# Distribution and diversity of fish species along the Sudanese Red Sea coast based on three combined trap and gillnet surveys 

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## A R T I C L E I N F O

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#### Abstract

On the western shore of the semi-enclosed coral-reef rich Red Sea, the 850 km coastline of the Red Sea State of the Republic of Sudan provides livelihoods to artisanal fishers, but the present state of the living natural resources and the impact of fisheries are poorly known. To provide a baseline on the biodiversity and fish abundance three fisheries research surveys spanning the entire Sudanese coast were carried out in 2012-13 designed around the seven Sudanese fisheries management areas. Baited traps and gillnets were employed to sample the various reef habitats and fish assemblages from inshore to deeper outer reef archipelagos. The highest species richness, functional diversity, as well and the highest catch rates with both traps and gillnets were observed in the protected Dungonab Bay area in the north, while the management area closest to the main population center along the coast - Port Sudan - showed the lowest levels of biodiversity and catch rates. The Dungonab bay area and adjacent northern areas therefore seem more pristine than areas closer to the main human population center. Thus the present study has provides a necessary knowledge baseline and highlights the opportunity for establishing effective ecosystem-based management before the resources and habitats are irreversibly impacted.


## 1. Introduction

With its semi-enclosed location, the waters of the Red Sea are warmer and more saline than many other marine tropical ecosystems (Ngugi et al., 2012; Raitsos et al., 2015; Roberts et al., 2016). Although there are large latitudinal gradients in environmental conditions with salinity increasing to the north and temperature increasing towards the south (Edwards and Rosewell, 1981; Tesfamichael and Pauly, 2016), the biological community changes comparatively little from north to south (Roberts et al., 1992, 2016). Here, the biodiversity is uniquely rich, with a high prevalence of endemic species (DiBattista et al., 2016a, 2016b). The Red Sea coral reef ecosystems are understudied compared to other extensive coral reef systems (Berumen et al., 2013). Within the Red Sea, the northern reef areas of Egypt and the Gulf of Aqaba and Eilat (Berumen et al., 2013; Loya et al., 2014), as well as the coast off Saudi Arabia (e.g. Coker et al., 2018; Nanninga et al., 2014; Roberts et al.,
2016), have received most of the scientific attention, while investigations of the Sudanese Red Sea coast are scarcer (Bamber, 1915; Edwards and Rosewell, 1981; Kattan et al., 2017; Spaet et al., 2016).

### 1.1. Sudan's Red Sea coast and fisheries

The Republic of the Sudan's Red Sea State includes 853 km of the 2250 km African (western) Red Sea shore (Fig. 1). Although the coast is long, the marine fisheries sector in Sudan is small with official annual catches at 5000 tons in 2012 and 4000 tons in 2013 (FAO, 2019). A catch reconstruction for 2010 of 2000 tons was low compared to the official catches statistics of 5700 tons, likely attributable to poor quality of available fisheries statistics in terms of degree of coverage and representativity (Tesfamichael and Elawad, 2016). Fisheries in the Sudanese Red Sea coast are dominated by artisanal handline and gillnet fisheries delivering the catches at a number of small informal landing

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Fig. 1. A bathymetric map of the Republic of the Sudan Red Sea coast, with the names and spatial extent of seven fisheries management areas (black polygons) shown.
Bathymetric data from NOAA National Geophysical Data Center. 2009: ETOPO1 1 Arc-Minute Global Relief Model. NOAA National Centers for Environmental Information. Accessed 9th April 2021.
sites and villages located along the entire coast. The management of the artisanal fishery is divided into seven geographical management areas (Fig. 1) covering the coast coral-reef dotted coast. The main population center and only major city is Port Sudan located in area 4. North of Port Sudan lies "Arakia" (Area 3), and further north the Dungonab Bay (area 2) which is is included in the UNESCO list of world heritage sites, and which since 2016 also includes the Sanganeb Atoll. Both areas are now designated marine parks: "Dungonab Bay - Mukkawar Island Marine National Park" and the "Sanganeb Marine National Park" (Claudino-Sales, 2019). Furthest north lies "Marsas north of Dungonab" (area 1) bordering with Egypt, while south of Port Sudan lies "Suakin" (area 5) where there also is a small city of the same name. Further south along the coast lies "Agig" (area 7) which covers the widest part of the continental shelf, while west of Suakin and Agig lies the "Suakin Archipelago" (area 6), the only management area not connected to the coast, but covering the offshore reef areas.

The Sudanese artisanal fleet currently consists of approximately two thousand fishers operating a total of about one thousand vessels ranging from 6 to 10 m length, each holding a $2-5$-person crew. Some of the vessels are equipped with $30-40 \mathrm{hp}$ outboard engines, the remaining are using sails (Marine Fisheries Administration, unpublished data). Fishing trips last from a few days up to two weeks. The main targets are finfish, particularly high-priced groupers, caught on the near- and offshore reef systems and in the archipelagos, while several crustacean and mollusc species are also caught. Fishing with handlines is the most common fishing method, followed by setting gillnets as barrier nets in lagoons and on reef flats for capturing roving herbivores such as parrotfish and surgeonfish that are chased into the nets using snorkeling gear. There are several published studies from Saudi Arabia pointing to the overexploitation of important artisanal fishery species, such as the roving coral grouper Plectropomus pessuliferus marisrubri and the squaretail coral grouper P. areolatus (Arabic names 'Najil' and 'Silimani', respectively) (Kattan et al., 2017; Spaet and Berumen, 2015; Shellem et al., 2021), but only a single study from Sudan indicating a similar potential overexploitation (Elamin, 2012). With calls to expand the Sudanses marine fisheries, the fish resources need to be sustainably managed to avoid the overexploitation, which in turn requires a comprehensive and updated knowledge base about the fisheries and fish resources (Nash and Graham, 2016) of the Sudanese Red Sea coast.

### 1.2. Aims

Specimen collectors and early natural scientists described the marine fauna of the Red Sea (Bamber, 1915; Berumen et al., 2013; Debelius, 2011; Randall, 1982), but there have been few large-scale studies systematically covering the coastal fish assemblages (see Kattan et al., 2017; Roberts et al., 1992 and Roberts et al., 2016). Other recent studies have provided new insight on localized diversity, distribution or abundance, albeit in limited geographic areas (e.g. Kessel et al., 2017), for a subset of taxa (e.g. Spaet et al., 2016), or focused on biodiversity rather than abundance (e.g. Klaus et al., 2009). The most extensive recent study was carried out by Kattan et al. (2017) as comparative UVC surveys of Sudanese and Saudi reefs, but only covered selected Sudanese reefs. So, to our knowledge there are no previous studies covering the inshore coastal zone along the entire Sudanese Red Sea coast. Thus, the understanding of fish species distribution and potential fisheries impact on biodiversity are limited for the Sudanese Red Sea coast, impeding sustainable management of the fishing sector there.

To contribute to closing these gaps in knowledge the present study aimed to quantify catch rates and biodiversity of a subset of fishes that are important fishery species from trap and gillnet catches in the seven management regions (Fig. 1) to provide fisheries independent baseline information on living marine resources along the coast of Sudan. This included identifying fish biodiversity hot spots, spatial distribution, and estimating indices of relative abundance.

## 2. Material and methods

### 2.1. Study area and surveys

Three surveys employing baited traps and gillnets to cover the watercolumn from surface to the bottom (up to 200 m maximum bottom depth), were carried in November 2012, May 2013 and November December 2013 (Table 1), covering the coast from the border with Egypt in the north to the border with Eritrea in the south (Fig. 2), with the sampling scheme stratified according to the seven defined fisheries management areas (Fig. 1).

Sampling locations at coral reefs within each management area were selected with the ambition of comparable depth coverage, as permitted by weather and current conditions. At each reef area, variable numbers of traps and gillnets were set, each individual gear set constituting a sampling station (Fig. 2).

A $10-\mathrm{m}$ sheltered fiberglass vessel with an inboard engine was used to deploy and retrieve traps while gillnets were deployed from a $6-\mathrm{m}$ fiberglass vessel equipped with an outboard engine. A comparable geographic coverage was achieved in areas $1-5$ (northern and central region) during all three surveys (Fig. 2), while challenging weather conditions and technical delays restricted the degree of coverage in the southernmost part of the study area (areas 6 and 7).

### 2.2. Fishing gear

### 2.2.1. Baited traps

The traps were constructed from steel frames with plastic coated square steel mesh with approximately 50 mm bar length, measuring $150 \times 180 \times 80 \mathrm{~cm}$ overall, and were baited with $\sim 500 \mathrm{~g}$ of frozen sardines. The number of traps deployed at each reef area ranged from 5 to 14 per survey, depending on the topography, reef length, and weather conditions at the time when traps were deployed. Median distance between traps by each area and survey ranged from 0.5 to 63.5 km (Fig. S1). Traps were set in the afternoon and hauled in the morning the following day (with some longer durations due to technical problems preventing retrieval of the traps the following morning).

### 2.2.2. Gillnets

Two types of pelagic gillnets were joined and set at each station: two multi-monofilament gillnets of $28.0-\mathrm{m}$ length and $10.5-\mathrm{m}$ height each with $89-\mathrm{mm}$ mesh size (stretched), and one multifilament gillnet of 40.0m length and $10.5-\mathrm{m}$ height with $76-\mathrm{mm}$ mesh size (stretched). As we had no prior information of the most appropriate mesh size to catch typical pelagic fish species in the Red Sea these two mesh sizes were chosen based on survey experience in other tropical regions of the Indian Ocean. The gillnets were anchored to the bottom at one end. Floats were attached in the float line at either end of the sets, with smaller floats running along the float line to ensure floatation of the float line. Nets were deployed in channels between reefs, in open waters inshore- or offshore of reefs. At particularly shallow stations the gillnets reached all the way from the surface to the bottom. The gillnets were deployed at dusk and hauled at dawn the next day. By setting the nets during the night their fishing time overlapped with the traps, also encompassing dusk/dawn when fish are most active. Also since fish see the nets during daytime gillnet catch rates are very low during daytime.

### 2.3. Biological measurements and data management

Catches were brought onboard immediately after hauling the fishing gear. Any sharks or moray eels were identified to species-level and released alive after estimating their individual total length. All other fish specimens were brought to the measuring lab where they were identified to species and measured for total length. The total weight of all fish specimens caught were estimated using published length-weight relationships (Froese and Pauly, 2000).

Table 1
Numbers of deployments (fishing stations) per fishing gear, as deployed in the seven management areas defined along the Sudanese coast, showing total fishing time (hours) and fishing depth for traps in each management area for each survey (Nov. 2012, May 2013 and Nov. 2013)

| Survey | Mgmt. Area | Number of stations (gear sets) |  | Hours fishing |  | Fishing depth of traps |  |  |  |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
|  |  | Traps | Gillnets | Traps | Gillnets | Mean | St.Dev. | Minimum | Maximum |
| Nov. 2012 | 1 | 22 | 0 | 694 | 0 | 42 | 27 | 13 | 142 |
|  | 2 | 54 | 3 | 722 | 62 | 41 | 17 | 0 | 71 |
|  | 3 | 26 | 1 | 451 | 14 | 31 | 19 | 8 | 95 |
|  | 4 | 5 | 0 | 77 | 0 | 23 | 18 | 10 | 54 |
|  | 5 | 31 | 4 | 678 | 78 | 21 | 6 | 7 | 30 |
|  | 6 | 36 | 1 | 850 | 38 | 32 | 24 | 0 | 88 |
|  | 7 | 31 | 8 | 712 | 136 | 31 | 17 | 5 | 66 |
|  | Sum | 205 | 17 | 4184 | 328 |  |  |  |  |
|  | With catch | 109 | 12 |  |  |  |  |  |  |
| May 2013 | 1 | 29 | 1 | 420 | 24 | 31 | 15 | 5 | 70 |
|  | 2 | 81 | 5 | 1102 | 222 | 27 | 14 | 5 | 145 |
|  | 3 | 32 | 1 | 546 | 24 | 29 | 16 | 0 | 60 |
|  | 4 | 13 | 10 | 160 | 138 | 30 | 23 | 9 | 67 |
|  | 5 | 33 | 5 | 209 | 196 | 20 | 11 | 7 | 50 |
|  | 6 | 45 | 2 | 642 | 78 | 35 | 22 | 9 | 88 |
|  | 7 | 39 | 0 | 666 | 0 | 33 | 20 | 5 | 76 |
| Nov. 2013 | Sum | 272 | 24 | 3746 | 681 |  |  |  |  |
|  | With catch | 141 | 16 |  |  |  |  |  |  |
|  | 1 | 23 | 4 | 272 | 84 | 30 | 13 | 10 | 80 |
|  | 2 | 57 | 6 | 500 | 156 | 38 | 18 | 7 | 80 |
|  | 3 | 9 | 2 | 123 | 36 | 27 | 21 | 9 | 70 |
|  | 4 | 16 | 4 | 151 | 143 | 33 | 18 | 12 | 68 |
|  | 5 | 30 | 3 | 317 | 147 | 26 | 10 | 11 | 65 |
|  | 6 | 40 | 2 | 444 | 72 | 40 | 26 | 6 | 89 |
|  | 7 | 22 | 2 | 172 | 203 | 35 | 17 | 11 | 54 |
|  | Sum | 197 | 23 | 1979 | 841 |  |  |  |  |
|  | With catch | 62 | 23 |  |  |  |  |  |  |



Fig. 2. Map showing all survey stations sampled from 2012 to 2013 overlaid over the seven fisheries management areas. PZU: the city of Port Sudan. Map data from Natural Earth (naturalearthdata.com).

All data from the surveys were entered into a NAN-SIS database (Strømme, 1992). The ecological traits of species in our samples were determined based on a list of traits of coral reef fish (Stuart-Smith et al.,
2013), amended with information from FishBase (Froese and Pauly, 2000) for the Red Sea species not covered in the original species traits list.

### 2.4. Analyses

The variability in catch rates and biodiversity between the seven management areas and three surveys was investigated using a range of methods. Catch-per-unit- effort (CPUE, numbers or kg per hours of fishing) was used as the measure of catch rates, while biodiversity was measured through calculation of species accumulation curves and functional diversity. To investigate the effect of depth on catch rates stations were classified as either shallow ( $0-30 \mathrm{~m}$ ) or deep (deeper than 30 m ).

All plotting and statistical analyses were carried out using the $R$ Statistical software package version 3.5.2 (Eggshell Igloo) (R-Team, 2000) implemented in R-Studio 1.1.419. Data files and R-scripts are deposited on GitHub: (https://github.com/erikjsolsen/Sudan).

Variability in fishing time and fishing depth were evaluated using the Kruskal-Wallis rank sum test, with the significance of pair-wise differences tested using the Conover-Iman test (Conover and Iman, 1979) with Holm correction, using the 'conover.test' package.

General Additive Models (GAM) (Hastie and Tibshirani, 1986) implemented in the GAMLSS package (Stasinopoulos et al., 2018) were used to parameterize the response of a variable to both continuous and factor variables. GAMLSS was chosen because it can test a large number of potential distributions to the data, and in particular due to its ability to model zero-adjusted distributions. For zero-adjusted data potential probability distributions were evaluated manually, while for other data the best-fitting distribution was chosen using the 'chooseDist' function in GAMLSS.

### 2.4.1. Catch-per-unit-effort

CPUE for each station was calculated both by weight (kg) and numbers of fish caught, divided by the fishing time (hours). Assuming that the catch coefficient remains constant, the CPUE is proportional to abundance (Tesfamichael and Pauly, 2016), although with caveats regarding hyperstability (CPUE remains stable while abundance is declining) and hyperdepletion (CPUE declines more than the actual decline in abundance, see Harley et al., 2001). Such effects are, however, not foreseen to have been a major source of error in the present analyses because the surveys only spanned 12 months for which a major change in abundance was unlikely.

### 2.4.2. Catch composition

The catch composition by trophic group and fish familie was measured by the species-specific CPUE-by-weight of traps and gillnets (excluding stations with no catches). Variability of catch composition by trophic group, area, survey and depth category of traps was further explored using Principal Component Analysis of the average CPUE-byweight per area and survey (averaging was necessary to create an data set with equal number of data points per varible which is required to carry out PCA). To evaluate effects of different predictor variables (management area, survey, trophic group and depth category of traps) on the catch composition, GAM models were developed separately for the station-wise trap and gillnet CPUE data.

### 2.4.3. Catch rates

Varibility in catch rates between all stations by areas and surveys were analyzed using zero-adjusted GAM models developed seperately for trap and gillnet CPUE-by-weight and CPUE-by-numbers, where the models using the "Zero Adjusted Gamma" (ZAGA) distribution, specified nu-function, and the variable 'survey' implemented as a normal factor were found to have the best fit.

### 2.4.4. Biodiveristy

The species numbers (the number of distinct species caught), species accumulation curves, and functional diversity were calculated using the catch data from both gear types. Functional diversity was estimated as Rao's Q functional diversity index which provides "a measure of
community-level dispersion of species in functional trait space weighted by their relative abundances [...] not mathematically constrained to be positively correlated with species richness" (Stuart-Smith et al., 2013). Rao's Q was calculated following the approach of Stuart-Smith et al. (2013) using the 'dbFD' function in the 'FD' package, utilizing CPUE-by-numbers as proxy for abundance. Data for all species occurring at three or more stations, combined for all surveys, were included in the analysis. The 'lingoes' correction was applied to attain a Euclidian species-by-species distance matrix. CPUE-by-numbers were used as a proxy for abundance, thereby weighing the species occurrence not just on hours of fishing, but also by the numbers of fish caught. Species caught were classified by trophic group, trophic level, maximum total length, relative vertical position in water column, diel activity, habitat and gregariousness in accordance with Stuart-Smith et al. (2013) (the traits table is available on the github repository). Dimensionality was limited to 10 PCoA (Principal Coordinates Analysis) axes to avoid integer overload.

## 3. Results

In total, 738 trap and gillnet stations were sampled during the three surveys (Table 1). The number of gear units deployed were increased during the second and third surveys, with traps being the most common gear with 674 sets, constituting $91 \%$ of the stations. However, $54 \%$ ( 362 traps) were empty when hauled, compared to $20 \%$ of the gillnets (Table 1). A total of 128 species of fish representing 40 families were caught (Table 2), with fish from 37 families caught in gillnets, while traps caught fish from 19 families. Gear deployments varied considerably with regard to soak time and depth. Trap fishing time averaged 17.9 h , but ranged from 7.9 to 46 hours (Fig. 3A) due to weather conditions and technical issues affecting when the traps could be hauled. Fishing times of traps varied significantly between areas and surveys (Kruskal Wallis rank test, $\mathrm{p}<0.05, \mathrm{df}=20$, chi-squared $=224.76$ ), with $33 \%$ of the 210 area - survey combinations found to be significantly different ( $\mathrm{p}<0.05$, Conover-Iman post-hoc test with Holm correction) (Table S1). Average fishing time for gillnets was 13.9 h , ranging from 10.3 to 24.1 hours (Fig. 3C). Fishing times of gillnets also varied between areas and surveys (Kruskal Wallis rank test, $\mathrm{p}<0.05$, df $=17$, chisquared $=32.04$ ), but only two of the pairwise area - survey combinations (area 2 and 5 for the Nov. 2013 survey) were found to be significantly different ( $\mathrm{p}<0.05$, Conover - Iman post-hoc test with Holm correction, Table S1).

The mean overall set depth for the traps was 21.5 m (range: $5-145 \mathrm{~m}$ ), with mean depth never exceeding 50 m (Fig. S2). Trap set depths varied significantly between areas and surveys (Kruskal Wallis rank test, $\mathrm{p}<0.05, \mathrm{df}=20$, chi-squared $=53.90$ ), with $2.4 \%$ of the 210 area-survey combinations (between areas 2 and 5 in all surveys) found to be significantly different (using the Conover - Iman post-hoc test with Holm Correction ( $\mathrm{p}<0.05$ ) (Table S1). Area 5 had the shallowest distribution of trap set depths, consistent with this area being inshore of the outermost reefs, hence characterized by shallower waters than in the management areas further offshore.

### 3.1. Catch composition

The catch composition of the traps and gillnets were markedly different, both in terms of trophic group and fish family composition (Fig. 4A \& B). Although carnivores dominated both gear types, traps had higher catches of invertivores than gillnets, but lacked herbivores and corallivores, and caught less planktivores than the gillnets (Fig. 4B). Gillnets had generally high catch rates of Carangidae and Scombridae, but caught relatively few Lutjanidae and Lethrinidae, whom together with the Serranidae and 'other species' made up the majority of the trap catches (Fig. 4B). The relative rank of the main fish families varied between the surveys for the gillnet catches, while for the traps it remained more stable (Fig. 4B). Catch composition by depth of the traps showed similar distribution of the trophic groups by depth category (Fig. 4A),

Table 2
Family, species and number of fish caught (No.), number of stations where caught (St.) in traps and gillnets during the three surveys along the coast of Sudan in Nov. 2012, May 2013 and Nov. 2013). Species names checked versus the recent checklist of Red Sea fish species (Golani and Fricke, 2018), names verified using the World Register of Marine Species (www.marinespecies.com) and FishBase (www.fishbase.com).

| Family | Species | Sum |  | Nov. 2012 |  |  |  | May 2013 |  |  |  | Nov. 2013 |  |  |  |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
|  |  |  |  | Gillnet |  | Trap |  | Gillnet |  | Trap |  | Gillnet |  | Trap |  |
|  |  | No. | St. | No. | St. | No. | St. | No. | St. | No. | St. | No. | St. | No. | St. |
| ACANTHURIDAE | Acanthurus gahhm | 105 | 16 | 0 | 0 | 14 | 4 | 0 | 0 | 29 | 5 | 7 | 1 | 55 | 6 |
|  | Acanthurus nigrofuscus | 18 | 6 | 0 | 0 | 0 | 0 | 0 | 0 | 18 | 6 | 0 | 0 | 0 | 0 |
|  | Naso elegans | 2 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 2 | 1 | 0 | 0 |
|  | Naso hexacanthus | 76 | 3 | 0 | 0 | 0 | 0 | 19 | 1 | 19 | 1 | 38 | 1 | 0 | 0 |
| ALBULIDAE | Albula glossodonta | 8 | 3 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 8 | 3 | 0 | 0 |
| ARIIDAE | Netuma thalassina | 16 | 7 | 0 | 0 | 10 | 4 | 0 | 0 | 4 | 2 | 2 | 1 | 0 | 0 |
| BALISTIDAE | Balistapus undulatus | 2 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 2 | 1 |
|  | Balistoides viridescens | 2 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 2 | 1 | 0 | 0 | 0 | 0 |
|  | Pseudobalistes flavimarginatus | 2 | 1 | 0 | 0 | 2 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| BATOIDEA | Taeniura lymma | 2 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 2 | 1 | 0 | 0 |
| BELONIDAE | Tylosurus choram | 11 | 5 | 3 | 1 | 0 | 0 | 8 | 4 | 0 | 0 | 0 | 0 | 0 | 0 |
| BOTHIDAE | Bothus pantherinus | 2 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 2 | 1 | 0 | 0 |
| CAESIONIDAE | Caesio caerulaurea | 17 | 2 | 0 | 0 | 0 | 0 | 17 | 2 | 0 | 0 | 0 | 0 | 0 | 0 |
|  | Caesio suevica | 2 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 2 | 1 | 0 | 0 |
| CARANGIDAE | Alectis indica | 2 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 2 | 1 | 0 | 0 |
|  | Alepes vari | 5 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 5 | 1 | 0 | 0 |
|  | Carangoides armatus | 5 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 5 | 1 | 0 | 0 |
|  | Carangoides bajad | 107 | 24 | 16 | 3 | 2 | 1 | 11 | 5 | 16 | 2 | 62 | 13 | 0 | 0 |
|  | Carangoides ferdau | 11 | 3 | 0 | 0 | 0 | 0 | 0 | 0 | 2 | 1 | 9 | 2 | 0 | 0 |
|  | Carangoides fulvoguttatus | 23 | 7 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 22 | 6 | 0 | 0 |
|  | Carangoides sp. | 2 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 2 | 1 | 0 | 0 |
|  | Caranx ignobilis | 4 | 2 | 0 | 0 | 0 | 0 | 0 | 0 | 2 | 1 | 2 | 1 | 0 | 0 |
|  | Caranx melampygus | 13 | 4 | 3 | 1 | 0 | 0 | 0 | 0 | 2 | 1 | 8 | 2 | 0 | 0 |
|  | Caranx sexfasciatus | 93 | 10 | 17 | 1 | 0 | 0 | 23 | 1 | 3 | 1 | 50 | 7 | 0 | 0 |
|  | Caranx sp | 2 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 2 | 1 | 0 | 0 |
|  | Decapterus macarellus | 2 | 1 | 0 | 0 | 0 | 0 | 2 | 1 | 0 | 0 | 0 | 0 | 0 | 0 |
|  | Decapterus russelli | 7 | 2 | 0 | 0 | 0 | 0 | 2 | 1 | 5 | 1 | 0 | 0 | 0 | 0 |
|  | Elagatis bipinnulata | 9 | 3 | 0 | 0 | 0 | 0 | 9 | 3 | 0 | 0 | 0 | 0 | 0 | 0 |
|  | Gnathanodon speciosus | 5 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 5 | 1 | 0 | 0 |
|  | Scomberoides lysan | 182 | 18 | 17 | 2 | 21 | 1 | 66 | 6 | 25 | 1 | 53 | 8 | 0 | 0 |
|  | Scomberoides tol | 82 | 4 | 0 | 0 | 0 | 0 | 5 | 1 | 0 | 0 | 77 | 3 | 0 | 0 |
| CARCHARHINIDAE | Carcharhinus albimarginatus | 3 | 1 | 3 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
|  | Carcharhinus melanopterus | 18 | 4 | 10 | 1 | 1 | 1 | 0 | 0 | 0 | 0 | 7 | 2 | 0 | 0 |
|  | Carcharhinus amblyrhynchos | 4 | 2 | 0 | 0 | 0 | 0 | 2 | 1 | 0 | 0 | 2 | 1 | 0 | 0 |
|  | Triaenodon obesus | 22 | 9 | 0 | 0 | 5 | 2 | 0 | 0 | 17 | 7 | 0 | 0 | 0 | 0 |
| CHAETODONTIDAE | Chaetodon auriga | 5 | 2 | 0 | 0 | 5 | 2 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
|  | Chaetodon semilarvatus | 20 | 2 | 0 | 0 | 0 | 0 | 17 | 1 | 3 | 1 | 0 | 0 | 0 | 0 |
| CHANIDAE | Chanos chanos | 2 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 2 | 1 | 0 | 0 |
| CHIROCENTRIDAE | Chirocentrus dorab | 104 | 12 | 19 | 4 | 0 | 0 | 20 | 3 | 0 | 0 | 65 | 5 | 0 | 0 |
| DIODONTIDAE | Diodon hystrix | 5 | 2 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 5 | 2 | 0 | 0 |
| ECHENEIDIDAE | Echeneis naucrates | 9 | 4 | 0 | 0 | 0 | 0 | 0 | 0 | 5 | 2 | 4 | 2 | 0 | 0 |
| EPHIPPIDAE | Platax boersii | 2 | 1 | 0 | 0 | 2 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
|  | Platax orbicularis | 13 | 6 | 0 | 0 | 4 | 2 | 0 | 0 | 3 | 1 | 2 | 1 | 4 | 2 |
| GERREIDAE | Gerres oyena | 10 | 3 | 0 | 0 | 0 | 0 | 2 | 1 | 0 | 0 | 8 | 2 | 0 | 0 |
| HAEMULIDAE | Diagramma pictum | 11 | 5 | 0 | 0 | 2 | 1 | 0 | 0 | 7 | 3 | 2 | 1 | 0 | 0 |
|  | Plectorhinchus gaterinus | 18 | 7 | 0 | 0 | 11 | 4 | 2 | 1 | 0 | 0 | 5 | 2 | 0 | 0 |
|  | Plectorhinchus schotaf | 2 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 2 | 1 | 0 | 0 |
| HEMIRAMPHIDAE | Hemiramphus far | 2 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 2 | 1 | 0 | 0 |
| HOLOCENTRIDAE | Myripristis murdjan | 10 | 3 | 0 | 0 | 0 | 0 | 4 | 1 | 0 | 0 | 6 | 2 | 0 | 0 |
|  | Sargocentron rubrum | 30 | 15 | 0 | 0 | 0 | 0 | 0 | 0 | 23 | 12 | 0 | 0 | 7 | 3 |
|  | Sargocentron spiniferum | 64 | 31 | 0 | 0 | 24 | 11 | 2 | 1 | 26 | 13 | 2 | 1 | 10 | 5 |
| KYPHOSIDAE | Kyphosus vaigiensis | 13 | 3 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 13 | 3 | 0 | 0 |
| LABRIDAE | Cheilinus lunulatus | 2 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 2 | 1 | 0 | 0 | 0 | 0 |
|  | Cheilinus quinquecinctus | 2 | 1 | 0 | 0 | 2 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| LETHRINIDAE | Gymnocranius grandoculis | 7 | 2 | 0 | 0 | 0 | 0 | 0 | 0 | 3 | 1 | 4 | 1 | 0 | 0 |
|  | Lethrinus microdon | 64 | 24 | 0 | 0 | 17 | 7 | 2 | 1 | 29 | 12 | 8 | 1 | 8 | 3 |
|  | Lethrinus harak | 12 | 2 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 12 | 2 | 0 | 0 |
|  | Lethrinus lentjan | 218 | 60 | 4 | 1 | 53 | 16 | 7 | 1 | 73 | 26 | 42 | 5 | 39 | 11 |
|  | Lethrinus mahsena | 97 | 42 | 0 | 0 | 30 | 14 | 3 | 1 | 36 | 17 | 0 | 0 | 28 | 10 |
|  | Lethrinus microdon | 2 | 1 | 0 | 0 | 0 | 0 | 2 | 1 | 0 | 0 | 0 | 0 | 0 | 0 |
|  | Lethrinus nebulosus | 2 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 2 | 1 |
|  | Lethrinus obsoletus | 6 | 3 | 0 | 0 | 0 | 0 | 2 | 1 | 2 | 1 | 0 | 0 | 2 | 1 |
|  | Lethrinus xanthochilus | 5 | 2 | 0 | 0 | 0 | 0 | 0 | 0 | 3 | 1 | 0 | 0 | 2 | 1 |
|  | Monotaxis grandoculis | 2 | 1 | 0 | 0 | 0 | 0 | 2 | 1 | 0 | 0 | 0 | 0 | 0 | 0 |
| LUTJANIDAE | Lutjanus argentimaculatus | 4 | 2 | 0 | 0 | 0 | 0 | 0 | 0 | 2 | 1 | 0 | 0 | 2 | 1 |
|  | Lutjanus bohar | 212 | 90 | 0 | 0 | 58 | 26 | 16 | 6 | 118 | 49 | 5 | 2 | 15 | 7 |
|  | Lutjanus ehrenbergii | 33 | 9 | 8 | 2 | 0 | 0 | 15 | 4 | 0 | 0 | 10 | 3 | 0 | 0 |
|  | Lutjanus fulviflamma | 3 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 3 | 1 | 0 | 0 |
|  | Lutjanus gibbus | 188 | 67 | 0 | 0 | 55 | 17 | 0 | 0 | 80 | 29 | 5 | 2 | 48 | 19 |
|  |  |  |  |  |  |  |  |  |  |  |  |  | ntin | on nex |  |

Table 2 (continued)

| Family | Species | Sum |  | Nov. 2012 |  |  |  | May 2013 |  |  |  | Nov. 2013 |  |  |  |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
|  |  |  |  | Gillnet |  | Trap |  | Gillnet |  | Trap |  | Gillnet |  | Trap |  |
|  |  | No. | St. | No. | St. | No. | St. | No. | St. | No. | St. | No. | St. | No. | St. |
|  | Lutjanus kasmira | 17 | 8 | 0 | 0 | 7 | 3 | 0 | 0 | 6 | 3 | 0 | 0 | 4 | 2 |
|  | Lutjanus monostigma | 19 | 9 | 3 | 1 | 8 | 4 | 0 | 0 | 6 | 3 | 0 | 0 | 2 | 1 |
|  | Lutjanus rivulatus | 2 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 2 | 1 | 0 | 0 | 0 | 0 |
|  | Lutjanus sebae | 2 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 2 | 1 | 0 | 0 | 0 | 0 |
|  | Lutjanus sp. | 2 | 1 | 0 | 0 | 2 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
|  | Macolor niger | 6 | 3 | 0 | 0 | 0 | 0 | 0 | 0 | 4 | 2 | 2 | 1 | 0 | 0 |
|  | Paracaesio sordidus | 3 | 1 | 0 | 0 | 3 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
|  | Pristipomoides multidens | 23 | 7 | 0 | 0 | 14 | 5 | 0 | 0 | 9 | 2 | 0 | 0 | 0 | 0 |
| MUGILIDAE MULLIDAE | Crenimugil crenilabis | 4 | 2 | 0 | 0 | 0 | 0 | 2 | 1 | 0 | 0 | 2 | 1 | 0 | 0 |
|  | Mulloidichthys flavolineatus | 2 | 1 | 0 | 0 | 0 | 0 | 2 | 1 | 0 | 0 | 0 | 0 | 0 | 0 |
|  | Mulloidichthys vanicolensis | 2 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 2 | 1 | 0 | 0 |
| MURAENIDAE | Gymnothorax flavimarginatus | 5 | 2 | 0 | 0 | 5 | 2 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
|  | Gymnothorax javanicus | 80 | 40 | 0 | 0 | 54 | 26 | 1 | 1 | 23 | 12 | 0 | 0 | 2 | 1 |
| PLATYCEPHALIDAE | Cociella crocodilus | 2 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 2 | 1 | 0 | 0 |
| PRIACANTHIDAE | Priacanthus hamrur | 6 | 2 | 0 | 0 | 0 | 0 | 6 | 2 | 0 | 0 | 0 | 0 | 0 | 0 |
| SCARIDAE | Hipposcarus harid | 10 | 2 | 0 | 0 | 0 | 0 | 5 | 1 | 0 | 0 | 5 | 1 | 0 | 0 |
|  | Scarus ferrugineus | 2 | 1 | 0 | 0 | 0 | 0 | 2 | 1 | 0 | 0 | 0 | 0 | 0 | 0 |
|  | Scarus frenatus | 6 | 2 | 0 | 0 | 0 | 0 | 3 | 1 | 0 | 0 | 3 | 1 | 0 | 0 |
|  | Scarus ghobban | 2 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 2 | 1 | 0 | 0 |
| SCOMBRIDAE | Auxis thazard | 15 | 1 | 15 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
|  | Euthynnus affinis | 9 | 2 | 0 | 0 | 0 | 0 | 5 | 1 | 0 | 0 | 4 | 1 | 0 | 0 |
|  | Grammatorcynus bilineatus | 48 | 10 | 29 | 3 | 3 | 1 | 8 | 3 | 0 | 0 | 8 | 3 | 0 | 0 |
|  | Gymnosarda unicolor | 14 | 4 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 14 | 4 | 0 | 0 |
|  | Katsuwonus pelamis | 2 | 1 | 2 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
|  | Rastrelliger kanagurta | 31 | 4 | 0 | 0 | 0 | 0 | 7 | 1 | 0 | 0 | 24 | 3 | 0 | 0 |
|  | Sarda orientalis | 2 | 1 | 0 | 0 | 0 | 0 | 2 | 1 | 0 | 0 | 0 | 0 | 0 | 0 |
|  | Scomber australasicus | 2 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 2 | 1 | 0 | 0 | 0 | 0 |
|  | Scomberomorus commerson | 51 | 5 | 39 | 2 | 0 | 0 | 0 | 0 | 0 | 0 | 12 | 3 | 0 | 0 |
|  | Thunnus albacares | 12 | 1 | 12 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| SERRANIDAE | Cephalopholis argus | 2 | 1 | 0 | 0 | 2 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
|  | Cephalopholis miniata | 2 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 2 | 1 | 0 | 0 |
|  | Aethaloperca rogaa | 23 | 10 | 0 | 0 | 4 | 2 | 0 | 0 | 17 | 7 | 0 | 0 | 2 | 1 |
|  | Epinephelus chlorostigma | 2 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 2 | 1 | 0 | 0 | 0 | 0 |
|  | Epinephelus fasciatus | 4 | 2 | 0 | 0 | 0 | 0 | 0 | 0 | 2 | 1 | 0 | 0 | 2 | 1 |
|  | Epinephelus fuscoguttatus | 34 | 17 | 0 | 0 | 12 | 5 | 0 | 0 | 16 | 9 | 2 | 1 | 4 | 2 |
|  | Epinephelus summana | 5 | 2 | 0 | 0 | 0 | 0 | 3 | 1 | 2 | 1 | 0 | 0 | 0 | 0 |
|  | Epinephelus tauvina | 48 | 23 | 2 | 1 | 21 | 10 | 7 | 3 | 8 | 4 | 6 | 3 | 4 | 2 |
|  | Plectropomus pessuliferus | 8 | 4 | 0 | 0 | 4 | 2 | 0 | 0 | 4 | 2 | 0 | 0 | 0 | 0 |
|  | Variola louti | 4 | 2 | 0 | 0 | 0 | 0 | 0 | 0 | 4 | 2 | 0 | 0 | 0 | 0 |
| SIGANIDAE | Siganus argenteus | 4 | 1 | 0 | 0 | 0 | 0 | 4 | 1 | 0 | 0 | 0 | 0 | 0 | 0 |
|  | Siganus luridus | 4 | 2 | 2 | 1 | 0 | 0 | 2 | 1 | 0 | 0 | 0 | 0 | 0 | 0 |
|  | Siganus rivulatus | 2 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 2 | 1 | 0 | 0 |
|  | Siganus stellatus | 5 | 2 | 0 | 0 | 0 | 0 | 2 | 1 | 0 | 0 | 0 | 0 | 3 | 1 |
| SOLEIDAE | Pardachirus sp. | 2 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 2 | 1 | 0 | 0 |
| SPARIDAE | Argyrops filamentosus | 9 | 2 | 0 | 0 | 0 | 0 | 0 | 0 | 9 | 2 | 0 | 0 | 0 | 0 |
|  | Argyrops sp. | 25 | 5 | 0 | 0 | 25 | 5 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
|  | Argyrops spinifer | 19 | 8 | 0 | 0 | 0 | 0 | 0 | 0 | 9 | 3 | 0 | 0 | 10 | 5 |
|  | Sparus sp. | 7 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 7 | 1 | 0 | 0 | 0 | 0 |
| SPHYRAENIDAE | Sphyraena forsteri | 2 | 1 | 0 | 0 | 0 | 0 | 2 | 1 | 0 | 0 | 0 | 0 | 0 | 0 |
|  | Sphyraena jello | 5 | 2 | 5 | 2 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
|  | Sphyraena putnamae | 2 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 2 | 1 | 0 | 0 |
|  | Sphyraena qenie | 15 | 5 | 0 | 0 | 0 | 0 | 8 | 2 | 0 | 0 | 7 | 3 | 0 | 0 |
| SPHYRNIDAE | Sphyrna lewini | 2 | 1 | 2 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |

while the fish families Acanthuridae and Carangidae were only caught in the shallow trap stations ( $<30 \mathrm{~m}$ ). For the other main fish families the catches were similar between the the deep ( $>30 \mathrm{~m}$ ) and shallow ( $<$ 30 m ) stations (Fig. 4B).

In the PCA analysis of average catch rates for both traps and gillnets the first two principal components (PCs) explained $88 \%$ of the variation. (Fig. 5A). A single large gillnet catch of Planktivores, 56.69 kg of Naso hexacanthus in area 2 during the Nov. 2013 survey, drove the variability along PC1, while PC2 was driven by high catches of carnivores in area 1 during the November 2013 survey (Fig. 5A and E). For most of the data the variability along PC2 was dominant, as seen by most datapoint (save four) aligning almost perfectly along a vertical line parallell to PC2 (Fig. 5A). Planktivores and carnivores drove most of the variabily along PC1 and PC2 respectively, while coralivores, invertivores and herbivores contributed little to the variability in either of the two first PCs
(Fig. 5E).
For the traps only PCA analysis the first two PCs explained $67.9 \%$ of the variability with PC1 and PC2 contributing fairly equally ( $35.9 \%$ and $32 \%$ respectively, see Fig. 5B), with most data points spread along PC1, while a single data point dominated the variability along PC2; a large shallow trap catch of planktivores ( 10.1 kg of Naso hexacanthus) in area 5 during the May 2013 survey (see Fig. 5B, D and F). As with the combined gear PCA neither area nor survey formed any clear groupings (Fig. 5B and D). Catches were not group by depth category either, but shallow stations contributed strongly to driving the variability along the PCs with shallow stations having both the maximum and minimum score values along both PCs (Fig. 5B). Catches of carnivores and invertivores drove the variability along PC1 while shallow catches of planktivores, specifically in May 2013 drove the variability along PC2 (Fig. 5B, D and F).


Fig. 3. Fishing gear deployment durations and catch rates by surveys and management areas. Boxplots of : A) duration of trap sets (hours), red circles show the mean; B) Trap catch rates (CPUE, kg-per-hour-of-fishing) ; C) Duration of gillnet sets (hours), red circles show the mean; D) Gillnet catch rates (CPUE, kg-per-hour-offishing). Median value is shown by the black horizontal line, while the lower and upper limits of the box denotes the $25 \%$ and $75 \%$ quantiles.

In the GAM model of trap CPUE-by-weight (for stations with catches only) only trophic group was a significant variables in the model when the smoothing function was dropped. Of the variables, the carnivores and corallivores were the significant factors (Inverse Gaussian distribution, AIC: -584, df: 12, see Table S2 for model details). For the similar GAM model of gillnet CPUE-by-weight the variables area, survey and trophic group were found to be significant when the smoothing function was dropped. Carnivores, herbivores, invertivores as well as areas 1,2 , 3, 4, 5 and 7 were significant factors (Exponential distribution, AIC $=-114, \mathrm{df}=10$, see Table S2 for model details).

The differences between the PCA and GAM results in relation to how the different variables contributed to the variability in the catch composition were likely due to the PCA analysis being based on the average CPUE rates per area area, while the GAM models used the raw station data. Few (14) sampling stations with planktivores caused this trophic group to have a low effect on the GAM models compared to other trophic groups that were caught at a higher number of stations.

### 3.2. Catch rates

### 3.2.1. Varibility in CPUE over all stations

Trap and gillnet CPUE-by-weight and numbers for all stations varied among management areas and between surveys (Fig. 3B and D). The Dungonab area (area 2) had the highest average CPUE-by-numbers for trap and gillnet ( 0.09 and 1.37 fish/hour respectively, see Table 3). The highest CPUEs by weight were $0.15 \mathrm{~kg} /$ hour for traps in area 2 and $1.65 \mathrm{~kg} /$ hour for gillnets in area 1 (Table 3).

Area and survey were significant variables in the traps CPUE-bynumbers GAM model (AIC $=400$, df $=21$ ), while for the CPUE-byweight model (AIC $=682, \mathrm{df}=21$ ) only the survey variable was
found to be significant when the smoothing function was dropped (see Table S2 for model details). The May 2013 survey was a significant factor in the CPUE-by-weight model, while the Nov. 2013 survey was a significant factors in CPUE-by-numbers model, while the Nov. 2012 survey was only a significant factor in the model of CPUE-by-numbers. For the gillnet GAM models, depth was the single significant variable identified when the smoothing function was dropped, and only for the CPUE-by-numbers model (AIC: 190, df $=21$ ). For the CPUE-by-weight model (AIC $=169, \mathrm{df}=21$ ), areas 3 and 6 were significant factors, while for the CPUE-by-numbers model only depth was a significant variable (see Table S2 for model details). Taken together the results from these four GAM models indicate a significant influence of surveys on CPUE, while the observed variability between areas was only significant for the CPUE-by-numbers and for a few areas.

### 3.2.2. Evaluation of the trap CPUE in relation to traits

Traits of species caught in traps varied between surveys and areas (see Figs. S3-S7 for plots of trophic group, place in water column, diel activity, gregariousness and maximum length, by area and survey). In a GAM model of trap CPUE-by-numbers in relation to traits (Box-Cox power exponential distribution, AIC $=-1384, \mathrm{df}=17$ ), all traits (trophic level, trophic group, place in water column, diel activity, habitat, gregariousness, and max length) were identified as significant variables of the model, both based on the p -values of the coefficients, and from evaluation of variables by dropping the smoothing function (see Table S2 for model details). This confirmed that the observed variability in CPUE by traits was not occurring by chance.


Fig. 4. Composition of catches (CPUE: kg-per-hour-of-fishing) for gillnets and traps, for each of the three surveys according to: A) trophic group, and B) main fish families in the catches. Bar colour identifies the depth range of the catches: $0-30 \mathrm{~m}$ (green), deeper than 30 m (blue).

### 3.3. Trophic level of trap catches

The trophic level in the catches ranged from 2 to 4.5 with a mean of 3.84 and averages per area and survey ranging from 3.20 (area 3, Nov. 2013 survey) to 3.97 (area 3, May 2013 survey) (see Table 3). When averaged across surveys the range in trophic level narrowed from 3.76 in area 6 to 3.83 in area 1 (Table 3). In a GAM model of trophic level dependent on the depth, survey and area, survey was the only significant variable when the smoothing function was dropped (Box-Cox power exponential distribution, AIC $=830, \mathrm{df}=11$, see Table S2 for model details). In this model area 3 and the intercept were the only significant factors affecting the trophic level. This indicated that trophic level remained stable over the time of the surveys and only varied to a limited degree between the seven management areas.

### 3.4. Biodiversity

The highest species richness in all trap catches across all surveys was 34 species observed in area 2, while only 11 species were observed in area 4 (Table 3). For gillnets the highest species richness was 40 species observed in area 2 , while area 3 had the lowest richness with only 5 observed species (Table 3). However, the large variability in the number of gillnet stations between areas should be taken into account when interpreting these results (Table 1).

### 3.4.1. Species accumulation curves

Across all areas and surveys, the accumulated number of species at the shallow trap stations plateaued at 49 species after 25 h (Fig. 6A), for the deep trap stations at 43 species after 23 h (Fig. 6B), and at 93 species after 16 h for the gillnet stations (Fig. 6C). Shallow and deep traps in area 2 had the steepest increase and highest species numbers (24 and 27)
while area 4 and area 5 had the least steep (and lowest species richness). For gillnets species numbers in areas 2,5 and 7 plateaued at similarly high levels (40, 36 and 38 respectively, see Table 3 and Fig. 6). The deep traps in area 2 showed a markedly steeper species accumulation curve (Fig. 6B) than any of the other areas, with the largest inter-area difference in species numbers ( 12 species) between this area and area 6 with 15 species. Neither shallow traps nor the gillnets showed as large interarea differences as those observed for the deep traps.

### 3.4.2. Functional diversity

The quality of the reduced vector space representation of the traits, $R^{2}$, was 0.533 when using all seven traits in the combined traps and gillnet model, and increased to 0.826 for the traps only model. To evaluate the contribution of individual traits on the functional diversity the model was rerun seven times for each of the two models excluding one trait at a time, but as it only lead to low ( $<10 \%$ ) increases in $\mathrm{R}^{2}$ it was decided to use the model with all traits included in the analysis.

The Rao's Q functional group richness index for the combined trap and gillnet model was highest in area 1 (0.090), closely followed by area 2 (0.087), and lowest in area 4 ( 0.038 ), which was $39 \%$ less than the second lowest ( 0.063 in area 6) (see Table 3). When calculated only for traps Rao's Q was highest in area 6 (0.084), second highest in area 1 (0.076), and lowest in area 4 ( 0.059 ), with a lower inter-area differences ( $5 \%$ ) between area 4 and the second lowest; area 7, than for the combined model (see Table 3).

## 4. Discussion

The three surveys conducted in 2012 and 2013 constitute one of the most extensive surveys of fishery species along the entire Sudanese coast. As such it represents a uniqe baseline of fish distributions, relative


Fig. 5. Principal component analysis of the average CPUE-by-weight (kg-per-hour-of-fishing) by trophic groups (variables in the analysis) per management area for trap and gillnet CPUE together, and separately for only the trap CPUE data. The scores and loadings are plotted along the first and second principal component (PC) with the percentage variations explained by each PC is shown in the axis legends. A) Scores of gillnet and trap catches by survey; B) Scores of the trap only catches per survey and by depth range ( $0-30 \mathrm{~m}$, and deeper than 30 m ); C) Scores of the gillnet and trap catches by management area (1-7); D) Scores of the trap only catches by depth range ( $0-30 \mathrm{~m}$, and deeper than 30 m ) and management area (1-7); E) Loadings of the trophic group variables for the PCA of the trap and gillnet catches; F) Loadings of the trophic group variables for the PCA of the trap only catches.

Table 3
Mean catch per unit effort (CPUE, kg-per-hour-of-fishing and number-of-fish per-hour-of-fishing); mean trophic level for traps and gillnet catches; species richness (number of species in traps and gillnets); and the functional diversity of catches (Rao's Q) for each of the seven management areas along the Sudanese Red Sea Coast (see Fig. 2).

| Mgmt. Area | CPUE (kg/hour) |  | CPUE (no. fish/hour) |  | Trophic level |  | No. Species |  | Rao's Q |  |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
|  | Traps | Gillnets | Traps | Gillnets | Traps | Gillnets | Traps | Gillnets | Traps \& Gillnets | Traps |
| 1 | 0.12 | 1.64 | 0.06 | 0.68 | 3.94 | 4.08 | 16 | 14 | 0.089 | 0.076 |
| 2 | 0.15 | 1.18 | 0.09 | 1.37 | 3.91 | 3.93 | 34 | 40 | 0.087 | 0.066 |
| 3 | 0.14 | 0.31 | 0.08 | 0.27 | 3.97 | 4.14 | 23 | 5 | 0.068 | 0.069 |
| 4 | 0.06 | 0.70 | 0.07 | 1.00 | 3.88 | 4.26 | 11 | 23 | 0.038 | 0.059 |
| 5 | 0.08 | 0.73 | 0.09 | 1.24 | 3.83 | 3.87 | 18 | 36 | 0.075 | 0.071 |
| 6 | 0.14 | 0.27 | 0.07 | 0.77 | 3.83 | 4.02 | 24 | 13 | 0.063 | 0.084 |
| 7 | 0.10 | 0.68 | 0.08 | 1.21 | 3.81 | 3.72 | 23 | 38 | 0.068 | 0.062 |

densities and biodiversity that can serve as a first starting point for future research and management efforts. Our results showed significant differences in both catch rates, species richness and functional diversity between the seven management regions and among the three surveys, also confirming the presence of species already known to inhabit the Sudanese coast (Table 2).

As expected, gillnets caught predominantly pelagic species, whereas traps caught predominantly benthic and demersal species. There were apparent and expected differences in catch composition compared to the
artisanal fishery that targets reef-dwelling species like groupers using hand line (Tesfamichael and Elawad, 2016), with snappers (Lutjanidae) dominating the trap catches (Fig. 4B). Our survey methods were chosen to cover a wider habitat (pelgagic and demersal) and depth ranges than the typical handline methods. Also, passive gears can be fished more uniformely, not being affected by the skill of the individual fisher to the degree that handlines are, and lastly using passive gear allowed us to cover a larger geographic area compared to using handlines where the boat would need to stay at each station for a much longer period of time.


Fig. 6. Species accumulation curves (accumulated number of species per hour of deployment of the fishing gears) for: A) Traps set at $0-30 \mathrm{~m}$ depth; B) Traps set deeper than 30 m ; C) Gillnets only. Accumulations curves are shown for each management area separately, as well as the combined accumulation curve for all areas.

With more data on abundance, distribution and biology there may be a potential for development of fisheries targeting the snappers, emperors and other species roaming between reefs by adapting the current artisanal fishery to utilize other gear types and fishing locations. Our gillnet catches caught a markedly different species composition than traps, particularly for Serranidae, Scombridae, Lutjanidae and Lethrinidae (Fig. 4B). Of particular interest in relation to the artisanal fisheries were Serranidae. During our surveys only 69 individuals of the Serranidae were caught using traps (none in the gillnets), with the highest catches (34 fish) obtained during the May 2013 survey, coinciding with the spawning season of the commercially important Plectropomus spp. (Elamin, 2012), and related species. The higher catches of Serranidae in the May 2013 survey might be explained by increased mobility and gear vulnerability during the time of spawning.

### 4.1. Catch rates (CPUE)

Our findings of the lowest trap CPUE-by-weight in the Port Sudan and Suakin areas (4 and 5) are consistent with Klaus et al. (2009). The three northernmost areas had the highest CPUE-by-weight for traps in addition to area 1 and 2 in the north having the highest functional diversity of the combined trap and gillnet catches, indicating that the north may be the most productive region along the coast. The Dungonab area (area 2) has the widest shelf and largest shallow-water region in the north, and a designated marine protected area covers most of management area 2, granting access to local fishers only, likely causing reduced fishing pressure in this area. Nevertheless, several previously known
spawning aggregations for Plectropomus spp. in this area are suspected lost due to past fishing (Sheikheldin M'Elamin, pers. comm.). Area 3, just south of Dungonab bay, had the second-highest trap CPUE (0.136), pointing to a possible ecological linkage of fish communities between the bay and the adjacent archipelago.

The two southernmost areas, Suakin Archipelago and Agig, had higher trap CPUE than Suakin and Port Sudan (areas 4 and 5), although lower than in the northernmost areas. Our results are thus similar to Kattan et al. (2017), who found a positive relationship between top predator biomass and distance to the nearest port. Kattan et al. (2017) hypothesized that fishing pressure diminishes with distance to port as fishermen prefer close and more nearshore reefs over more distant offshore reef areas, or gradually move to more distant fishing grounds as home reefs are depleted. However, the results from the present analysis are not consistent, exemplified by the high CPUE estimated for the nearshore Dungonab bay (area 2). This may, however, be explained by the higher level of protection and management in this area compared to other inshore areas. Nevertheless, our results, taken together with Klaus et al. (2009) and Kattan et al. (2017), may imply that local artisanal fishing pressure has been sufficient to impact local fish populations to a certain degree, though more focused studies on population dynamics are warranted to confirm this.

In contrast to Klaus et al. (2009), who noted the low abundance of large snappers, groupers and emperors in the UVC surveys that they conducted, the present surveys found these species in abundance (although large individuals were relatively rare). Trap-based surveys differ fundamentally from UVC in that fish are attracted to the bait in the trap, while UVCs give a snapshot of the fish present in the UVC transect (Connell et al., 1998). Furthermore, UVCs are only carried out during daytime, while traps were fished overnight. The differences can be further explained by the more extensive geographic coverage, the greater depth of the sampling gear compared to UVC depths, the larger number of sampling stations, and difference in catchability of fishing gear in our study compared to the UVC survey by Klaus et al. (2009). In addition, snappers and emperors, and to a lesser degree groupers, all showed roving behaviour between reefs, often keeping a distance from divers (Emslie et al., 2018, personal observations), similar to what Colton and Swearer (2010) observed for mobile predators, possibly making them less available in UVC transect paths. These species were attracted to baited traps, possibly explaining their common occurrence in catches in the present study.

### 4.2. Species richness and functional diversity

There were clear differences in species richness among the seven management areas (Table 3), highest in Dungonab bay (area 2) and lowest in the Port Sudan (area 4) for both traps and gillnets. However, the species richness in Port Sudan is probably an underestimate due to the fewer sampling stations in this area. Still, the differences in species richness between the Dungonab bay (area 2) and the Port Sudan (area 4) are large, and the species accumulation curve (Fig. 6) indicated a clear plateauing, wich together indicates that even with comparable sampling it is likely that the Port Sudan area has a lower species richness than the Dungonab bay area. Functional diversity showed a similar pattern, with the three northernmost areas, and in particular the protected Dungonab bay area (area 2) having higher functional diversities than the Port Sudan area. These results support the findings of Kattan et al.'s (2017) that suggested relatively higher numbers of species per UVC transect in remote areas of the coast compared to closer to population centers.

Klaus et al. (2009) identified the $70-\mathrm{km}$ coastal region between Port Sudan and Suakin as being the most heavily affected by coastal and harbour developments and claimed that this affected the reefs in this area. This is further supported by Kattan et al. (2017), who found that biomass and species richness increased with distance from the main port of Port Sudan. Our results showed a lower species richness and functional diversity in the Port Sudan management area. This supports the
hypothesis that increased urban development and proximity to population centers have resulted in decline in catchable fish biomass and reduced productivity of reefs. The higher human populations and number of fishermen based in the regions of management area 4 have likely increased all kinds of anthopogenic impact more than in other areas, likely explaining the low species richness, functional diversity, and lower catch rates in these regions.

### 4.3. Limitations

Gear selectivity greatly impacted the catch composition. With traps constituting $91 \%$ of our stations, it was unsurprising that the major trophic group caught was carnivores, as these were the species most likely to be attracted to bait. Additionally, small fish caught in the traps may act as bait attracting larger carnivore fish. Thus, predation of smaller fish in the trap may cause an underestimate of CPUE of smaller fish with increasing soak time. Our trap-based method was thus suboptimal to survey herbivorous fish species, as well as fish closely associated with coral reef habitats. For such species, underwater visual census (UVC) methods, or baited remote under-water video (BRUVs) remain the only current alternatives. However, for certain vagile species such as snappers (Lutjanidae), emperors (Lethrinidae) and Scombridae, the use of baited traps proved appropriate, filling a gap where gillnets were proven inefficient or difficult to deploy (e.g., close to coral reefs).

It is also inevitable that the capture-based methodologies employed to cover the entire coast during surveys have resulted in missing cryptic, locally rare or endemic species. There are other issues pertaining to gillnet and trap fishing in coral reef areas that make them less desirable from a biodiversity and fisheries conservation perspective, such as ghost fishing, and bycatch of vulnerable species (e.g., sharks). Selective passive gears, like traps, can, however, be employed with less environmental impact or bycatch of threatened elasmobranch species than pelagic gillnets or long-lines. Still, physical damage to reefs during deployment and ghost fishing if lost, particularly if deployed without bio-degradable openings, may represent considerable drawbacks.

Whether traps are more appropriate for estimation of species abundance than visual census methods, which may underestimate species that actively avoid divers doing the census (Colton and Swearer, 2010), or are reluctant to approach a baited camera rig (BRUV) during the relatively short recording time, remains to be properly tested for species typically targeted by Sudan's artisanal coral reef fishery. In a study comparing the relative efficiency of commercial fish traps and BRUVs in sampling tropical demersal fishes in Western Australia, Harvey et al. (2012) found that BRUVs had greater statistical power to detect changes in abundance than an equivalent number of traps. Harvey et al. (2012) also found that among five commercially important Indo-Pacific species (Epinephelus bilobatus, Epinephelus multinotatus, Lethrinus punctulatus, Lutjanus russelli and Lutjanus sebae) only emperor red snapper (L. sebae) was more efficiently sampled with commercial traps. Still, a monitoring system based on traps requires lower skill levels and less infrastructure than UVC and BRUV methodology, and most species will survive capture and subsequent release if a non-extractive approach to monitoring is desired. Traps also have their drawbacks in being bulky, requiring a winch to haul and will involve more sea time if soaked overnight. Evaluating such practical constraints is essential when planning and designing fish monitoring programs in countries with poor institutional capacities and limited resources like Sudan.

### 4.4. Conclusions

The observed differences in species richness, species accumulation curves, functional diversity and catch rates demonstrate clear variabilities between areas and surveys that can be hypothesized to some degree to be caused by varying degrees of human impacts along the coast of Sudan. The methods presented here should be further developed by improving the sampling design by means of complementing the catch-
based approaches with remote video or visual census-based methods to more fully cover habitats and species. The strong gear selectivity evident in our trap and gillnet catches indicate a potential for using gear regulations as means of fisheries management to contribute towards an ecosystem approach to management of the Sudanese marine waters. In addition to monitoring the state of the fisheries resources through scientific investigations akin to the surveys here presented we strongly advocate for a comprehensive, statistically rigorous and continuous monitoring of the Sudanese fisheries catches. Whereas scientific surveys are expensive and resource intensive, catch monitoring programs can be designed and implemented with low cost and resource demands. Together this would improve our understanding of the fish community and fisheries along the coast of Sudan, for which the present study provides a first baseline. Surveys like these are a necessary part of the beginning of an extensive monitoring and management plan that can be used to manage the increasing pressures from a growing population pushing for increases in coastal developments and fisheries, to avoid overfishing, habitat destruction and associated negative socioeconomic impacts.

## CRediT authorship contribution statement

Erik Olsen: Conceptualization, Methodology, Investigation, Data curation, Software, Formal analysis, Visualization, Writing - original draft, Writing - review \& editing, Project administration, Funding acquisition. Bjørn Erik Axelsen: Conceptualization, Methodology, Investigation, Writing - original draft, Writing - review \& editing. Even Moland: Conceptualization, Methodology, Investigation, Writing original draft, Writing - review \& editing. Anne Christine Utne-Palm: Conceptualization, Methodology, Investigation, Writing - original draft, Writing - review \& editing. Elamin Mohammed Elamin: Conceptualization, Methodology, Investigation, Writing - original draft. Motassim Ali Mukhtar: Conceptualization, Methodology, Investigation, Writing original draft. Adel Mohamed Saleh: Conceptualization, Methodology, Investigation, Writing - original draft. Sheikheldin Mohamed Elamin: Conceptualization, Methodology, Investigation, Writing - original draft. Mohamed Abdelhameed Iragi: Conceptualization, Methodology, Investigation, Writing - original draft. Said Gumaa Fadul Gumaa: Conceptualization, Methodology, Investigation, Writing - original draft.

## Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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## Appendix A. Supplementary data

Supplementary material related to this article can be found, in the online version, at doi:https://doi.org/10.1016/j.fishres.2021.106032.

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