* 24, 118–124.
- Hadj-Hammou, J., McClanahan, T.R., Graham, N.A., 2021. Decadal shifts in traits of reef fish communities in marine reserves. *Sci. Rep.* 11 (1), 23470.
- Hamilton, R.J., Almany, G.R., Stevens, D., Bode, M., Pita, J., Peterson, N.A., Choat, J.H., 2016. Hyperstability masks declines in bumphead parrotfish (*Bolbometopon muricatum*) populations. *Coral Reefs* 35, 751–763.
- Hamner, W.M., Jones, M.S., Carleton, J.H., Hauri, I.R., Williams, D.M., 1988. Zooplankton, planktivorous fish, and water currents on a windward reef face: Great Barrier Reef, Australia. *Bull. Mar. Sci.* 42 (3), 459–479.
- Harvey, D., 1981. The spatial fix—Hegel, von Thünen, and Marx. *Antipode* 13 (3), 1–12.
- Hawkins, J.P., Roberts, C.M., 2004. Effects of artisanal fishing on Caribbean coral reefs. *Conserv. Biol.* 18 (1), 215–226.
- Hoon, V., 2003. A case study from Lakshadweep. *Poverty and Reefs* 2, 187–226.
- Hughes, T.P., 1994. Catastrophes, phase shifts, and large-scale degradation of a Caribbean coral reef. *Science* 265 (5178), 1547–1551.
- Islam, D., Berkes, F., 2016. Can small-scale commercial and subsistence fisheries co-exist? Lessons from an indigenous community in northern Manitoba, Canada. *Maritime studies* 15, 1–16.
- Jaini, M., Advani, S., Shanker, K., Oommen, M.A., Namboothri, N., 2018. History, culture, infrastructure and export markets shape fisheries and reef accessibility in India's contrasting oceanic islands. *Environ. Conserv.* 45 (1), 41–48.
- Johannes, R.E., 1978. Traditional marine conservation methods in Oceania and their demise. *Annu. Rev. Ecol. Syst.* 9, 349–364.
- Johannes, R.E., 1998. The case for data-less marine resource management: examples from tropical nearshore finfisheries. *Trends Ecol. Evol.* 13 (6), 243–246.
- Johannes, R.E., 2002. The renaissance of community-based marine resource management in Oceania. *Annu. Rev. Ecol. Syst.* 33 (1), 317–340.
- Karkarey, R., Boström Einarsson, L., Graham, N.A., Mukrikkakudi, I., Bilutheth, M.N., Chekkillam, A.R., Keith, S.A., 2024. Do risk-prone behaviours compromise reproduction and increase vulnerability of fish aggregations exposed to fishing? *Biol. Lett.* 20 (8), 20240292.
- Karkarey, R., Kelkar, N., Lobo, A.S., Alcoverro, T., Arthur, R., 2014. Long-lived groupers require structurally stable reefs in the face of repeated climate change disturbances. *Coral Reefs* 33, 289–302.
- Karnad, D., Barnes, A., Mukherji, S., Narayani, S., Jabado, R.W., 2024. Fisher insights into rhino ray status, utilisation, and conservation at five major fishing harbours in India. *Endanger. Species Res.* 53, 49–66.
- Karnad, D., Sutaria, D., Jabado, R.W., 2020. Local drivers of declining shark fisheries in India. *Ambio* 49 (2), 616–627.
- Khan, M., 2024. Lakshadweep. In: *The Territories and States of India 2024*. Routledge, pp. 400–406.
- Leach, M., Mearns, R., Scoones, I., 1999. Environmental entitlements: dynamics and institutions in community-based natural resource management. *World Dev.* 27 (2), 225–247.
- Legendre, P., Gallagher, E.D., 2001. Ecologically meaningful transformations for ordination of species data. *Oecologia* 129, 271–280.
- Lokrantz, J., Nystrom, M., Norstrom, A.V., Folke, C., Cinner, J.E., 2009. Impacts of artisanal fishing on key functional groups and the potential vulnerability of coral reefs. *Environ. Conserv.* 36 (4), 327–337. <https://doi.org/10.1017/S0376892910000147>.
- Lüdtke, et al., 2021. performance: an R package for assessment, comparison and testing of statistical models. *J. Open Source Softw.* 6 (60), 3139. <https://doi.org/10.21105/joss.03139>.
- Ludwig, D., Hilborn, R., Walters, C., 1993. Uncertainty, resource exploitation, and conservation: lessons from history. *Science* 260 (5104), 17–36.
- Madin, E.M., Gaines, S.D., Warner, R.R., 2010. Field evidence for pervasive indirect effects of fishing on prey foraging behavior. *Ecology* 91 (12), 3563–3571.
- Mangi, S.C., Roberts, C.M., 2006. Quantifying the environmental impacts of artisanal fishing gear on Kenya's coral reef ecosystems. *Mar. Pollut. Bull.* 52 (12), 1646–1660.
- McClanahan, T.R., 1995. A coral reef ecosystem-fisheries model: impacts of fishing intensity and catch selection on reef structure and processes. *Ecol. Model.* 80 (1), 1–19.
- McClanahan, T.R., Friedlander, A.M., Graham, N.A., Chabanet, P., Bruggemann, J.H., 2021. Variability in coral reef fish baseline and benchmark biomass in the central and western Indian Ocean provinces. *Aquat. Conserv. Mar. Freshwat. Ecosyst.* 31 (1), 28–42.
- Muallil, R.N., Mamaug, S.S., Cababaro, J.T., Arceo, H.O., Aliño, P.M., 2014. Catch trends in Philippine small-scale fisheries over the last five decades: The fishers' perspectives. *Mar. Policy* 47, 110–117.
- Mustak, M.S., Rai, N., Naveen, M.R., Prakash, S., Carlus, S.J., Pasupuleti, N., Thangaraj, K., 2019. The peopling of Lakshadweep archipelago. *Sci. Rep.* 9 (1), 6968.
- Oksanen, J., Simpson, G., Blanchet, F., Kindt, R., Legendre, P., Minchin, P., O'Hara, R., Solymos, P., Stevens, M., Szoecs, E., Wagner, H., Barbour, M., Bedward, M., Bolker, B., Borcard, D., Borman, T., Carvalho, G., Chirico, M., De Caceres, M., Durand, S., Evangelista, H., FitzJohn, R., Friendly, M., Furneaux, B., Hannigan, G., Hill, M., Lahti, L., Martino, C., McGlenn, D., Ouellette, M., Ribeiro Cunha, E., Smith, T., Stier, A., Ter Braak, C., Weedon, J., 2025. *vegan: Community Ecology Package*. In: R package version 2.8-0. <https://vegandevs.github.io/vegan/>.
- Pratchett, M.S., Hoey, A.S., Wilson, S.K., 2014. Reef degradation and the loss of critical ecosystem goods and services provided by coral reef fishes. *Curr. Opin. Environ. Sustain.* 7, 37–43.
- Purcell, S.W., Pomeroy, R.S., 2015. Driving small-scale fisheries in developing countries. *Front. Mar. Sci.* 2, 44.
- Rizvi, A.N., Raghunathan, C., Banerjee, D., Sureshan, P.M., 2024. Current Status of Faunal Diversity in Lakshadweep: An Overview. In: *Current Status of Faunal Diversity in Lakshadweep*, pp. 1–24.
- Russ, G.R., 2003. Grazer biomass correlates more strongly with production than with biomass of algal turfs on a coral reef. *Coral Reefs* 22, 63–67.
- Sadovy, Y., 2005. Trouble on the reef: the imperative for managing vulnerable and valuable fisheries. *Fish. Fish.* 6 (3), 167–185.
- Sadovy, Y., Domeier, M., 2005. Are aggregation-fisheries sustainable? Reef fish fisheries as a case study. *Coral Reefs* 24, 254–262.
- Salas, S., Gaertner, D., 2004. The behavioural dynamics of fishers: management implications. *Fish. Fish.* 5 (2), 153–167.
- Sattar, S., Andrefouet, S., Ahsan, M., Adam, S., Anderson, C.R., Scott, L., 2012. Status of the coral reef fishery in an atoll country under tourism development: the case of Central Maldives.
- Schmitz, O.J., Hawlena, D., Trussell, G.C., 2010. Predator control of ecosystem nutrient dynamics. *Ecol. Lett.* 13 (10), 1199–1209.
- Schneider, C.A., Rasband, W.S., Eliceiri, K.W., 2012. NIH Image to ImageJ: 25 years of image analysis. *Nat. Methods* 9 (7), 671–675.
- Schoenberger, E., 2004. The spatial fix revisited. *Antipode* 36 (3).
- Stuart-Smith, R.D., Barrett, N.S., Crawford, C.M., Frusher, S.D., Stevenson, D.G., Edgar, G.J., 2008. Spatial patterns in impacts of fishing on temperate rocky reefs: Are fish abundance and mean size related to proximity to fisher access points? *J. Exp. Mar. Biol. Ecol.* 365 (2), 116–125.
- Syms, C., Jones, G.P., 2000. Disturbance, habitat structure, and the dynamics of a coral-reef fish community. *Ecology* 81 (10), 2714–2729.
- Tamelander, J., Hoon, V., 2008. The Artisanal Reef Fishery on Agatti Island, Union Territory of Lakshadweep, India. *Coastal Oceans Research and Development in the Indian Ocean*, pp. 293–308.
- Teh, L.C., Teh, L.S., Meitner, M.J., 2012. Preferred resource spaces and fisher flexibility: Implications for spatial management of small-scale fisheries. *Hum. Ecol.* 40, 213–226.
- Teh, L.S., Teh, L.C., Sumaila, U.R., 2013. A global estimate of the number of coral reef fishers. *PLoS One* 8 (6), e65397.
- Tootell, J.S., Steele, M.A., 2016. Distribution, behavior, and condition of herbivorous fishes on coral reefs track algal resources. *Oecologia* 181 (1), 13–24.
- Trenkel, V.M., Rochet, M.J., 2003. Performance of indicators derived from abundance estimates for detecting the impact of fishing on a fish community. *Can. J. Fish. Aquat. Sci.* 60 (1), 67–85.
- U.T Administration of Lakshadweep, 2025. *Departments: Fisheries*. <https://lakshadweep.gov.in/departments/fisheries/>.
- Ulate, K., Alcoverro, T., Arthur, R., Aburto-Oropeza, O., Sánchez, C., Huato-Soberanis, L., 2018. Conventional MPAs are not as effective as community co-managed areas in conserving top-down control in the Gulf of California. *Biol. Conserv.* 228, 100–109.
- Venables, W.N., Ripley, B.D., 2002. *Modern Applied Statistics With S*, Fourth edition. Springer, New York. ISBN 0-387-95457-0. <https://www.stats.ox.ac.uk/pub/MASS4/>.
- Virgen-Urcelay, A., Donner, S.D., 2023. Increase in the extent of mass coral bleaching over the past half-century, based on an updated global database. *PLoS One* 18 (2), e0281719.
- Ward, H.G., Askey, P.J., Post, J.R., 2013. A mechanistic understanding of hyperstability in catch per unit effort and density-dependent catchability in a multistock recreational fishery. *Can. J. Fish. Aquat. Sci.* 70 (10), 1542–1550.
- Wickham, H., Averick, M., Bryan, J., Chang, W., McGowan, L.D., François, R., Grolemund, G., Hayes, A., Henry, L., Hester, J., Kuhn, M., Pedersen, T.L., Miller, E., Bache, S.M., Müller, K., Ooms, J., Robinson, D., Seidel, D.P., Spinu, V., Takahashi, K.,

- Vaughan, D., Wilke, C., Woo, K., Yutani, H., 2019. Welcome to the tidyverse. *J. Open Source Softw.* 4 (43), 1686. <https://doi.org/10.21105/joss.01686>.
- Wilson, S.K., Fisher, R., Pratchett, M.S., Graham, N.A.J., Dulvy, N.K., Turner, R.A., Polunin, N.V., 2010. Habitat degradation and fishing effects on the size structure of coral reef fish communities. *Ecol. Appl.* 20 (2), 442–451.
- Yadav, S., Alcoverro, T., Arthur, R., 2018. Coral reefs respond to repeated ENSO events with increasing resistance but reduced recovery capacities in the Lakshadweep archipelago. *Coral Reefs* 37, 1245–1257.
- Zamborain-Mason, J., Cinner, J.E., MacNeil, M.A., Graham, N.A., Hoey, A.S., Bejer, M., Connolly, S.R., 2023. Sustainable reference points for multispecies coral reef fisheries. *Nat. Commun.* 14 (1), 5368.