Functional traits illuminate the selective impacts of different fishing gears on coral reefs

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Abstract

1. Unsustainable fishing is a major driver of change in marine ecosystems. The ways that fishing gears target fishes with different ecological functions are unclear, particularly in complex multi-species fisheries.
2. Here, we examine whether artisanal fishing gears compete for fishes with unique combinations of ecological traits (diet, body size, depth, position in water column, period of activity, schooling behaviour) in a coral reef ecosystem. We use coral reef fish landing data from 25 sites along the Kenyan coast collected over a seven year period.
3. All fishing gears targeted a wide diversity of traits, but with some differentiation among gears. Fish assemblages captured by spearguns were significantly different from the other gear types, specialising on diurnal species that feed on sessile invertivores. Nets, including gillnets and beachseines, targeted the most functional diversity. Escape slot traps targeted the least functionally-diverse assemblages. Basket traps and escape-slot traps targeted the most functionally similar species of all two-gear combinations.
4. There were 163 functional entities (unique combinations of traits) captured in the fishery, however 50% of the catch by each gear was from only 2-6 functional entities. Most of the differences in gear selectivity were due to unique and rarely targeted functional entities, that made up only a small proportion of the catch.
5. Synthesis and applications. Coral reef fisheries target a breadth of functional entities, but catches are heavily skewed towards relatively few functional entities. While banning specific gears will benefit rare functional entities in the catch, effort reductions will be necessary to alleviate pressure on commonly targeted functional entities.

Key words: ecosystem-based management, functional diversity, gear-based management, gear interactions, niche breadth, trait-based approach

Introduction

Fishing is a major driver of marine ecosystem change worldwide (Worm *et al.* 2006). Consequently, a variety of tools have been proposed to evaluate the environmental effects of fishing on marine ecosystems (McClanahan, Hicks & Darling 2008; Guillemot *et al.* 2014). Most work aimed at understanding the effects of fishing on the marine environment tends to focus on species abundances and catch composition (Jennings, Greenstreet & Reynolds 1999; Hiddink *et al.* 2006). Yet, the growing interest in an ecosystem-based approach has stressed maintaining and sustaining ecological functions (Sinclair *et al.* 2002; Tillin *et al.* 2006). Trait-based ecology has much to offer to this objective. Indeed, choosing relevant traits that represent the complementary roles of organisms has become a cornerstone of functional ecology (McGill *et al.* 2006; Violle *et al.* 2007). By considering biological traits as proxies for function, the trait-based approach (Mouillot *et al.* 2013; Villéger *et al.* 2017) may help uncover ecosystem processes and functional implications of changes in fisheries assemblages.

Trait-based approaches were initially applied in plant ecology (Cornwell, Schwilk & Ackerly 2006) and are now widely used across other organisms, such as birds (Naeem, Duffy & Zavaleta 2012), bats (Norberg 1994), corals (Darling et al. 2012), insects (Poff *et al.* 2006), and fish (Albouy *et al.* 2011). The approach has proven to be exceptionally versatile, offering functional insights into changes in assemblages through time (Friedman 2009; Villéger, Novack-Gottshall & Mouillot 2011), the impacts of species invasions (Olden, Poff & Bestgen 2006; Corbin & D'Antonio 2010), and responses to environmental change (Laughlin *et al.* 2011; Graham *et al.* 2015).

Several studies have used traits to assess how fishing modifies aquatic ecosystems, however most are based on in-situ observations in temperate countries, and none have assessed how different fishing gears remove specific ecological traits from the ecosystem (Tillin *et al.* 2006; Guillemot *et al.* 2014; Koutsidi *et al.* 2016). In multi-species coral reef fisheries, fishing gears are known to exhibit some degree of overlap in the species they capture (McClanahan & Mangi 2001) and to reduce fish biodiversity (McClanahan 2015) highlighting the need to understand how competitive interactions among gear types affect outcomes (McClanahan & Kosgei 2018). However, the degree to which specific fishing gears target different traits remains unclear.

Here, we employ a trait-based approach to assess the functional selectivity of seven fishing gears, many of which are commonly used in small scale coral reef fisheries around the world. Specifically, we ask the following questions; (i) do specific fishing gears target certain traits and (ii) what overlaps are there in trait composition among gears? We use field data on fisheries landings collected over a seven-year period from 25 coral reef and lagoon sites in Kenya.

Material and Methods

Catch sampling

We used catch data from 25 landing sites conducted monthly between 2010 and 2016 (Fig. 1). Observers identified landed catch to species level and recorded the number, size (total length in cm), gear used, landing site name, and date. Although all sampling was conducted during daylight hours, these include catches attributed to night-time fishing activities as observers also intercepted fishers returning from their overnight fishing. At least 8 days of data collection were achieved every month, translating into a total of 599 sampling days over the survey period. We excluded 60 species that were represented by only one individual in any gear to avoid potential misidentification. Our analysis is based on 19,401 fish representing 245 species from 25 families, with a mean of 777 ± 546 fish per site. We produced cumulative frequency curves to determine whether enough samples were collected to reach asymptotes of observed functional entities. All curves reached saturation as evidenced by the asymptote plateaus in the number of functional entities (unique combinations of traits), suggesting that our sampling for each gear was adequate (Fig. 2).

We assessed functional selectivity of seven fishing gears: hook and line, speargun, gillnet, beach seine, basket trap, and escape slot trap (modified basket traps that allows juveniles and narrow-bodied species to escape through a gap). Apart from gillnet and beach seine, artisanal fishers use a variety of other nets, such as ringnets, scoop nets, cast nets, and mosquito nets; we therefore include a separate gear category of other nets. Gillnets and beach seines were separated from ‘other nets’ because they are more frequently used.

Associations of gears with traits

Fish species were assigned to a set of categorical trait values relating to their diet, body-size, mobility, time of activity, schooling behaviour, and position in the water column (Table S1). These ecological traits are thought to be important for determining trophic role and have been used in other studies examining functional diversity, vulnerability, and redundancy of fish assemblages in tropical ecosystems (Micheli *et al.* 2014; Mouillot *et al.* 2014). While we use ecological traits to calculate these widely used metrics, we acknowledge uncertainties regarding specific links to ecosystem function and the need for more detailed ecological studies to refine such approaches in the future (Bellwood *et al.* 2018). Each unique combination of these six traits is considered a distinct functional entity (which may be comprised of one or more species) (Mouillot *et al.* 2014). Of the 245 species sampled, we derived 163 unique functional entities (FEs).

Associations between traits and fishing gears were examined using Principal Component Analysis (PCA) based on the fourth root transformation of Wisconsin double standardized abundance data (sum of all species). In this standardization, the fourth root of each element is calculated after each element is divided by its column maximum and then divided by the row total. This standardization is recommended for ordination of species data that exhibit substantial differences in sample sizes across sampling units (Legendre & Gallagher 2001). A permutational multivariate analysis of variance (PERMANOVA, Anderson 2001) on trait categories (i.e., the category within each trait, such as size class) was performed to examine the overall trait structure between the six traits. Differences in trait categories across gear types for each of the six traits were determined using six separate PERMANOVA tests. These analyses were based on Euclidean distances on fourth root transformation of Wisconsin double standardized abundance data for each trait category (n = 999 permutations). Pairwise comparisons between trait categories were carried out to determine differences in trait categories within the six traits. All pair-wise comparisons were carried out at the site level based on unrestricted permutation of raw data to allow for a sufficient number of unique permutations (>258) to be tested.

Functional structure

A trait-based ordination analysis was used to describe variation in fish assemblage trait structure among gear types. To build a multidimensional trait space (Mouillot *et al.* 2013), we performed a Principal Coordinates Analysis (PCoA) using a FEs x traits matrix. FEs coordinates on the first four principal axes of this PCoA were used to construct a synthetic multidimensional ordination based on pairwise Gower's distances between functional entities (Legendre & Legendre 2012) (Fig. 3). Gower's distances allows mixing of different types of variables while giving them equal weight (Legendre & Legendre 1998). A square root correction for negative eigenvalues was applied for Euclidean representation of distance relationships among entities in order to avoid biased estimations of distances (Legendre & Legendre 2012). Although there is no rule to choose *a priori* the number of dimensions, spaces with higher dimensionality (i.e., with at least four dimensions) provide the best assessment of diversity (Maire *et al.* 2015). We therefore selected *a posteriori* the first four dimensions of the ordination, keeping a manageable number that reduced computing time and allowed graphical representation. The third and fourth PCoA axes are presented as Fig. S1.

Associations of gears with assemblage functioning

In describing how gears affect assemblage trait functioning, we utilised three indices: functional volume (FV), functional redundancy (FR) and rarely targeted functional entities (RFEs) (Mouillot *et al.* 2014). We define FV for each gear as the proportion of the functional space the gear occupies relative to that of all fish caught (Villéger, Mason & Mouillot 2008). Functional redundancy (FR) is the mean number of individuals per functional entity. Others have used functional originality as a proxy of functional redundancy (Buisson *et al.* 2013; Brandl *et al.* 2016). Here, we found a strong correlation between mean values of functional originality and mean number of individuals per functional entity ($r = 0.95$, $n = 7$, $p < 0.001$) (SI). The RFE index is expressed as the proportion of FEs that constitute less than 1% of catch (total number of individuals) within a gear. With n_p being the relative abundance of a functional entity in a gear, we express RFEs as the following ratio:

$$n_p = \frac{n_i}{N_g}$$

$$RFEs = \frac{FE - \sum_{i=1}^{FE} \min(n_p - 1,\ 1)}{FE}$$

N_g denotes the total number of individuals in a gear, *FE* the total number of functional entities, and n_i the number of individuals in a functional entity *i* (Mouillot *et al.* 2014). We also compute the number of unique FEs targeted by the different gear types.

In examining the distribution of catch by FEs, we found a very long tail i.e., although each gear type caught dozens of FEs, the majority of the catch was typically comprised of only a few functional entities. Consequently, we provide complementary analyses where we examine, i) the entire catch, ii) the top 75% of the catch (i.e., the FEs representing the top 75% of catch abundance), and iii) the top 50% of the catch (i.e., only the most dominant FEs).

Gear overlaps and exclusion analysis

To show the levels of overlap in trait composition among gears, we quantified the number of FEs and FV shared among gear types. Overlap in composition of FEs among gears was visualised using Venn diagrams based on all catch, 75% and 50% of catch. Because of the complexity in interpreting Venn diagrams with more than four elements, we only present numbers and proportions of overlaps from the resultant groupings. To examine the potential influence of gear restriction policies on functional diversity, we explored two sequential gear exclusion case scenarios: i) one that minimises the number of FEs harvested by one or combinations of gears regardless of overlaps across gears; and ii) one that minimises overlaps notwithstanding the number of FEs targeted by a combination of two gears or more. All values of FV are computed from the first four dimensions of the ordination.

Robustness analysis

To determine whether our results are robust to the number and choice of traits, we reran all analyses using all combinations of five traits out of six. We avoided reducing the number of traits lower than five so as to retain important dimensions of the functional space defining fish niches (Mouillot *et al.* 2013). As such, an over simplistic definition of FEs was avoided. We further performed a crude categorization potentially inducing high functional redundancy (many species in each FE) whereas a fine categorization would lead to few species in each FE (Mouillot *et al.* 2014). For, example, instead of using all six categories on body size, we reran the analysis testing the association between gears and three size categories (SI). In this analysis, we reduced the number of categories for each trait and re-ran all analyses with 64 FEs (crude categorization) instead of 163 (fine categorization). To show the robustness of our findings, we present the distribution of FEs contained in the entire catch, in addition to the number of FEs and species in 50, 75, and 99% of the catch considering the reduced number of FEs (163 – 64) for each gear (SI). We also show the proportion of RFEs and levels of FR (SI).

Simulated random assignment models

We tested whether the observed values of RFEs were significantly different from the null hypothesis that individuals are randomly distributed into FEs. In each of the seven gears, we simulated a random assignment of individuals to FEs while ensuring that each functional entity had at least one individual. We simulated 999 random assemblages for each gear, and, for each simulation, we computed rarely targeted FEs while the number of individuals and the number of FEs were kept constant. All calculation of indices and statistical analyses were performed with R statistical software (R Development Core Team, 2018) using packages *cluster, ade4, stats,* and *vegan.* PERMANOVA tests were performed using the function *‘adonis’* implemented in the R package vegan. Graphical representations were performed with R and Sigma plot version 11.

Results

Trait composition in landed catch

The majority of the fished assemblages were benthic species, species active during the day and species actively mobile within reefs (Table S2; Fig. S2). Pelagics, species moving in pairs, and those that feed on plants, animals, or plankton were rarely caught. Fish assemblages with size ranges of 30-50 cm were disproportionately targeted whereas larger species >80 cm were least caught (Fig. S2). Overall differences in trait structure between the six traits were identified by the PERMANOVA (F = 2.71, $p<0.001$, 978 permutations) (Table S3). However, pairwise comparisons indicated differences in abundance between trait categories for diet, activity, and mobility ($P\leq 0.05$; Table S4). No differences in abundance of trait categories were detected for schooling behaviour and body size ($P>0.05$).

Associations of gears with traits

Associations between gears and traits identified in the PCA were supported by the PERMANOVA analyses with significant differences in trait composition between gears ($P\leq 0.05$; Table S3; Fig. S3; Fig. 3a). Pairwise comparisons indicate that a vast majority of categories within all six traits, except size, schooling behaviour, and mobility differed among gear types (Table S5). Basket traps and escape slot traps predominately targeted benthic herbivores/detritivores (e.g., rabbitfishes and parrotfishes) (Table S5; Fig. 3a). Sessile invertivores (e.g., wrasses and porgies) and diurnal species were largely captured by spearguns. A combination of other nets, including ring nets and cast nets, as well as hook and lines, harvested species moving in large groups and feeding on plankton (e.g., mackerels and jacks). Gillnet and beachseines were largely associated with pelagic species (e.g., mackerels and jacks).

Patterns of association between gears and traits did not change much when considering the dominant 75% of the catch compared to those of all catch (Fig. S4a). For example, spearguns and gillnets were consistently associated with diurnal species and fishes that moved between reefs, respectively (Fig. S4a). Considering 50% of the catch, all types of nets (i.e., gillnets, beachseines and other nets) exhibited substantial similarities in trait composition. Substantial deviations in trait composition were observed between hook and line and spearguns (Fig. S4b). Considering the dominant 75 or 50% of the catch, other nets were consistently associated with pelagics (Fig. S4 a & b). There was no statistically significant difference in traits composition among gear types when considering only 50% ($P = 0.18$) and 75% of catch ($P = 0.77$).

Functional diversity

We detected substantial variability in the number of FEs (functional diversity) targeted by gear types, ranging from 86 for spearguns to 57 for hook and line (Fig. 4). Distribution of individuals among FEs was largely skewed with a few FEs containing a large number of individuals, while the majority of FEs contained relatively few (Fig. 4). Having shown that abundance was heavily packed in few FEs across all gear types, we decided to compare functional diversity in the dominant catch, i.e., 75% and 50% of the total catch in each gear. Here, we show that escape slot traps hosted the fewest FEs in 50% (2 FEs; six species) and 75% of catch (6 FEs; 31 species) (Fig. 5). The proportion of RFEs ranged between 11.9% for gillnets and 25% for basket traps, and observed values were all significantly higher than expected when abundance was randomly assigned to FEs (Fig. 4; Fig. S4b). Functional redundancy, i.e. mean number of individuals per functional entity, ranged between 39.3 in escape slot traps to 16.3 in gillnets (Fig. 4) with a species-functional entity gradient between 1.41 for escape slot traps to 0.87 for spearguns. This means that on average an escape slot trap fisher had to catch about 40 fish individuals in order to remove one additional functional entity from the ecosystem. In contrast, an additional functional entity was harvested when 16-18 fish individuals were captured by fishers using beachseines, gillnets, or spearguns.

Functional space and assemblage functioning

The distribution of traits in the functional space showed that social grouping broadly changed from left to right along the first axis of the PCoA, whereas fish body-size and mobility increased from top to bottom along the second axis of the PCoA (Fig. 5). Herbivores, detritivores and omnivores, typically associated closely with the benthos, were positioned top-left in the functional space; sedentary, territorial and macroalgal herbivores were positioned middle right; pairing invertivores targeting sessile invertebrates typically active during the day were positioned to the top right; invertivores targeting mobile invertebrates typically mobile within the reef in the top-right; planktivores in the middle-right; and larger carnivores that were largely pelagic and typically mobile across reefs were located in the bottom-left. The first four dimensions of the PCoA cumulatively explained 47.5% of the projected inertia in the distribution of fish species traits (first two independent axes accounted for 29.7% of the variance). Explained variances were not more than 17% per axis (Fig 5).

Nets in general (i.e. gillnets, beachseines, and other nets) filled more functional space (44.6-50.7%), but did so targeting relatively fewer species (71-77 species) and FEs (59–64) than many of the other gear types. For example, spearguns targeted 86 FEs comprised of 113 species, but only filled 34.3% of the FV. Similarly, hook and line targeted a slightly greater number of species than nets (75 and 57, respectively), but occupied a much smaller FV (28.2%). Trends in functional spaces occupied by the different gear types in the first two dimensions of the ordination were mirrored in the third and fourth PCoA axes (Fig. 5; Fig. S1).

RFEs in basket traps and spearguns affected a larger proportion of assemblage functioning (48.8 – 55%). Only escape slot traps removed less than 20% of the total FV (assemblage functioning) from the RFEs (Table 1). Spearguns had the highest number of unique FEs (12) affecting 49.2% of the FV. Other gears caught between one (other nets) and eight (basket traps) unique FEs, potentially affecting up to 38% of assemblage functioning. Unique FEs associated with nets, such as gillnets and other nets, occupied the least FV (<4%) (Table 1).

Gear overlaps, exclusion and functional optimization analyses

Gear overlap harvested 19 FEs, representing 12% of the functional diversity (i.e., the total number of FEs) in this fishery (Fig. 3a). This shared component included 45 out of 245 species, representing an 18% overlap among gear types. This gear overlap represented 47.3% of the total FV targeted by fishing. There was substantial similarity in traits captured by fishing gears whose mode of operation and fishing grounds were related, e.g., basket traps and escape slot traps (64% similarity); gillnet and other nets (53% similarity) (Fig. 3a). Despite a reduction of two FEs (19 vs. 17) when considering 75% of the catch, the total FV of the shared catch component remained the same (Fig. S4a). The 17 out of 29 FEs shared across all gears represents a 59% overlap. Of the 63 species present in 75% of the catch, 42 were shared across all gear types, representing a 67% overlap. When considering 50% of the catch, all gears together shared nine out of 11 FEs, representing 82% overlap (Fig. S4c). This catch component included 29 out of 31 species and affected 30% of assemblage functioning.

Functional diversity (number of FEs) in the landed catch decreased when one or combinations of gears were excluded from the analysis (Fig. 3b). However, the levels of overlap across gears increased when one or combinations of gears were excluded from the analysis (Fig. 3c). For example, about 157 (±2.3) FEs on average were captured when one gear was excluded from the fishery, representing a 3.9% decrease in functions removed from the ecosystem relative to all gear types (Fig. 3b). As more gears were excluded from the fishery, the number of FEs conserved (i.e. not removed from the ecosystem) gradually increased from 9.3 (2 gears removed) to 58 (6 gears removed)% (Fig. 3b). Conversely, the number of shared FEs gradually increased from 12.6% to 37.4% when combinations of two to five gears were excluded from the fishery (Fig. 3c). The number of FEs harvested by various combinations of six gears (i.e., random removal of one gear), notwithstanding overlaps, were lowest when spearguns were excluded (Fig. 3b). In order to sequentially conserve the optimal number of fish functions by removing more than one gear, the other gears to be excluded were basket traps, escape slot traps, hook and lines, and gillnets in that order (Fig. 3b). When considering a sequence of gear exclusion that minimizes the number of shared FEs (overlaps), a totally different trend emerged. Other nets were the first candidates, followed by basket traps, beachseines, gillnets, and spearguns (Fig. 3c).

Robustness analysis

Using the crude functional categorisations, the level of RFEs was surprisingly close to that observed with a much finer categorization (Fig. S5 & S6). The observed distribution of abundance between FEs was more right skewed than expected, with a long tail with few individuals (Fig. S6). Overall, our sensitivity analyses showed the consistent and uneven distribution of some FEs, regardless of the number, identity, or categorization of traits. We also reran all analyses with all combinations of five traits out of six (Fig. S5). Whatever the combination, all patterns were still close to those observed with six traits (Fig. S5).

Discussion

Fished assemblages in this fishery were characterized by high capture of multiple functional groups (e.g., rabbitfishes, parrotfishes, and emperors). However, a vast majority of the catch was dominated by a few FEs overlapping across all gears to make up the largest proportion of the catch. The breadth of functional diversity represented by unique and RFEs varied greatly among gears. This indicates that differences in gear selectivity along with specific impacts of fishing are driven by depauperate FEs represented by species that are opportunistically caught. Findings highlight the need to manage fishing of rare taxa with potentially important ecological functions because overfishing these species could alter ecosystem functioning.

On average, one gear has the potential to affect at least 43% of functional diversity in the overall catch landed. Importantly, most of the catch for each gear is represented by very few dominant FEs. Our study presents the first empirical evidence that shows that beyond the number of species (Mouillot *et al.* 2014), abundance also packs into a few FEs. Gears that are less selective, such as gillnets and beachseines, targeted the greatest breadth of functional diversity. This was not surprising because nets in general target a larger portion of the water column and habitat, thus increasing the likelihood of catching many species and high functional diversity. Gillnets and beachseines also seem to catch FEs in more even proportions. Besides differences in selectivity in terms of functional diversity, there were differences in the actual level of catch among gear types. The very few FEs that dominated the landings, however, occupy less functional volume - at least for some gears such as traps and hook and lines. This means that gears that are more selective, such as escape slot traps and hook and lines, rarely captured species that are functionally diverse. Our results indicate that these more selective gear types target a narrow range of ecosystem functions (Murawski 2000).

Only two gears, spearguns and other nets, exert strong trait specialization in this fishery. Spearguns specialised on diurnal and sedentary/territorial species that feed on plankton. Spearguns disproportionately caught species that move in pairs (e.g., butterflyfishes) and diurnal invertivores that feed on sessile invertebrates (Kruer & Causey 2005). Differences in selectivity between gears show that other nets disproportionately targeted pelagic species (e.g., bonitos) because nets (e.g., ring nets) are often used further offshore – habitats that are typically associated with pelagic fishes (Fock, Pusch & Ehrich 2004). Basket traps targeted more herbivorous detritivores than hook and lines because trap fishers in Kenya use a mixture of plants and animals (seagrass, algae, crushed sea urchins, brittle stars and molluscs) as bait (Mbaru & McClanahan 2013). In sum, physical and operational differences, in addition to behavioural activity among species can provide clear insights into the differences in gear selectivity on coral reef fishes.

The identification of unique and rarely targeted traits or their combinations can have significant fisheries management implications. Unique or rarely targeted species in fished assemblages occupied a higher proportion of functional volume, even for some selective gears such as hook and lines and spearguns. In heavily exploited areas, depauperate functional entities can be represented by few opportunistic and tolerant fish species in the community (Mouillot *et al.* 2014). Previous ecological investigations on in-situ fish data show that rare species tend to represent a high level of functional diversity within communities (Micheli *et al.* 2014). These findings suggest that functional volume removed by unique functional entities and rarely targeted functional entities can significantly amplify the effect of specific fishing gears on ecosystem functioning. Future management priorities should include monitoring of gears such as hook and lines that are traditionally assumed to be selective, especially on the type and size of hooks used.

Previous studies show that species diversity, functional diversity, and assemblage functioning are intricately linked (Villéger, Mason & Mouillot 2008; Mouillot *et al.* 2013). Here, we show that these relationships in fished assemblages are not linear. For example, we show that beachseines captured slightly fewer species than other nets, yet had more FEs that occupied slightly less FV. Fish assemblages in escape slot traps had the third highest number of species, yet had the most redundant FEs and occupied the lowest FV compared to all gear types. This implies that capturing a high species diversity for some gears may not strongly contribute to loss of ecosystem functioning (Wackernagel & Rees 1998; Murawski 2000; Cumming, Cumming & Redman 2006). The number of species, FEs and FV was lower in escape slots compared to basket traps. The inclusion of escape slots in basket traps therefore has the potential to increase selectivity in traps.

The overrepresentation of functional groups associated with benthic-attached species is consistent with the role played by tropical coral reefs in supporting demersal fish diversity (Micheli & Halpern 2005). This is not surprising because a majority of the gears analysed here are associated with the bottom habitat (McClanahan & Mangi 2004). Because a vast majority of demersal species do not often share common traits (Elleouet *et al.* 2014), this perhaps explains why the landings are characterized by a high capture of multiple functional groups. Our catch data contained few pelagics, macroalgae feeders, and large body sized fish moving in pairs. Given the high fishing intensity in Kenya (Hicks & McClanahan 2012; McClanahan 2018), low prevalence of functional redundancy in trait combinations is likely a result of low abundance and diversity, and hence availability for capture. Specifically, it is highly likely that the low prevalence of herbivorous fishes and large body sized fish is due to chronic overfishing. However, the low prevalence of ecological traits associated with the pelagic environment is likely because only a small proportion of fishers use fishing techniques that target pelagic stocks in Kenya (Mbaru 2012).

The extent of overlap suggests that all gears together can affect >47% of the total breadth of functional diversity targeted. This is not surprising because the mode of operation of the fishing gears analysed and fishing grounds are related to traits of the catches, like type of movement, predation, or habitat (McClanahan & Cinner 2008). There is hardly any change in FV among shared FEs in 75% of the catch (47 vs 48.4%). Proportions of shared FEs increase substantially when considering the dominant 50% of the catch suggesting that >80% of FEs can potentially be harvested by just one gear. This shared component however affects only 27% of the total FV – emphasizing the point that the differences between fishing gears is primarily from the non-dominant part of the catch.

To minimize the number of overlapping FEs based on all catch, we developed a sequential gear exclusion process. Other nets were the first candidate gear to exclude, followed by basket traps, beachseines, gillnets, and spearguns. However, given the extent of overlap in functional diversity, we show that even just using two gears (i.e., excluding five gears) still targets >60% of total FV. These findings indicate that the risk of targeting certain fish functions is not necessarily or substantially reduced when one or more gears are excluded from the fishery. Thus, initiatives to reduce overall effort should reduce pressure on important trait combinations.

Conclusion

Multi-species, multi-gear small-scale fisheries are common in coral reef ecosystems around the globe (McClanahan & Mangi 2004; Cinner *et al.* 2009). This study is the first attempt to connect traits to catches of fishing gears in multispecies coral reef fisheries and provide insights on how fishing can modify ecosystem biodiversity in tropical regions. Key findings unveiled here could shape future assessments of the ecological implications of fishing in multi-gear and multi-species fisheries. Across all gears, the distribution of individuals across FEs is largely skewed, with the majority of the catch comprising relatively few FEs. Although there was over-redundancy in the few functional entities in the dominant portion of the catch, the low redundancy in the long-tail of FEs removed by fishing can potentially affect ecosystem functioning. We show that gear selectivity in coral reef fisheries is primarily due to unique, and rarely targeted species. Considering fished assemblages as one monolithic catch component can be a weak indicator of differences in gear selectivity. The addition of a traits approach to standard analyses could provide a concrete foundation for the formulation of the Ecosystem Approach to Fisheries Management in tropical multispecies fisheries.

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Author Contributions

E.K.M, N.A.G, J.E.C conceived the idea and designed the methodology. T.R.M provided the data. E.K.M analysed the data and led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for the publication.

Data Accessibility

All data from the manuscript will be made publicly available on the Knowledge Network for Biocomplexity.

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Tables

Table 1. Number of functional entities, species (in parenthesis), and functional volume (FV) in unique and rarely targeted functional entities (RFEs) for each gear. FV is expressed as a percentage of volume occupied by all fish caught.

	Unique FEs		**Rarely targeted FEs**	
Fishing gear	No. FEs(species)	% Functional volume	No. FEs(species)	% Functional volume
Escape slot trap	6(6)	16	6(6)	19.9
Basket trap	8(9)	37.9	13(13)	48.8
Hook and line	7(7)	21.5	8(8)	39.2
Speargun	12(12)	49.2	11(12)	55
Gillnet	3(4)	3.6	7(7)	22.2
Beachseine	7(9)	20.1	10(10)	53.2
Other nets	1(1)	-	7(7)	32.5

Figures

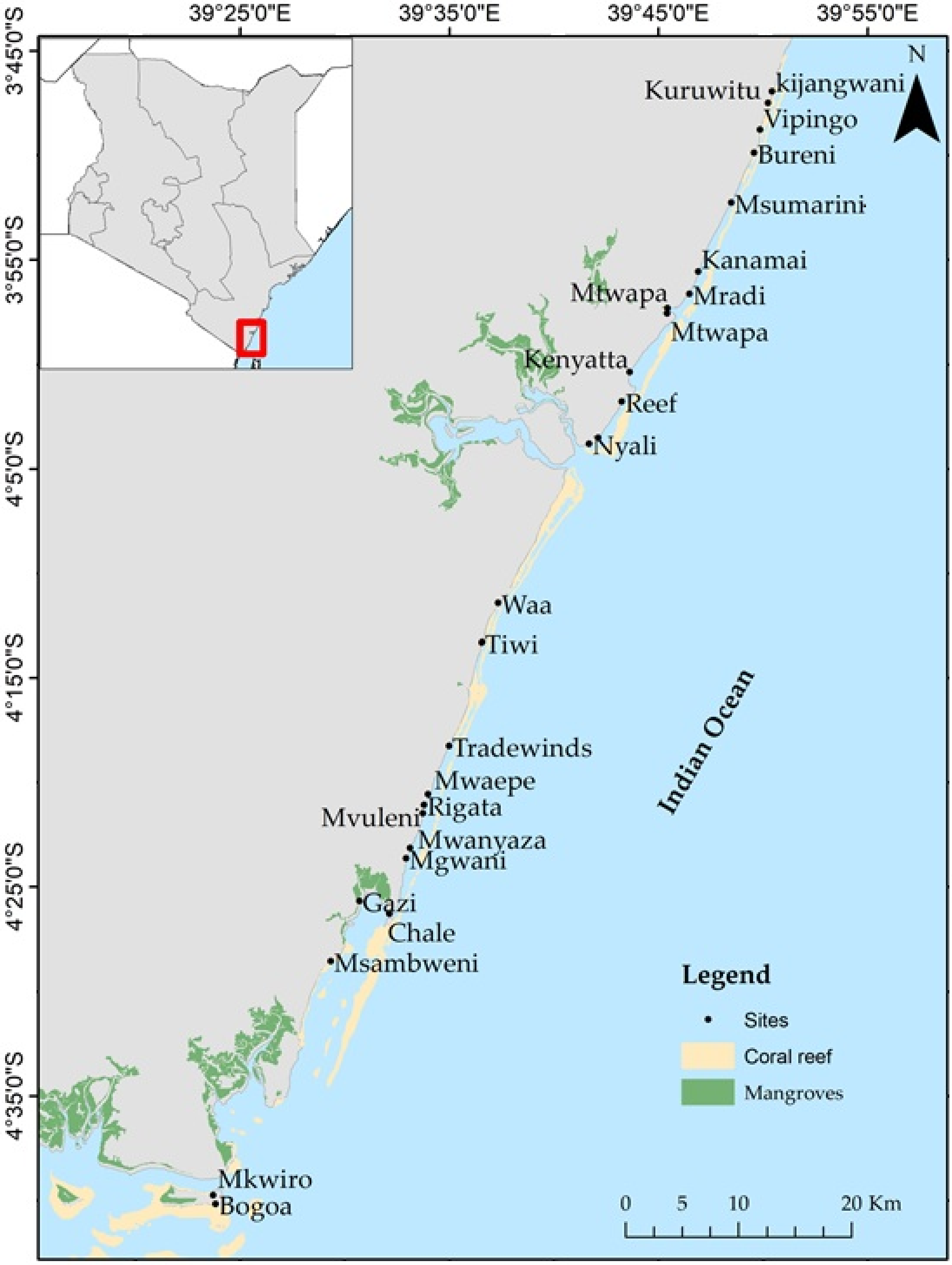


Fig. 1. Map of sampling sites

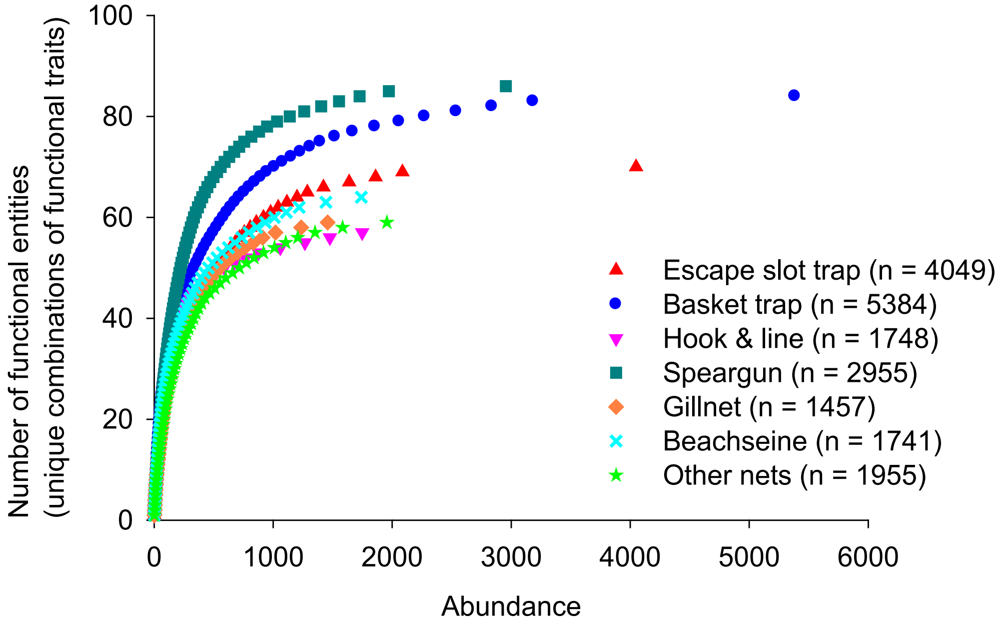
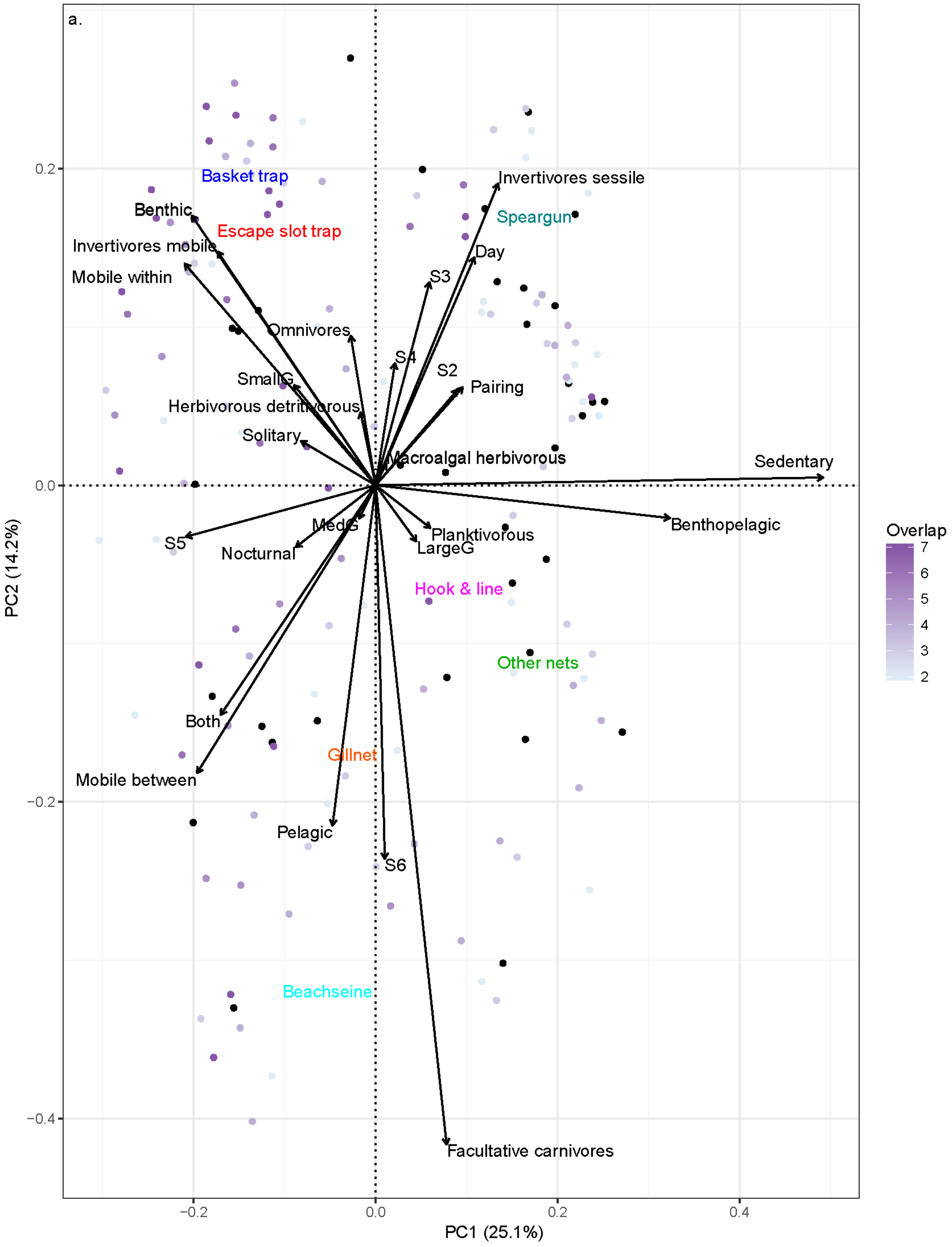


Fig. 2. Cumulative frequency curves of the number of functional entities (i.e., unique combinations of traits) present in sampled fish assemblages per gear. Sample sizes are displayed in parenthesis.


a.
Basket trap
Benthic
Escape slot trap
Invertivores mobile
Mobile within
Invertivores sessile
Speargun
Day
S3
Omnivores
S4
S2
Pairing
SmallG
Herbivorous detritivorous
Solitary
Macroalgal herbivorous
Sedentary
Benthopelagic
MedG
Planktivorous
LargeG
S5
Nocturnal
Hook & line
Other nets
Both
Gillnet
Mobile between
Pelagic
S6
Beachseine
Facultative carnivores
Overlap
7
6
5
4
3
2
PC2 (14.2%)
0.2
0.0
−0.2
−0.4
PC1 (25.1%)
−0.2
0.0
0.2
0.4

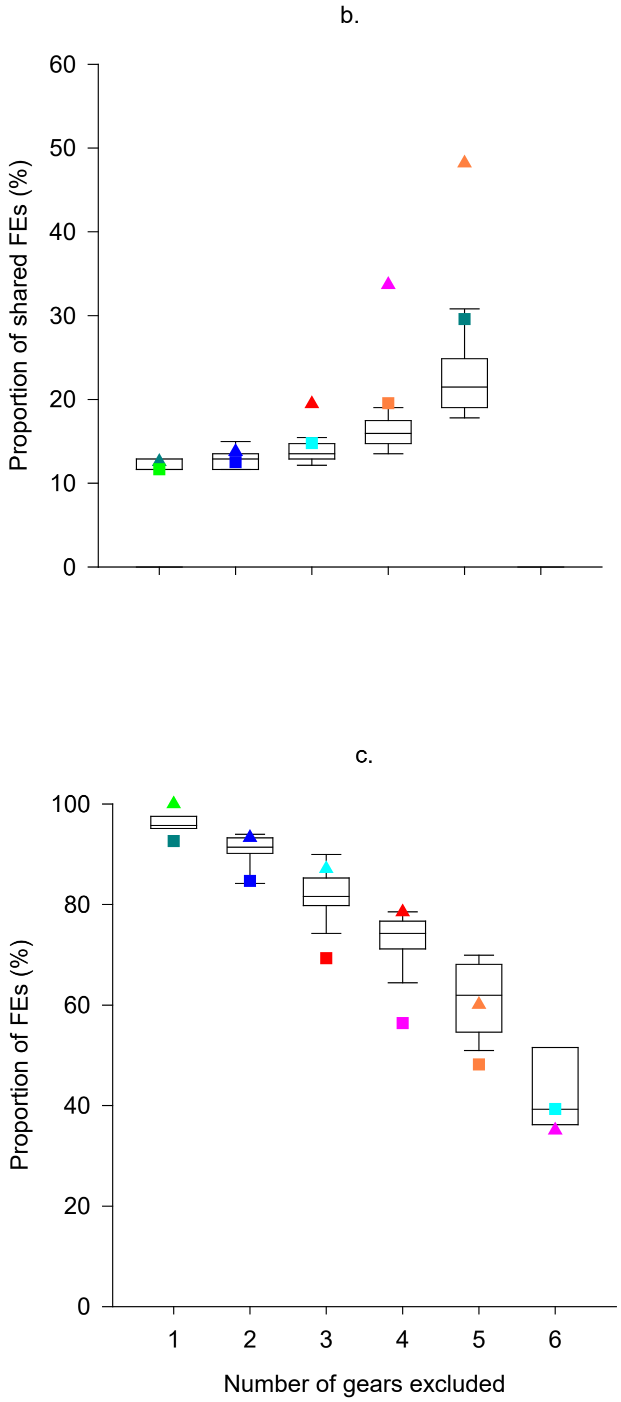
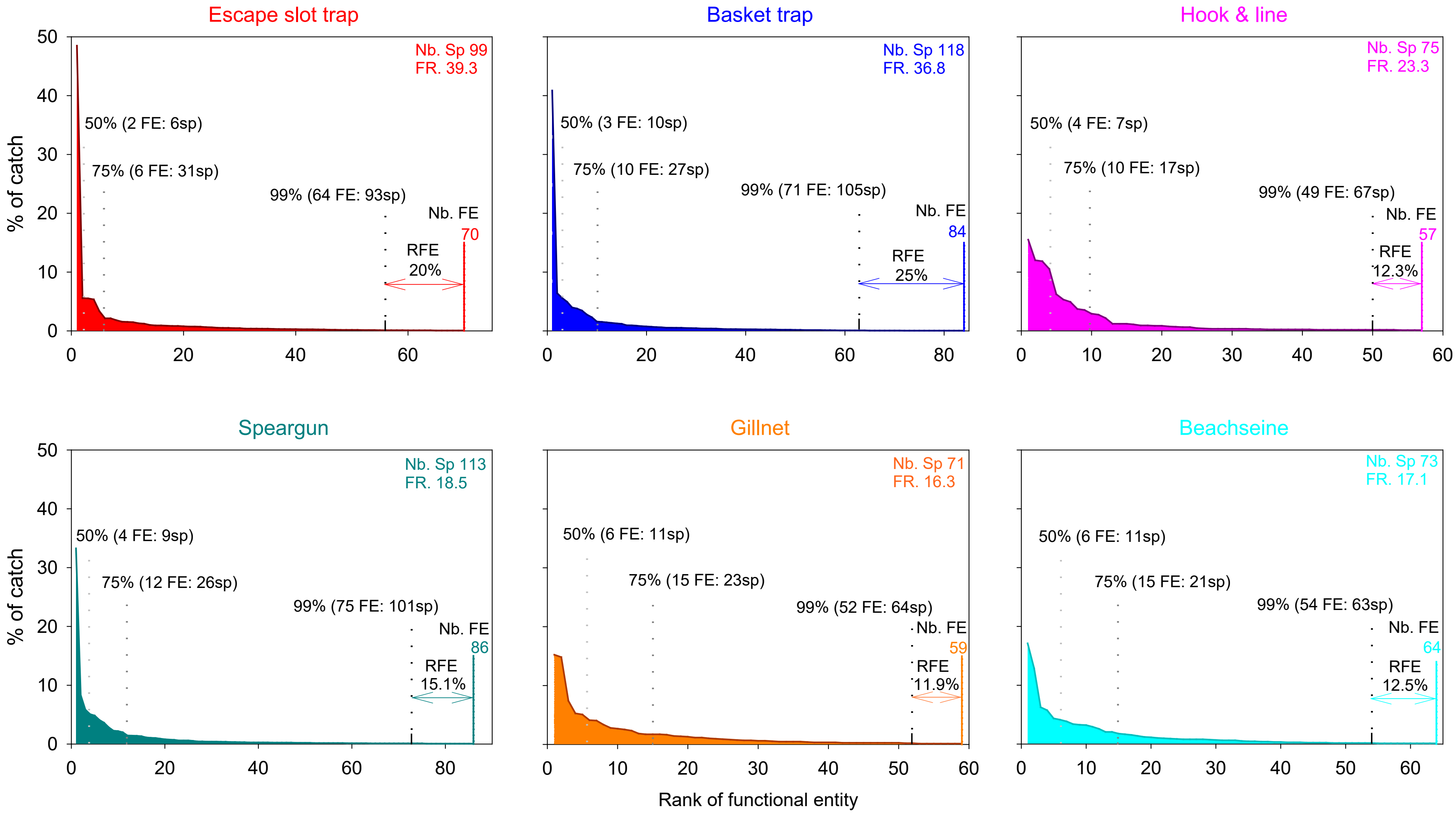


Fig. 3. (a). Principal component analysis of functional entities (FEs) contained in the entire catch (n=163). Coloured dots represent FEs captured by the seven gear types analysed. Colour gradient represents FEs shared across a range of gear combinations. Black dots represent unique FEs targeted by a single gear. LargeG (>50 individuals), MedG (20-50 individuals), and SmallG (3-20 individuals) indicate

schooling behaviour. Fish size is coded using six categories: 7.1-15 cm (S2), 15.1-30 cm (S3), 30.1-50 cm (S4), 50.1-80 cm (S5), and >80 cm (S6). ‘Both’ denotes species active during the day and night. (b). Proportion of FEs targeted when one or a combination of gears are excluded from the analysis (box plot). Coloured squares denote the minimum number of FEs targeted by one or a combination of gears. Coloured triangles denote the number of FEs targeted by one or a combination of gears when the number of shared FEs (overlaps) is minimized. (c). Box plot shows the proportional distribution of shared FEs for each number of gear removal. Coloured squares show the lowest proportions of shared FEs when the number of overlapping FEs is minimized on the gear exclusion process. Coloured triangles depict the lowest proportions of shared FEs when the number of FEs targeted is minimized. Minimum values of targeted and shared FEs were based on all possible permutations of in the gear exclusion process. Colour codes represent gears as in Fig 2.


Escape slot trap
Nb. Sp 99
FR. 39.3
50% (2 FE: 6sp)
75% (6 FE: 31sp)
99% (64 FE: 93sp)
Nb. FE
70
RFE
20%
Basket trap
Nb. Sp 118
FR. 36.8
50% (3 FE: 10sp)
75% (10 FE: 27sp)
99% (71 FE: 105sp)
Nb. FE
84
RFE
25%
Hook & line
Nb. Sp 75
FR. 23.3
50% (4 FE: 7sp)
75% (10 FE: 17sp)
99% (49 FE: 67sp)
Nb. FE
57
RFE
12.3%
Speargun
Nb. Sp 113
FR. 18.5
50% (4 FE: 9sp)
75% (12 FE: 26sp)
99% (75 FE: 101sp)
Nb. FE
86
RFE
15.1%
Gillnet
Nb. Sp 71
FR. 16.3
50% (6 FE: 11sp)
75% (15 FE: 23sp)
99% (52 FE: 64sp)
Nb. FE
59
RFE
11.9%
Beachseine
Nb. Sp 73
FR. 17.1
50% (6 FE: 11sp)
75% (15 FE: 21sp)
99% (54 FE: 63sp)
Nb. FE
64
RFE
12.5%
% of catch
0
10
20
30
40
50
Rank of functional entity
0
20
40
60
80
0
10
20
30
40
50
60

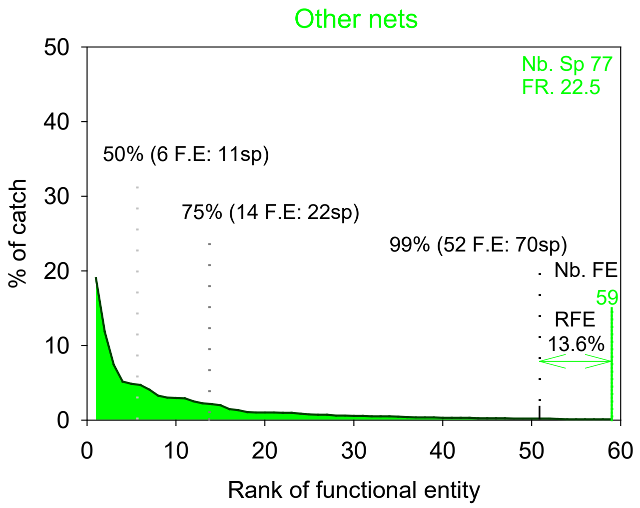


Fig. 4. The distribution of fish individuals into functional entities (FEs) is displayed for each gear type. The number of functional entities ("Nb FE.") present in each gear is shown at the bottom right of the distribution. Functional redundancy (FR) (i.e., the mean number of individuals per functional entity) and number of species are displayed at far right top corner. The light grey dashed line illustrates number of FEs contained in 50% of catch. The grey dashed line illustrates number of FEs contained in 75% of catch while the black dashed line illustrates number of FEs contained in 99% of catch. Rarely targeted functional entities (RFE) i.e., functional entities contained in 1% of total number of individuals captured in each gear is illustrated in double arrows displayed at far right bottom corner.

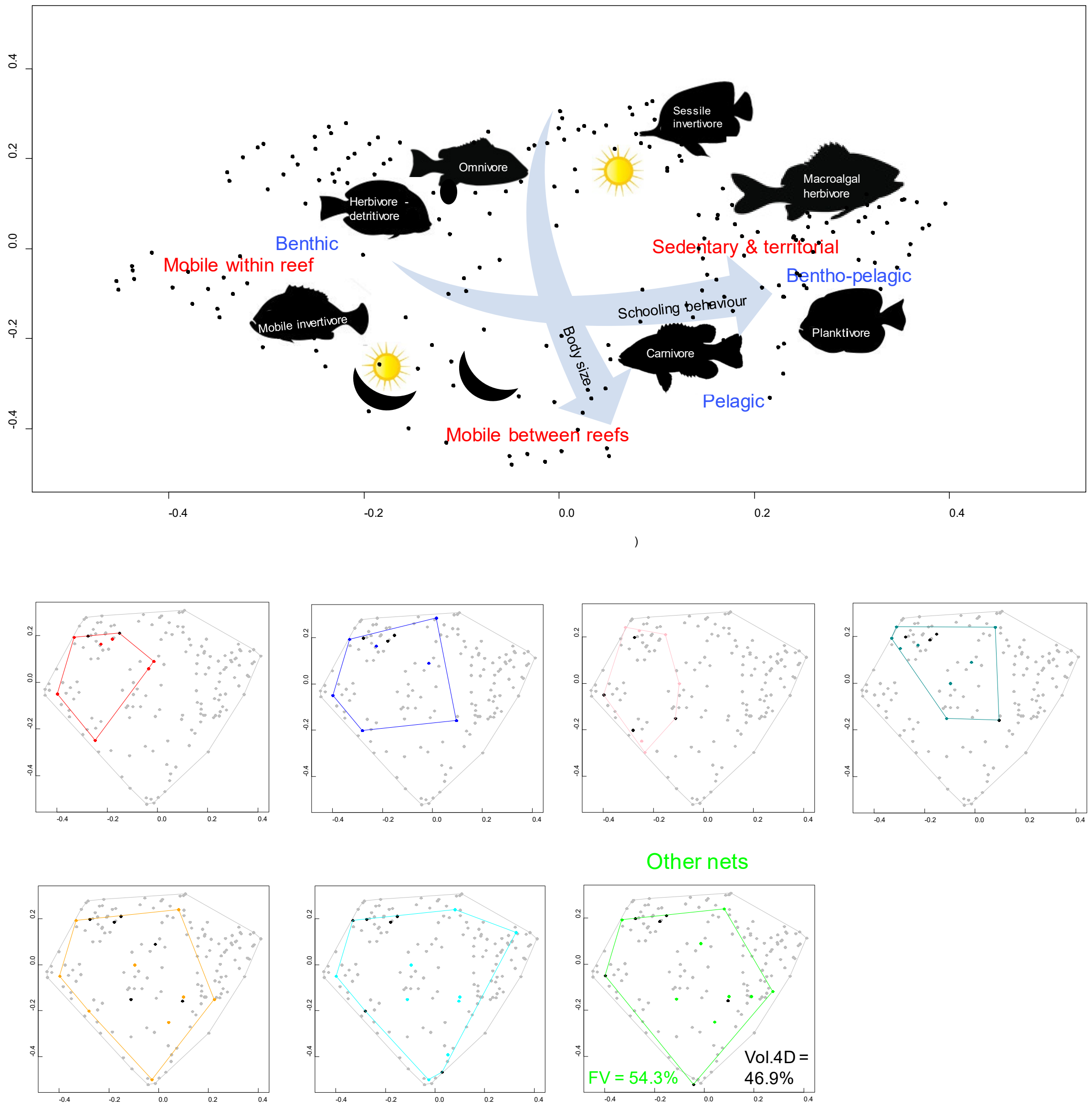


Fig. 5. Distribution of functional entities is shown in functional space from a Principal Coordinate Analysis on traits based on all catch. 163 computed functional entities (black dots) plotted in the first two dimensions (four total) of functional space defined by six traits: body size (arrow indicating increasing body length), diet; mobility (red text); time of activity (sun and moon); social grouping (arrow indicating increasing size of fish school); and position in the water column (blue text). Illustrations and text show the position of average trait levels in the functional space. Distribution of functional entities is shown in functional spaces for each gear from a Principal

Coordinate Analysis on traits (bottom convex hulls). Colour filled points are FEs present in the catch of each gear while grey filled points are FEs absent in the 75% catch of each gear. The total convex hull, including the 245 species split into 163 FEs, is enclosed by grey continuous lines joining vertices of the convex hull that shape edges. Continuous coloured lines outline the FV (FV) determined by coloured points representing the most abundant FEs comprising 75% of the catch for each gear. Coloured text in the bottom convex hulls show FV for the first two dimensions whereas black text indicate FV considering all four dimensions. FV is expressed as a percentage relative to all fish caught. Black points are FEs representing the most abundant FEs comprising 50% of the catch for each gear.