Ecological indicators for coral reef fisheries management

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- Using ecological indicators to assess coral reef fisheries
- Building blocks for coral reef fisheries management: exploring ecological indicators

Authors: Kirsty L. Nash[1,2*] and Nicholas A. J. Graham[1,3]

[1]ARC Centre of Excellence for Coral Reef Studies, James Cook University, Townsville, QLD, 4811, Australia

[2] Centre for Marine Socioecology, Institute for Marine and Antarctic Studies, University of Tasmania, Hobart, TAS 7000, Australia

[3]Lancaster Environment Centre, Lancaster University, Lancaster, LA1 4YQ, UK

*Corresponding author: Kirsty Nash, Tel: +61 439783383, Email: nashkirsty@gmail.com

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Abstract

Coral reef fisheries are of great importance both economically and for food security, but many reefs are showing evidence of overfishing, with significant ecosystem-level consequences for reef condition. In response, ecological indicators have been developed to assess the state of reef fisheries and their broader ecosystem-level impacts. To date, use of fisheries indicators for coral reefs has been rather piecemeal, with no overarching understanding of their performance with respect to highlighting fishing effects. Here we provide a review of multi-species fishery-independent indicators used to evaluate fishing impacts on coral reefs. We investigate the consistency with which indicators highlight fishing effects on coral reefs. We then address questions of statistical power and uncertainty, type of fishing gradient, scale of analysis, the influence of other variables, and the need for more work to set reference points for empirical, fisheries-independent indicators on coral reefs. Our review provides knowledge that will help underpin the assessment of the ecological effects of fishing, offering essential support for the development and implementation of coral reef fisheries management plans.

Keywords: artisanal fisheries, ecosystem function, indicator selection, reference points, sensitivity, specificity.

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Introduction

Fisheries management and data-poor fisheries

Fisheries management is underpinned by knowledge of the state of fisheries resources. There has been a progressive shift in the type of information desired by management from population-level stock assessments to ecosystem-based approaches that encompass system-wide interactions and effects (Travis et al., 2014, Thrush and Dayton, 2010). This shift has driven the development of metrics of different aspects of the fish community and the wider ecosystem that are likely to be impacted by fishing (e.g. those reviewed in Rochet and Trenkel, 2003). These metrics are used as indicators (the term we use hereafter) to support fisheries management, by integrating them with information on pressures affecting the system and management responses (FAO, 1999, Rogers and Greenaway, 2005). This provides a framework for monitoring the state of an ecosystem and evaluating progress in achieving management objectives (Jennings, 2005), where management objectives are measureable targets that represent the 'desired' state of a system (Sainsbury et al., 2000). The process of setting targets and other reference points (e.g. limits to be avoided) for ecological indicators is complex, requiring an understanding of trade-offs between factors such as yields, sustainability and ecosystem health (Mardle and Pascoe, 2002, Jennings and Dulvy, 2005). Nonetheless, there is an emerging literature on approaches to support this process by identifying values beyond which environmental damage may be significant or hard to counteract (Rice, 2003, Martin et al., 2009). Research on indicator development and reference points has primarily been linked to data-rich fisheries (e.g. Yemane et al., 2005, Shin et al., 2012), however, there is an expanding body of work focusing on assessment of data-poor resources.

Data-poor fisheries are characterized by few or unreliable data. This lack of information may be due to either the low value of the fishery, its new or opportunistic nature, the presence of few fishers, or a lack of monitoring capacity (Smith et al., 2009). Importantly, the lack of data prevents quantitative stock modelling, and potentially gives considerable uncertainty when using proposed fishery indicators and reference points to inform management (Erisman et al., 2014). Studies to support management of data-limited fisheries have predominantly focused on temperate systems (e.g.

Caddy, 1998, Wiedenmann et al., 2013). There has been considerably less emphasis on low income, small-scale, tropical fisheries in developing nations, such as those found on coral reefs, with significant implications for the effective implementation of fisheries management in this context (Johnson et al., 2013).

Coral reef fisheries

Despite the often artisanal nature of individual coral reef fisheries, globally they are estimated to generate revenue in excess of US$5.7 billion annually, supporting 6 million fishers distributed across nearly 100 countries (Cesar et al., 2003, Teh et al., 2013), and provide a broad portfolio of ecosystem services (Hicks & Cinner 2014). Some coral reef fisheries occur in the jurisdictions of developed nations where research capacity is relatively strong, fishers often target specific species and stocks are frequently managed at the species level (e.g. coral trout fishery in Australia; Leigh et al., 2014). However, coral reefs are commonly found in developing countries, and are subject to artisanal, multispecies, multi-gear fisheries that are data-poor and not amenable to traditional single-stock management (Worm and Branch, 2012). In this context, management is expected to benefit from information derived from community-level assessments (Fulton et al., 2005, Mangi et al., 2007, McClanahan and Hicks, 2011). The tight coupling between reef fish and the benthic habitat (Bellwood et al., 2004, Graham and Nash, 2013) suggests that management efforts may meet limited success unless the broader ecosystem effects of fishing are considered (McClanahan et al., 2011, Mumby, 2014). Implementing ecosystem-based approaches to fisheries management has already proved challenging in jurisdictions with strong governance structures and research capacity (Ruckelshaus et al., 2008, Tallis et al., 2010). Implementing such approaches for coral reef fisheries in resource-poor countries, and where the high diversity reef system gives rise to complex indirect relationships (Yodzis, 2000, Clua et al., 2005), may prove particularly difficult. Nonetheless, examples do exist of ecosystem based management being implemented for coral reef systems (e.g. Raja Ampat, Tallis et al., 2010).

A diversity of approaches are being employed to improve coral reef fisheries management. Governance strategies span spatial scales from national level fisheries agencies to decentralised management operating at the local level (Cinner et al., 2012). Co-management of resources and strategies built around customary tenure are gaining increasing traction (Christie et al., 2009, Jupiter et al., 2014). A range of management controls have been implemented, including networks of no-take areas (Galal et al., 2002, Harborne et al., 2008), periodic closures (Cohen and Foale, 2013) and gear restrictions (Hicks and McClanahan, 2012, Lindfield et al., 2014). Despite these efforts, fifty-five percent of island-based coral reef fish communities are fished in an unsustainable manner (Newton et al., 2007), and a review of artisanal coral reef fishery research found that nearly 90% of studies listed overfishing as a concern (Johnson et al., 2013). A number of strategies have the potential to improve management outcomes, such as strengthening governance, developing a more nuanced understanding of the interaction between fishing, alternative livelihoods and wellbeing, and explicitly linking gear selectivity to ecosystem effects (Sadovy, 2005, Coulthard et al., 2011, Bejarano et al., 2013, Hilborn, 2007). From an ecological standpoint, management efforts are constrained by a poor understanding of cause-and-effect relationships between fishing (and other variables) and ecosystem responses, and the difficulties in prescribing ‘desirable’ states (Aswani et al., 2015, Karr et al., 2015). Thus, building knowledge of the application and utility of indicators to assess the state of the ecosystem, the effects of fishing, and to evaluate the success of management actions, is critical (Costello et al., 2012, McClanahan et al., 2015). Here we, 1) review indicators of the effects of fishing on coral reefs, and 2) discuss a range of factors that should be considered in such work.

Review approach and structure

While a number of publications have discussed the effects of fishing on coral reefs (e.g. Jennings and Polunin, 1996, Guillemot et al., 2014, Karnauskas and Babcock, 2014), there has not been a review of the expanding literature presenting indicators available to assess these effects. In our study, we address this gap by presenting a systematic review of research using fishery-independent, fish community and ecosystem indicators to assess fishing impacts on reefs. This synthesis provides an understanding of the consistency with which different indicators highlight fishing effects (for example whether there is a decline in fish biomass in response to increased fishing pressure across studies). We also explore how factors other than fishing may influence indicators.

Such knowledge is foundational to understanding the performance of indicators in different contexts (Rice, 2003). Key components of performance are the sensitivity of an indicator to fishing, for example whether it is insensitive or sensitive to the extraction of fish, and the specificity of an indicator to fishing: whether it is affected primarily by fishing or is also influenced by other factors (Houle et al., 2012). A lack of knowledge regarding sensitivity and specificity has the potential to result in misleading or erroneous interpretations from indicator trends (Rice, 2003). The risk of producing errors can be thought of using a signal detection framework: the likelihood of hits, misses, false alarms or true negatives (terms explained further in Fig. 1A; Helstrom, 1968). Knowledge of these probabilities and the relative costs of false alarms or misses will help managers to select indicators to optimise the likelihood of hits and true negatives whilst minimising the costs of errors, giving a more precautionary approach (Peterman and M'Gonigle, 1992, Piet and Rice, 2004). Before exploration of such trade-offs can occur, an important first step is building knowledge of the consistency with which indicators highlight fishing effects, as provided in our study. In this context, outcomes are characterised as consistent when the effect of fishing on an indicator is demonstrated across multiple studies, and there is homogeneity in the positive or negative change of an indicator in response to fishing. To move beyond simply characterising indicator trends, we also discuss a range of additional factors that are pertinent to the use of ecological indicators on coral reefs. Fig. 1B illustrates how this information may feed into a fisheries management framework.

We focus on fish community indicators, because, as mentioned earlier, coral reef fisheries are predominantly multispecies: reef fishers may be less selective than fishers based in other environments, and even where certain species are preferred, these are often found at lower densities than target species in temperate systems (Mangi et al., 2007). Thus, single-species management may be insufficient to address the multispecies nature of the fishery. We concentrate on fishery-independent indicators because although specific fishery-independent survey methods vary in their selectivity, for example underwater visuals surveys do not adequately account for cryptic species (Willis, 2001), it is relatively easy to identify such biases. In contrast, indicators derived from fishery-dependent information are influenced by spatio-temporal variations in gear usage, selectivity of gear, spatial behaviour of fishers, and catchability of fishes (Punt et al., 2001, Hicks and

McClanahan, 2012). These changes introduce biases that should be controlled for via comprehensive monitoring of fishing practices through time, introducing additional data collection needs that may be impractical in low-capacity, multi-gear coral reef settings (Clua et al., 2005, Starr et al., 2010, Karnauskas et al., 2011). Similarly, fishery-dependent data is often limited in providing information on broader ecosystem effects, such as benthic condition or the state of the non-target fish assemblage.

Review methodology

A comprehensive search of the ISI Web of Science database (1972-2014) was conducted using the following keywords: (coral AND reef*) AND ((fishing OR fisheries OR fishery) NEAR/5 (impact* OR gradient* OR indicator* OR pressure* OR effect*)). We used this range of search terms to address potential changes over time in the language used in peer-reviewed publications exploring fishing effects. We focused on ISI Web of Science (WoS) because it searches articles over a longer time period than other databases such as Scopus (Scopus is limited to articles published since 1995), and WoS provides more consistent search results than Google Scholar (Falagas et al., 2008). However, WoS does not encompass all peer-reviewed journals, therefore, as a second step, the reference lists of publications returned from our search of WoS were checked for other relevant studies that were not identified in the initial search (note, throughout the text we use the terms ‘studies’ and ‘publications’ interchangeably, whereas reports refer to individual results within publications).

Four hundred and twenty four studies were identified in our two part search. From this literature only those publications specifically related to fishery-independent, multi-species or community indicators of fishing effects on coral reef ecosystems were retained. Few modelling studies and studies using experimental removals of targeted species were found, therefore these studies were excluded to maximise comparability among the publications incorporated in our review. This resulted in 105 publications examining the effect of gradients in fishing pressure on fish and benthic reef communities (Table S1). Details of the type of fishing gradients studied, methods used to collect data, the indicators used to assess fishing effects, the component of the community (e.g. family, functional group or community) for which these indicators were estimated, and the methods for setting reference points, were sourced from each article. We used functional groups identified in the source publications; these groupings were based on fish diets and are therefore linked to trophic-level. Where more than one fishing gradient was studied, the gradient was classified as ‘multiple’. Where more than one indicator or community component was studied, all were recorded.

Information from 65 of these publications (Table S1), detailing data from 41 different locations, were extracted for further evaluation (hereafter termed ‘in-depth’ review) based on the following criteria: (i) the analysis provided a clear and explicit comparison between different fishing intensities; (ii) the study was spatial (data collected at multiple sites) and/or temporal (data collected over time at a site); (iii) indicators were empirical and not derived from system modelling to reduce the potential for incorrect assumptions in data-poor situations (Kelly and Codling, 2006); and (iv) research examining differences inside versus outside protected areas were included unless these studies primarily focused on recovery within the no-take areas, there was a breakdown of protection over time, or spillover from reserves was described in associated fished areas. This ensured that clear, quantified gradients or categories of fishing pressure were inherent to the retained studies.

Data were extracted on the fishery and methods used, specifically whether the fishing gradient was categorical or continuous in nature, and information on any statistical power analyses presented. The scale of the study was also noted using the categories local, regional or global. These classifications were based on the spatial extent of sites, rather than linked to the resolution of the sampling undertaken in the study. For example, a study that looked at sites spread throughout the Caribbean and a study that looked at two sites located at the northern and southern extent of the Caribbean would both be classified as regional studies. Next, the effects of fishing on the indicators were explored: where the authors specified in the study’s introduction their qualitative expectations regarding the effect of fishing on the indicators described, it was noted whether these expectations were met. Specifically, we noted whether significant indicator trends found in the analyses of fishing impacts corresponded to the authors’ expectations of indicator behaviour. For all studies, the effect of fishing (or lack thereof) on the indicators was recorded. Finally, the presentation of factors other than fishing that may have affected the indicators, were noted. Where multiple publications presented data from the same location, duplicates were excluded, with the larger or newer dataset retained.

Due to the wide range of different methodological and analytical approaches used in the studies, and low replication within these different approaches, it was not possible to provide a quantitative measure of the effect of fishing on the different indicators. Thus, qualitative scales are presented: the impact of fishing on the indicator was classified as ‘decrease’, ‘no change’, ‘mixed’, ‘ increase’ or ‘shift’ based on the relationships described in the original publications. Where a single study described either consistent declines or a mix of declines and no change for a specific indicator, the effect of fishing on that indicator was classified as ‘decrease’. ‘Mixed’ indicated studies that presented both increases and declines for an indicator across a fishing gradient. Where a single study described either consistent increases or a mix of increases and no change for a specific indicator, the effect of fishing was classified as ‘increase’. ‘Shift’ was used for indicators such as fish community composition, where changes occurred in response to variations in fishing pressure but there was no clear negative and positive direction.

Fisheries indicators on coral reefs

Since 1989, there has been a steady growth in the number of publications documenting indicators of fishing effects on reefs (Fig. 2A); no research was found prior to 1989, whereas, 60 studies have been published in the last decade. This growth in research may be an artefact of changing terminology over time such that our search terms were not capturing early studies, however we believe the range of terms used in the literature search makes this unlikely. The majority of studies (63%) were focused on extremes of fishing pressure, comparing no-take zones with fished areas; fewer publications (26%) looked across gradients where fishing was permitted at all locations (Fig. 2A). There has been an emphasis on spatial studies (72 publications) rather than temporal or spatio-temporal comparisons (33 studies; Table S2). The majority of these fishery-independent studies (97%) used underwater surveys, with the remainder relying on research-derived catch data (Table S3).

Density (number or biomass per unit area, hereafter termed simply ‘abundance’ or ‘biomass’), community composition (e.g. diversity), and ecosystem (e.g. coral cover) indicators have consistently been presented in the literature over time (Fig. 2B). For example, density indicators have been reported in at least 30% of records for each time period. In contrast, size (e.g. mean size) and function-based (e.g. herbivore biomass) indicators have been reported in an increasing number of publications over the last 15 years. For example, function-based indicators were not recorded prior to the late 1990s but had increased to 15% of the indicators presented between 2011 and 2015. Research has commonly focused on the whole community for fish-related indicators (Fig. 2C). Over the last decade, there has been a shift in emphasis from indicators calculated at the family-level to those estimated for functional groups: between 1996 and 2000, 13 studies reported family-level indicators, but only 8 presented functional group indicators, whereas from 2011-2015, 7 studies provided family-level analyses compared with 15 giving functional measures.

Where expectations of the effects of fishing on indicators were provided by the authors, 60% of those expectations were met, and 9% were met for some but not all reports of indicators within a study (Fig. 3A). Thirty one % of expectations were not met, suggesting that further knowledge of how indicators respond to fishing is required. A lack of knowledge is not surprising considering the high number of indicators that have been used and the very low replication among studies (53% of indicators had fewer than 5 replicates among studies; Table S4), giving little opportunity to build understanding in the literature of how indicators respond to fishing. When the results are examined with respect to the type of indicator, it is possible to see that expectations of the effect of fishing on fish biomass, size distributions and community composition were met more often than not (>65% of expectations met; Fig. 3B). In contrast, expectations of the effect of fishing on fish abundance, species richness and coral cover were not met or only partially met more than 66% of the time. Only 56% of results reported in the publications found an effect of fishing on indicator values (Fig. 3C), suggesting that the sensitivity or specificity of many of these indicators to fishing may be low (Rice, 2003). Although, in some instances, the study design may have been inappropriate to detect fishing effects, for example where there is a scale mismatch between the sampling program and the fishing impact.

In the following sections, we explore the consistency with which specific indicators track fishing effects across studies, highlighting the potential utility of these indicators in the coral reef context. It should be noted that where multiple publications detailed the same indicator from the same location (12 pairs of publications), and thus duplicates were excluded from the ‘in-depth’ analysis, the selection of which paper to exclude made little difference to the overall findings. Only 3 pairs of publications showed varying results and these differences were based on findings of ‘no change’ versus ‘decrease’.

Density based indicators

Fishing removes individuals and is likely to result in a decline in the abundance and biomass of target species (Jennings and Kaiser, 1998), unless compensatory mechanisms such as growth and recruitment counteract removals (Gonzalez and Loreau, 2009, Thorson et al., 2012). At the community level we found that biomass (per unit area) showed more consistent responses to fishing than abundance (per unit area), with all studies recording either ‘decrease’ (91%), ‘no change’ (30%) or ‘mixed’ (9%) with increasing fishing effort for biomass, but both decreases (39%) and increases (8%) in response to greater exploitation for abundance (Fig. 4A). Although, fishing removes individuals and thus has the potential to reduce fish abundance, targeting of large individuals may drive greater losses in biomass than abundance per unit area (Friedlander and DeMartini, 2002), potentially giving more consistent evidence of fishing effects on biomass than on abundance. However, the more consistent findings for biomass compared to abundance trends was not apparent at the level of fish families (2% and 4% of studies detailed increases, for biomass and abundance respectively; Fig. 5). This lack of consistency for biomass at the family level may reflect different fishing practices and gears employed among locations, resulting in variable selectivity for specific species and families. Research is now needed to explore how family-level indicators respond in different fishery contexts where specific groups of species may be targeted or particular gears are employed. When the community level results were split across different spatial scales, biomass showed more consistent declines in response to exploitation at regional scales than at local scales (89% and 56% of studies, respectively; Fig. S1). Similarly, when these results were partitioned among different fishing gradients, the effect of fishing on the density indicators (abundance or biomass) was most consistent across gradients where fishing is permitted at all locations (all records showed declines or ‘no change’), rather than for gradients including extremes of fishing (from no-take to fished; ‘decrease’, ‘mixed’ and ‘increase’ reported) (Fig. S2).

Density-based metrics are easy to communicate to stakeholders and give an indication of the resource potential of a fishery, a common management focus (Shin et al., 2010). However, fish density (biomass or abundance) may be influenced by factors other than fishing, such as habitat changes, variability in recruitment, growth rates and schooling behaviour of fishes (Rochet and Trenkel, 2003).

Community composition indicators

In targeting large individuals and showing preferences for particular species, fishers may influence the composition of fish communities, affecting the relative dominance of species (Link et al., 2002, Yemane et al., 2005, Shin et al., 2010). Although there is considerable evidence of fishing affecting community composition across a range of ecosystems (e.g. Beets, 1997, Trenkel and Rochet, 2003), there is controversy in the literature regarding the benefits of using species richness (number of species) and diversity metrics (number of species and how evenly individuals are distributed among those species) as indicators of fishing pressure, due to their inconsistent response to exploitation within and among studies (Gislason and Rice, 1998, Greenstreet and Rogers, 2006). Unlike species richness, diversity changes do not solely rely on localised extinctions, rather they may be influenced by changing dominance and thus may be more sensitive to the effects of fishing (Rice, 2003).

Indicators of fish diversity showed the effects of fishing more consistently than species richness. All studies estimating fish diversity reported ‘decrease’ (17%) or ‘no change’ (83%) in response to increased fishing pressure, compared with 10% of publications that detailed species richness indicating ‘mixed’ responses or increases in response to greater fisheries exploitation (Fig. 4B). However, it must be noted that few studies estimated diversity (6), and thus more research is needed to confirm this outcome. Nonetheless, the apparent inconsistent response of species richness to fishing pressure is important when considered in concert with the prevalence of publications using species richness to assess fishing impacts on fish communities: after biomass and abundance, species richness was the most commonly used indicator across the 105 publications incorporated in the initial review (presented in 39% of publications; Table S4). This prevalence may reflect the ease with which species richness may be estimated. Nonetheless, it appears that this indicator may represent fishing effects on coral reefs in an ambiguous manner.

Species diversity is relatively easy to communicate to stakeholders and may underpin management objectives focused on conserving biodiversity (Shin et al., 2005, Greenstreet and Rogers, 2006). Nonetheless, diversity and other community composition indicators are generally non-specific, such that variables other than fishing (e.g. habitat differences and pollution) may also influence trends (Rochet and Trenkel, 2003). Furthermore, 97% of studies used underwater surveys to collect fish data; these methods are likely to underestimate the abundance and diversity of certain species, for example visual censuses underestimate cryptic species (Willis, 2001). Moreover, there may be significant cost implications associated with monitoring fish communities accurately to species-level (Bianchi et al., 2000).

Size based indicators

Fishing may be strongly size selective, with fishers preferentially targeting larger fish, and a greater vulnerability of large individuals to a given fishing pressure due to low rates of population increase (Jennings et al., 1998, Pauly et al., 1998, Shin et al., 2005). Few studies we reviewed (35 of 105) reported the results of size-based indicators. At the community level, size distributions and the slope of size spectra were recorded as either ‘decrease’, ‘no change’ or ‘mixed’ in response to increased fishing effort in all studies (Fig. 4C). Mean size showed both decreases (95%) and increases (5%) in response to greater exploitation, but the negative effects of fishing on mean size became more consistent when the community-level results were split across different spatial scales (Fig. S1). All studies reported a ‘decrease’ or ‘no change’ at regional scales, whereas 10% of studies reported an increase in mean size with increasing fishing pressure at local scales .

A number of other size-based indicators were reported, but are presented in too few studies to qualitatively explore consistency across studies (e.g. mean maximum size was reported in only 5 of the publications incorporated in the initial review; Table S4), but the findings of these publications suggest further work is warranted in exploring the response of these indicators to fishing pressure.

For example, whereas the abundance of fish is not a consistent indicator of fishing effects on reefs, the abundance of large individuals and mean maximum fish size are potentially more sensitive and/or specific to fishing on coral reefs, showing declines in response to increased exploitation (Dulvy et al., 2004b, Clua and Legendre, 2008, Guillemot et al., 2014). Where sequential hermaphrodites, such as parrotfishes, are important fishery targets, mean length at sex change has been found to be lower at intensively fished sites compared with areas subject to less exploitation (Taylor, 2014). Similarly, fishing was shown to drive declines in the lengths at which parrotfish mature (Taylor et al., 2014). Ratios between these size-based indicators also provide useful information. For example the ratio between mean length and length at maturity indicates the likelihood of catching individuals before they mature and can reproduce. Where many fish are caught before maturity there will be little chance for reproduction and thus continuation of the resource (Froese, 2004, Babcock et al., 2013). There were too few studies reporting mean size of different fish families (9 estimates across all families) to explore the response of family mean size to fishing pressure. Nonetheless, work by Vallès and Oxenford (2014) highlights the importance of understanding the differential rate of response of fish families to fishing pressure (Fig. 6): the size of preferentially targeted families such as groupers may show decline at light to moderate fishing pressure but these declines level out at high fishing pressure (Fig. 6B). At locations where fishing pressure is moderate to heavy, trends in the size of parrotfish may be important to elucidate differences in exploitation among sites (Fig. 6C).

Size-based indicators are important in the coral reef context because larger fish may provide greater functional impact. For example, larger herbivores may remove disproportionately more algae per unit body mass (Lokrantz et al., 2008) and forage over larger areas (Nash et al., 2013a). Size-based indicators are intuitive and thus easy to communicate to stakeholders, and many are based solely on size and abundance data so species identification skills are not required (Rochet and Trenkel, 2003, Shin et al., 2010). In view of the low data requirements of size-based indicators, their apparent usefulness in temperate marine systems (Jennings, 2005, Jennings and Dulvy, 2005), and early evidence of their value in reef systems (e.g. Dulvy et al., 2004b, Graham et al., 2005), there is certainly support for more research in this area.

Life-history based indicators

Many life history traits are correlated with size (Abesamis et al., 2014). Thus, targeting of large individuals and the vulnerability of these individuals to fishing will have knock-on consequences for other life history traits (Jennings and Kaiser, 1998, Mullon et al., 2012). Varying fishing intensities are expected to drive differences in the life history composition of fish communities: fast growing, rapidly maturing species will be found in heavily fished areas, whereas slow growing, late maturing species will be more prevalent in lightly fished, or unexploited areas (King and McFarlane, 2003, Winemiller, 2005). While work evaluating the impact of fishing on life history traits in coral reef fish communities has gathered momentum in recent years (e.g. Taylor, 2014, Vallès and Oxenford, 2014), the focus has remained on size-based traits and there were insufficient studies in our review to compare findings for other traits such as growth rate or age at maturity, across studies (all indicators reported <4 times). Nonetheless, research looking at the relationship between fishing protection and shifts in life history traits over time and space suggest a wide range of traits may be consistently affected by fishing (McClanahan and Humphries, 2012), and age at maturity may prove more responsive to fishing effects than many size-based indicators (Taylor et al., 2014). Unfortunately, information such as age and growth data are currently lacking for many species (Abesamis et al., 2014), so estimating these indicators is difficult. However, as knowledge of these traits grows, the potential of life-history indicators will increase.

Function based indicators

An ecosystem based approach to management is reliant on understanding how fishing is affecting broader ecosystem structure and function (Friedlander and DeMartini, 2002, Henriques et al., 2014). For example, loss of herbivores that are critical for mediating competition between coral and macroalgae on coral reefs, can result in regime shifts from coral to macroalgal dominated states (Steneck et al., 2014). The switch to an increased interest in functional rather than family-level indicators over time likely represents the expanding research focus on how coral reef ecosystems function, and the importance of fishes in performing roles such as herbivory (Bellwood et al., 2004). The effect of fishing on the biomass and proportion of different functional groups within the community were most consistent for higher trophic levels. All studies indicated a ‘decrease’ or ‘no change’ in response to greater exploitation for piscivores and piscivore-invertivores, whereas 1 study reported increases for herbivore biomass and 2 studies report increases for the proportion of herbivores in the community (Fig. 7A&B). Abundance of functional groups both increased and decreased in response to increased fishing pressure. In contrast, all functional groups across all reviewed studies showed either a ‘decrease’ or ‘no change’ in mean size in response to greater fishing pressure (Fig. 7C). However, there was a shift in the predominance of the ‘no change’ classification to ‘decrease’ between lower (herbivores – 25% of studies reported a ‘decrease’) and higher (piscivores – 60% of studies reported a ‘decrease’) trophic levels.

Only one coral reef publication estimated functional redundancy and richness metrics (Table S4), demonstrating that exploitation may result in a decline in both (Micheli et al., 2014). However, the functional indicators used by Micheli (2014) are based on presence/absence data and thus will not be sensitive to fishing reducing numbers or biomass unless localised extinctions occur. The expanding literature using metrics of functional diversity weighted by biomass or abundance (Villéger et al., 2008, Laliberté and Legendre, 2010), may present useful alternatives to indicators based on presence/absence data. Indicators weighted by biomass or abundance account for fishing-driven declines in density and are not reliant on localised extinctions. However, to our knowledge, no studies have explicitly used this approach to examine fishing effects on coral reefs. Importantly, the response of functional indicators to fishing pressure will be influenced by how functions are defined; whether they are based solely on trophic group as used here, or encompass other information such as mobility and size (Amand et al., 2004, Mouillot et al., 2014). Furthermore, the distribution and prevalence of different functions within the community will be affected by impacts such as climate change (Graham et al., 2015), as well as fishing.

In many marine systems, feeding is strongly size structured, with larger individuals feeding higher in the food chain (Sheldon et al., 1972, Dickie et al., 1987, Jennings et al., 2001). Thus, a decline in the mean trophic-level (MTL) of the fish community may be driven by a loss of large individuals to fishing, or where MTL is estimated from landings data, an increase in the catch of lower trophic levels (Jennings et al., 2001, Christensen et al., 1996, Essington et al., 2006). Indeed, there has been a reported global decline in the mean trophic-level (MTL) of fisheries landings over time (Pauly et al., 1998). These findings have underscored the popularity of MTL as an indicator of fishing effects, although work by Branch et al. (2010) highlights that MTL estimates based on catch data may not accurately reflect ecosystem changes captured by fishery-independent methods. On tropical coral reefs, decline in MTL may be ambiguous due to the unselective nature of fisheries (Mangi et al., 2007), the relatively large size of some species feeding at low trophic levels such as parrotfishes, and the complex range of trophic cascades observed to result from exploiting predatory species on coral reefs (Salomon et al., 2011). It is perhaps not surprising, therefore, that we found only 4 studies in the initial search and 3 studies in the 'in-depth' review, which estimated MTL on coral reefs. Of these latter 3 studies, there were records of 'no change' and 'increase' in response to increased fishing pressure (Karnauskas and Babcock, 2014, Guillemot et al., 2014, McClanahan and Humphries, 2012). Although, MTL may not be an appropriate indicator of the effects of fisheries on coral reefs (but see Weijerman et al., 2013), investigations into trophic interactions using tools such as stable isotope analysis will complement suites of ecological indicators employed in fisheries management. These techniques help provide an understanding of how coral reef fisheries affect and are affected by the structure and function of food webs on reefs (Jennings and Kaiser, 1998, Frisch et al., 2014, Pestle, 2013). Indeed, due to the complex trophic relationships characterizing reef ecosystems, this type of approach is critical.

Ecosystem indicators

Fishing may have direct impacts on the benthos through destructive fishing practices, or indirect effects through removal of fishes that perform specific functional roles (Jennings and Kaiser, 1998, Micheli et al., 2014). Overall, our findings indicate variability in the effects of fishing on the benthic community (Fig. 8). Structural complexity, which is easy and quick to measure when using a visual scale (Wilson et al., 2007), was found to show the most consistent response to fishing pressure, with all studies reporting either a 'decrease' (11%) or 'no change' (89%) in response to increased fishing pressure. In contrast, the expectations of few authors (20%) were met regarding the effect of fishing on coral cover (Fig. 3B), and this indicator responded inconsistently to fishing pressure across studies (Fig. 8B). There has been concern raised about the reliance of many monitoring programs on the relatively coarse metric of coral cover as a measure of ecosystem health (Hughes et al., 2010). Darling et al. (2013) highlight the potential for differential responses to stressors within coral communities. These differential responses suggest that indicators assessing changes in the life-history composition of coral communities, rather than coral cover *per se*, may be more sensitive indicators to fishing effects. Work from Kenya demonstrates that urchin density may respond to fishing impacts, with removal of invertivorous fish resulting in increased urchin numbers (e.g. McClanahan and Mutere, 1994). However, there were insufficient studies (4 studies estimating abundance and 3 studies estimating biomass) using this indicator for us to evaluate it more thoroughly.

Important issues in the use of fisheries indicators on coral reefs

Statistical power and uncertainty

Almost 50% of the indicators reported in the coral reef literature did not highlight any effects of fishing (Fig. 3C). ‘No change’ needs to be interpreted with caution because the lack of any trend may simply be a function of insufficient statistical power (Jennings and Kaiser, 1998, Wagner et al., 2013). The capacity to detect change depends on the sampling program, and should be explicitly addressed at the survey planning stage (Levine and Ensom, 2001). In the ‘in-depth’ section of our review we found only 5 out of the 65 studies reported *a priori* power analyses in relation to survey methods for the indicators used. Few studies discussed statistical power in relation to survey design or interpretation of results (12 and 9 respectively). This apparent lack of *a priori* investigation into the power to detect change may simply reflect a lack of reporting of these analyses in published studies. Nonetheless, such information is important when presenting indicator results in order to understand whether the sample size was adequate to detect a pre-specified magnitude of change within a particular length of time (Levine and Ensom, 2001, Wagner et al., 2013). This provides fundamental knowledge needed to build an understanding of how different indicators respond to fishing on coral reefs. When presenting indicator trends to stakeholders this knowledge allows discussion of the trade-offs between costs associated with overlooking fishery effects versus responding to noise (Jennings, 2005). Where *a priori* power analyses have not been performed, post-hoc approaches are not advised as these can give rise to incorrect interpretations of the probability of false negatives; in this instance confidence limit analysis is more appropriate (see Smith and Bates, 1992, Colegrave and Ruxton, 2003 for more details).

Issues associated with a low statistical power to detect trends sit within the broader problem of uncertainty in fisheries management. In the context of the estimation and use of ecological indicators, uncertainty may arise from a range of different sources: natural variability, and measurement, modelling and estimation error (implementation of management controls may produce additional sources of uncertainty; see Francis and Shotton, 1997 for further details). Importantly, in using our qualitative review of the response of indicators to fishing effects we were not able to account for or estimate any of these sources of uncertainty, for example through incorporation of model standard errors in meta-analytic summaries (Thorson et al., 2015, Gurevitch and Hedges, 1999). Quantifying uncertainty is critical for assessing and communicating the risk associated with different fisheries management options (Francis and Shotton, 1997, Babcock et al., 2013). In the context of understanding the performance of fisheries-independent indicators on coral reefs, there is a clear need to move towards quantitative summaries of indicator behaviour across studies.

Fishing gradients

Understanding the response (and variability of responses) of an indicator across a wide range of fishing mortalities underpins knowledge of indicator sensitivity and specificity to fishing (Fig. 6; Houle et al., 2012). For example, there is evidence that declines in community biomass may only be visible across gradients spanning no-take to lightly fished sites: large changes in biomass may occur at low fishing mortality but this rate of change declines at moderate to high mortality, making it harder to detect differences (Fig. 6B; Houle et al., 2012). Where catch data are lacking or management programs rely on fishery-independent indicators such as those reviewed here, characterisation of gradients in fishing mortality may be based on fishing pressure proxies such as number of fishing vessels, rather than on mortality itself.

We found an emphasis on categorical classifications of fishing pressure, with 65% of studies in our review providing qualitative descriptions such as low or high fishing pressure. These types of classifications make it impossible to build an understanding of the shape of the relationship between fishing pressure and a specific indicator. Furthermore, where quantitative estimates were used, there was no consistent proxy of exploitation; studies used a wide range of variables as surrogates such as human population density or degree of coastal development. There have been recent moves to use surrogates of exploitation that are more nuanced than simple measures such as human population density, for example by accounting for reef area (Dulvy et al., 2004b), or by exploring how humans interact with fishery resources (Grace-McCaskey, 2012). For example, access to markets has been shown to be a strong predictor of exploitation on reefs even at low human population densities (Cinner et al., 2013). There is now a need to link the use of such proxies in the context of fishery-independent indicators with information derived from studies that focus on catch data and directly characterise fishing mortality. This will help build an understanding of which of these proxies are most representative of fishing mortality and thus might be recommended more universally for application in coral reef fisheries research.

An additional issue is the reliance on spatial comparisons to investigate the effects of fishing on indicators (69% of studies; Table S2), with no accounting for confounding habitat effects that may also impact indicator values. As a result, trends in indicators across space cannot be attributed solely to fishing effects (see section on indicator specificity below; Russ, 2002, Greenstreet and Rogers, 2006). This is a significant problem when comparing no-take with fished areas since the design and siting of reserves may be based on baseline differences in the condition of specific areas, an issue that may be addressed through the use of Before-After-Control-Impact (BACI) studies (Abesamis et al., 2014).

Scale

Reefs are multi-scale, hierarchical ecosystems (Hatcher, 1997), and it is important to understand how scale of analysis affects indicator findings (Appeldoorn, 2008). The majority of studies (65%) examined fishing indicators at local scales, with the remainder primarily focusing on regional scales (Table S5). We found more consistent effects of fishing on fish biomass and mean size, at the regional scale. Whether this is an artefact of larger gradients in exploitation at locations that were incorporated into regional scale studies, or reflects the predominant scale of fishery impacts is not clear. Furthermore, our scale specific findings need to be interpreted with care due to the coarse, qualitative nature of the scale categories used, which focused purely on the spatial extent of each study. As with the quantification of fishing gradients, understanding of indicator behaviour would benefit from future research that quantitatively explores the effect of both the study extent and resolution (grain) on indicator trends. If the grain of surveys is too coarse then it may not be possible to discern spatially discrete fish communities that respond ‘independently’ to fishing. Understanding this spatial arrangement is important for designating appropriate management units (Cope and Punt, 2009). In contrast, a grain that is too fine may result in a noisy dataset with high variability that masks signals in fish or benthic indicators (Chabanet et al., 2005), unless this is accounted for in the analysis using a graduated approach with the data analysed at multiple resolutions. Chabanet et al. (2005) provide examples of sampling protocols for a range of different spatial scales when exploring the effect of human disturbance on reef ecosystems.

Temporal mismatches between fishing effects and monitoring may also hide important signals. For example, a number of the studies looked at fishing effects in relation to periodic closures (e.g. Bartlett et al., 2009); if monitoring does not account for the timing of openings, indicator values will not reflect this temporal variation in exploitation. Finally, because extrapolating results across scales may be misleading, the scale at which indicators are estimated needs to be relevant to the scale of management. This concordance among scales will help ensure actions taken in response to indicator outcomes achieve pre-defined objectives.

Indicator specificity

Reef ecosystems are not only influenced by fishing effects, they will also be affected by a range of other drivers such as coastal development and elevated sea surface temperatures. These drivers may in turn influence aspects of the reef community such as habitat condition which will have knock-on consequences for indicator behaviour (Table 1; Jennings and Kaiser, 1998, Link et al., 2010, Rouyer et al., 2008). For example, fish size distributions are influenced by fishing and the availability of refuge provided by the reefs structure (Nash et al., 2013b, Shin et al., 2005). Teasing apart the comparative impacts of fishing versus these other factors (the specificity of the indicator) may be difficult, but is imperative to build an understanding of indicator performance (Rochet and Trenkel, 2003, Houle et al., 2012). In the absence of specificity to fishing, any actions taken by managers may show no corresponding changes in indicator outcomes. In this instance, the effect of the management action cannot be adequately evaluated (Trenkel and Rochet, 2003).

Almost 50% of publications incorporated in the ‘in-depth’ section of our review did not evaluate the effect of other factors on the indicator values. Another 15% only tested the effect of other factors on a subset of the indicators presented. Where other factors were accounted for, several influenced indicator values (Table 1). Anecdotally, it appears that benthic variables such as coral cover and, to a lesser extent seascape variables, may be particularly important. There was insufficient consistency among studies to allow a more rigorous quantitative analysis of these trends, as such there is now a clear need for research that focuses on exploring the consistency with which factors other than fishing affect indicator behaviour over time and space in coral reef ecosystems.

The process of separating out the effect of fishing on indicator behaviour from the influence of other variables is complicated by feedbacks among factors, for example fishing may make coral reefs more susceptible to other disturbances (Dulvy et al., 2004a, Salomon et al., 2011, Nyström et al., 2012). Similarly, impacts on reef structural complexity and resultant loss of refuges may alter the behaviour and survival of smaller fishes and invertebrates (Madin et al., 2010, Graham and Nash, 2013). These changes will modify interactions among organisms and affect detection during underwater visual surveys. Predicted increases in disturbances on coral reefs, such as bleaching events or acidification, are likely to add further challenges (Jennings and Kaiser, 1998, Hoegh-Guldberg et al., 2007). Methods for unravelling the relative impacts of different factors should be essential components of any fishery assessment. Structural equation modelling, redundancy analysis and BIO-ENV are examples of techniques that allow the variance in indicator values to be separated among different explanatory variables (Clarke and Ainsworth, 1993, Clua and Legendre, 2008, Link et al., 2010).

Indicator selection

We have discussed a wide range of metrics that have been used as indicators of fishing effects on coral reefs (Table S4). Methods for calculating these indicators are provided in Table S6. Estimating all indicators that are likely to be specific and sensitive to fishing effects is impractical or unnecessary to address specific management or research goals, thus, scientists and managers must choose suites of ecological indicators from the extensive list (Rice, 2003). An understanding of what attributes of the reef ecosystem are reflected in specific indicators, the correlation among indicators, and their relative advantages and disadvantages is essential. For example, fish community biomass may show recovery following cessation of fishing when a no-take area is implemented, but biomass trends will not reflect trends in the life history attributes of the community: recovery of life-history characteristics may lag behind increases in biomass (McClanahan and Graham, 2015). Thus, both biomass and life history indicators are required to track the influence of designating a no-take area on the local fish community. Although such knowledge may focus indicator choice, final selection is reliant on management objectives and context-specific constraints such as the availability of resources (e.g. data and manpower; Newson et al., 2009). This process of selecting indicators for a specific management context is beyond the scope of our review, and we direct readers to Rice & Rochet (2005) who outline a practical framework to guide this process, and to Newson et al. (2009) who provide an example of how this framework may be implemented.

Setting measurable management objectives for ecological indicators

Reference points are the translation of management objectives into specific, measurable values that may be used to evaluate the state of an ecosystem (Caddy and Mahon, 1995, Edwards et al., 2012). The success of management actions can be assessed by comparing changes in indicator values relative to these reference levels (Punt et al., 2001). Traditional fisheries management has relied on the modelling of fish stocks and the subsequent estimation of reference points for fishing mortality or biomass (Caddy and Mahon, 1995). Setting equivalent reference levels for empirical indicators presents a considerable challenge because it requires an understanding of the causative relationships between fishing and the full suite of ecosystem indicators used (Link, 2005). In our search, we found very little research explicitly looked at setting reference points for multi-species coral reef fisheries (see work by Ault and colleagues for examples of single stock reference points in US jurisdictions, e.g. Ault et al., 2014): only four coral reef publications provided reference levels or methods for determining them for multispecies indicators (Friedlander et al., 2007, Karr et al., 2015, McClanahan et al., 2015, McClanahan et al., 2011). This lack of studies is likely to reflect, to some degree, our focus on the peer-reviewed, fisheries-independent indicator literature. The grey literature, including technical reports detailing monitoring of specific fisheries, would provide more data in this area. Unfortunately the dispersed nature of such sources means a comprehensive search of this broader body of work was beyond the scope of our study. Nonetheless, the few publications detailing reference points found in our search suggest a gap between coral reef studies and the expanding body of fisheries research aimed at developing methods to support the setting of measurable management objectives for ecological indicators (e.g. Jennings and Dulvy, 2005, Large et al., 2013, Pazhayamadom et al., 2013). This gap might be bridged by exploring these methods for coral reefs in relation to fishery-independent ecological indicators. Potential methods include: 1) reference directions, which concentrate on how indicators and thus the underlying ecosystem attributes are changing: are they ‘improving’ or ‘declining’ in response to management actions (where designation of 'improvement' is based on managment goals; Scandol, 2004, Martin et al., 2009, Bundy et al., 2010); 2) trigger points, which in limited research capacity contexts provoke further data collection or analysis at specific values of an indicator (e.g. Dowling et al., 2008, Dowling et al., 2015); or 3) setting specific reference points to be aimed for or avoided. Methods supporting this latter process include: comparison of indicator values between fished and no-take areas (Pauly, 1995, Babcock and MacCall, 2011, MacNeil et al., 2015, McGilliard et al., 2010); setting multispecies maximum sustainable yield estimates (McClanahan et al., 2011, Worm et al., 2009); or identifying ecological thresholds in exploitation-indicator relationships (Samhouri et al., 2010, Martin et al., 2009, McClanahan et al., 2015).

Recommendations

Our review highlights considerable scope for innovative and important work in the realm of understanding the sensitivity and specificity of coral reef fisheries indicators. Here we highlight research directions that we feel are fundamental to moving the field forward:

1. Quantification of fisheries pressure gradients to allow effective comparison of fisheries-independent indicator results among locations and studies, and to provide a better understanding of uncertainty concerning indicator estimation and modelling.
2. A more judicious selection of fisheries indicators on coral reefs, for example focusing on fish biomass rather than fish abundance, to improve assessments of fishery effects and to increase knowledge about specific indicators.
3. Explicit incorporation of habitat effects into studies of fishing impacts on indicators through the addition of habitat characteristics as explanatory variables in analyses of indicator trends. This will help to tease apart the separate factors influencing indicator behaviour.
4. Modelling of indicator specificity and sensitivity in coral reef settings to give a better understanding of indicator performance (e.g. Houle et al., 2012), and to identify the potential for misleading or erroneous interpretations from indicator trends.
5. Examination of how the wide range of fishing gears used on coral reefs influence different indicators.
6. Consideration of how biases inherent to particular fishery-independent survey methods may influence indicator patterns. Similarly, although we focus on fisheries-independent indicators, catch data may be more readily available in some locations, and there is a need to build knowledge of how the potential biases inherent to fisheries-dependent indicators, such as spatial or temporal changes in gear usage, may be accounted for when interpreting indicator patterns on coral reefs. This will increase the utility of fishery-dependent methods in this context.

7. Further exploration of the different methods for supporting coral reef managers tasked with setting reference points and harvest control rules in relation to fisheries-independent indicators.

8. Incorporation of ecological indicators into multidisciplinary indicator frameworks is currently lacking for coral reefs (Johnson et al., 2013). While we focus here on ecological state indicators, effective management of fisheries requires their integration into a pressure-state-response framework (e.g. Mangi et al., 2007).

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Table 1. Factors, other than fishing, found to influence indicators presented in the coral reef literature.

Factors	**Examples**
Seascape variables	Reef area, reef type, exposure
Habitat variables	Benthic cover, structural complexity, depth
Temporal variables	Season
Anthropogenic variables	Pollution, size of no-take area

FIGURE LEGENDS

Figure 1. A) Signal detection framework to explore the potential for correctly identifying a fishing effect (hit), missing a fishing effect (miss), incorrectly identifying a fishing effect (false alarm) or correctly showing no effect of fishing (true negative). B) Schematic of a framework for fishery management (grey boxes) and how this fits with and is supported by the ecological indicator information covered in this review (white box). Figure is adapted from Hoggarth et al. (2006).

Figure 2. Temporal distribution of publications A) presenting indicators of fishing effects across different fishing gradients (n=105); B) estimating different types of indicators e.g. density-based indicators; C) estimating indicators for different components of the fish community, e.g. family-level. In B) & C) frequencies are representative of all indicators presented, therefore a single publication may have more than one indicator type. LHT – life history trait; Other – Ecosystem indicators, e.g. benthic cover; FG – functional group. Note, indicators calculated at the level of functional group may be considered functional indicators even though they are not explicitly accounted for as such in B, e.g. fish biomass estimated for herbivores will be listed under ‘density’ in B and FG in C. Function indicators in B are metrics such as functional richness, calculated across the whole community.

Figure 3. A) Whether expectations were met for those publications providing *a priori* expectations of the impact of fishing on indicators (n=207); B) Whether expectations were met for those publications providing *a priori* expectations of the impact of fishing split by indicator type (only those indicators with at least five samples in B are presented). C) Observed effect of fishing on indicators presented in publications (n=803). In all plots frequencies are representative of all indicators presented in a study, therefore a single publication may have more than one entry.

Figure 4. Number of publications showing different effects of fishing on indicators estimated at the community-level: A) density; B) community composition; and C) size based indicators. X-axis represents change in indicator value in response to an increase in fishing pressure, either along a fishing gradient or from no-take to fished areas. Only those indicators presented more than 5 times in

the literature are shown. Note a ‘decrease’ for size distribution indicates a shift in size to smaller size classes. A ‘decrease’ in size spectra slope means a shift to a more negative slope, e.g. from -1 to -1.5.

Figure 5. Number of publications showing different effects of fishing on family density. X-axis represents change in indicator value in response to an increase in fishing pressure, either along a fishing gradient or from no-take to fished areas. Only those indicators presented more than 5 times within a family in the literature are shown. Figure includes data for indicators calculated using subsets of the families in some instances.

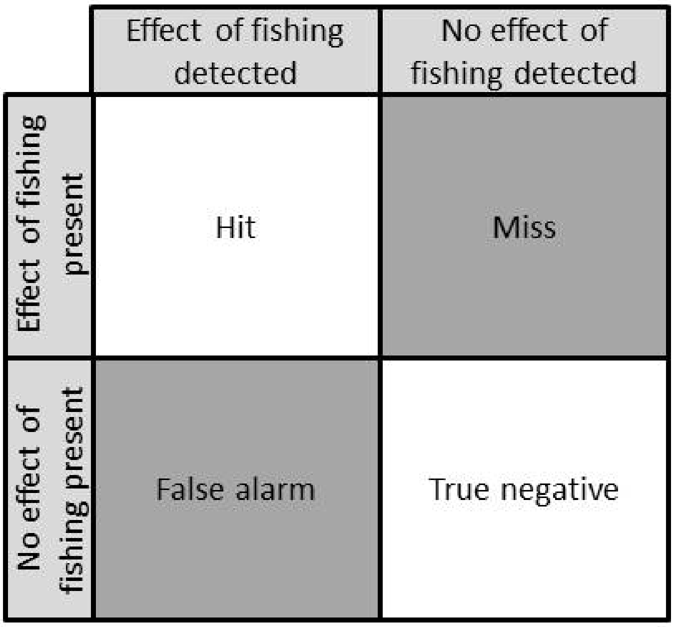
Figure 6. Different types of relationships between fishing pressure and indicators. Changes in indicator in response to fishing evident across A) the full spectrum of fishing pressures; B) no-take to lightly fished sites; and C) moderate to heavy exploitation. Grey arrow indicates effective range of indicator.

Figure 7. Number of publications showing different effects of fishing on functional indicators: A) density; B) community composition; and C) size based indicators. X-axis represents change in indicator value in response to an increase in fishing pressure, either along a fishing gradient or from no-take to fished areas. Only those indicators presented more than 5 times with a trophic group in the literature are shown. Classifications to specific groups (e.g. piscivores) are as provided by each publication’s authors. Figure includes data for indicators calculated using subsets of the functional groups in some instances.

Figure 8. Number of publications showing different effects of fishing on ecosystem indicators: A) coral cover; B) macroalgal cover; and C) structural complexity. X-axis represents change in indicator value in response to an increase in fishing pressure. Only those indicators presented more than 5 times with a benthic category in the literature are shown.

FIGURE 1

A



	Effect of fishing detected	No effect of fishing detected
Effect of fishing present	Hit	Miss
No effect of fishing present	False alarm	True negative

B

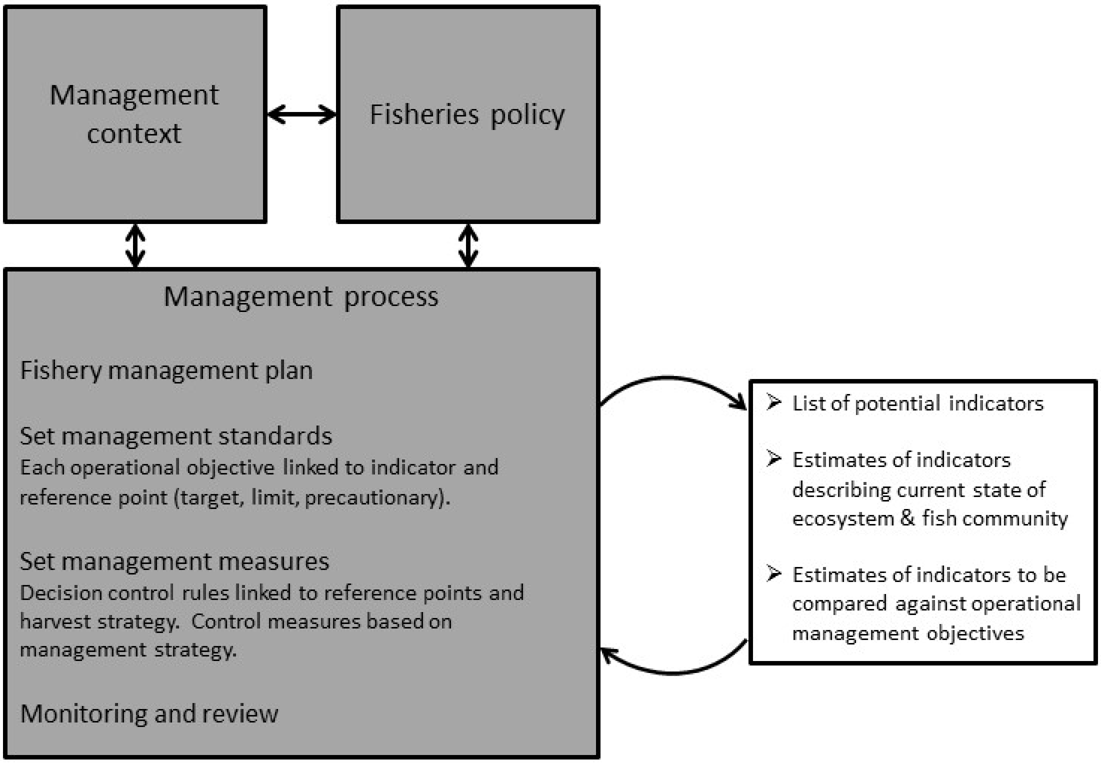
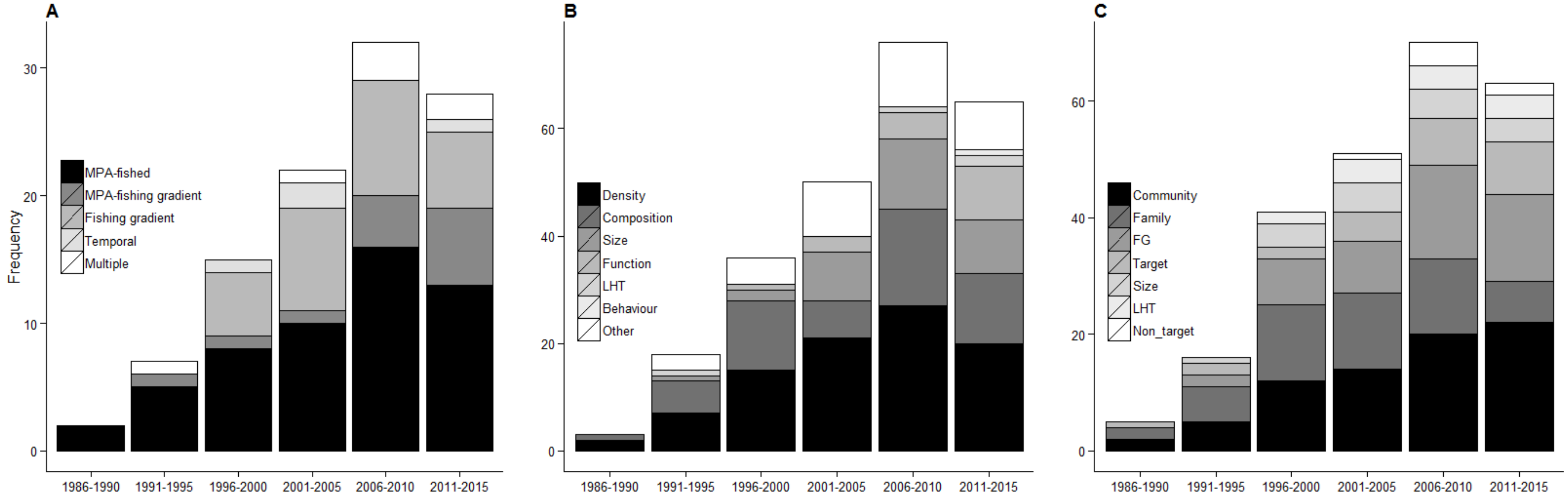
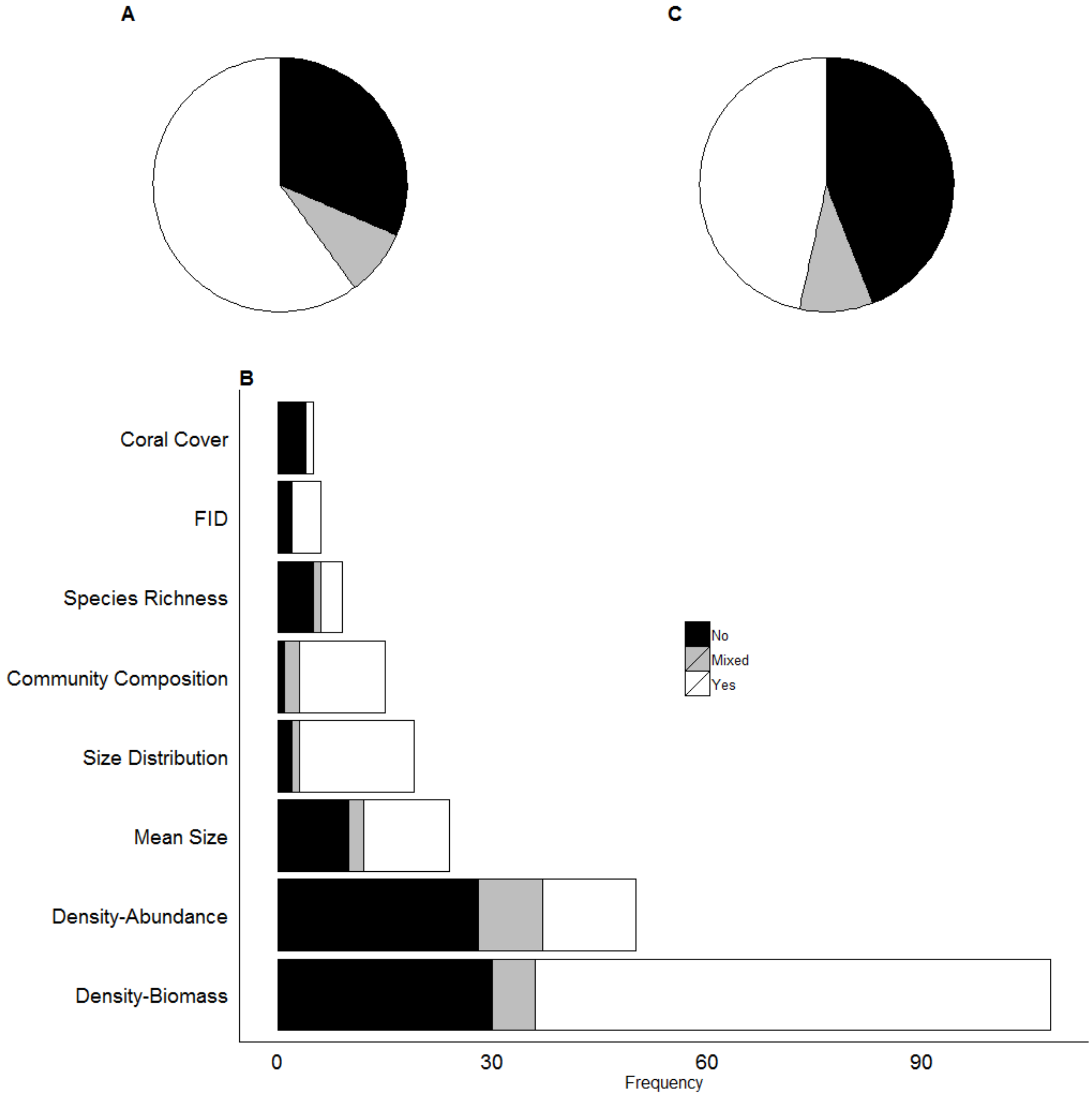


FIGURE 2


A
B
C
Frequency
0
10
20
30
40
60
MPA-fished
MPA-fishing gradient
Fishing gradient
Temporal
Multiple
Density
Composition
Size
Function
LHT
Behaviour
Other
Community
Family
FG
Target
Size
LHT
Non_target
1986-1990
1991-1995
1996-2000
2001-2005
2006-2010
2011-2015

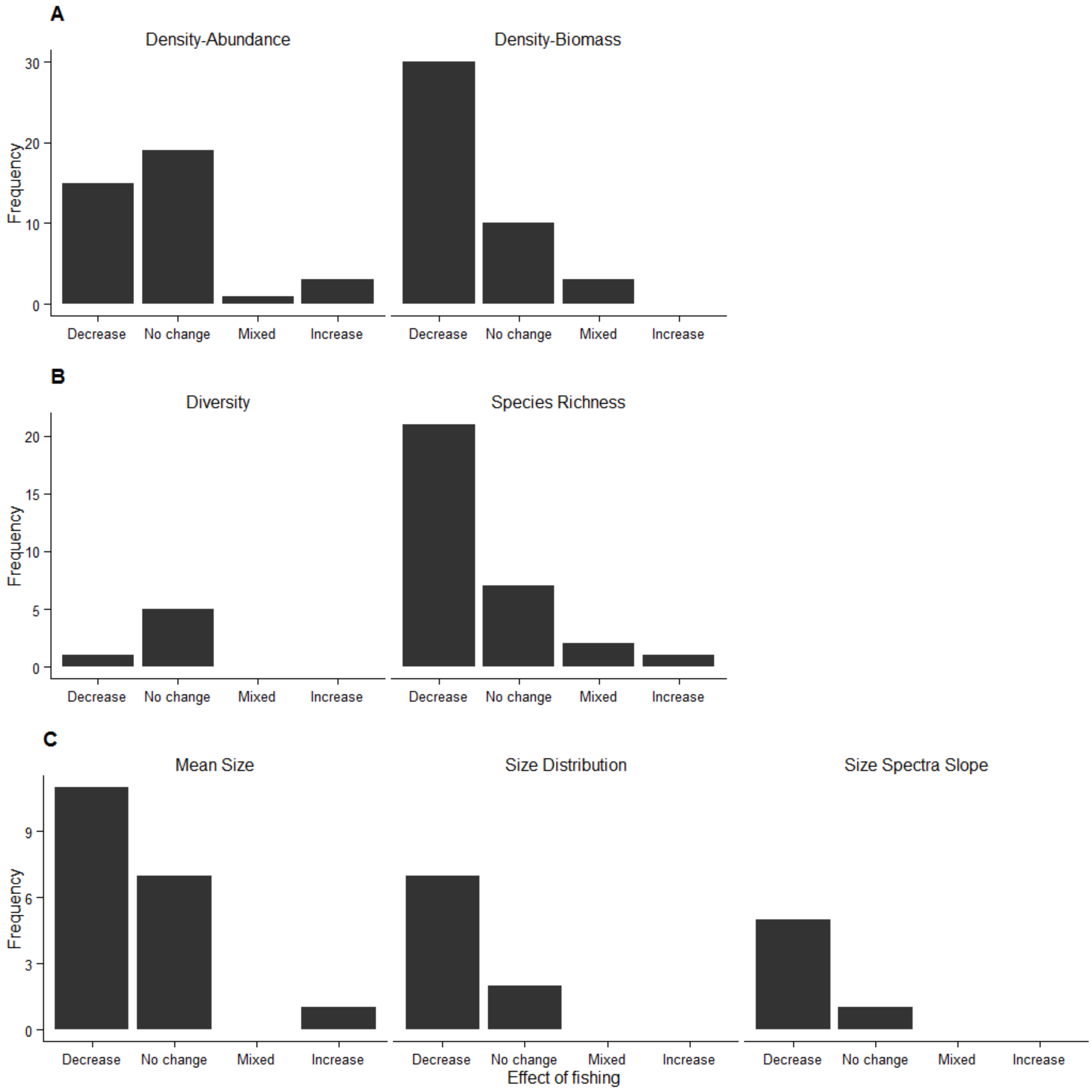
1134 **FIGURE 3**

1135

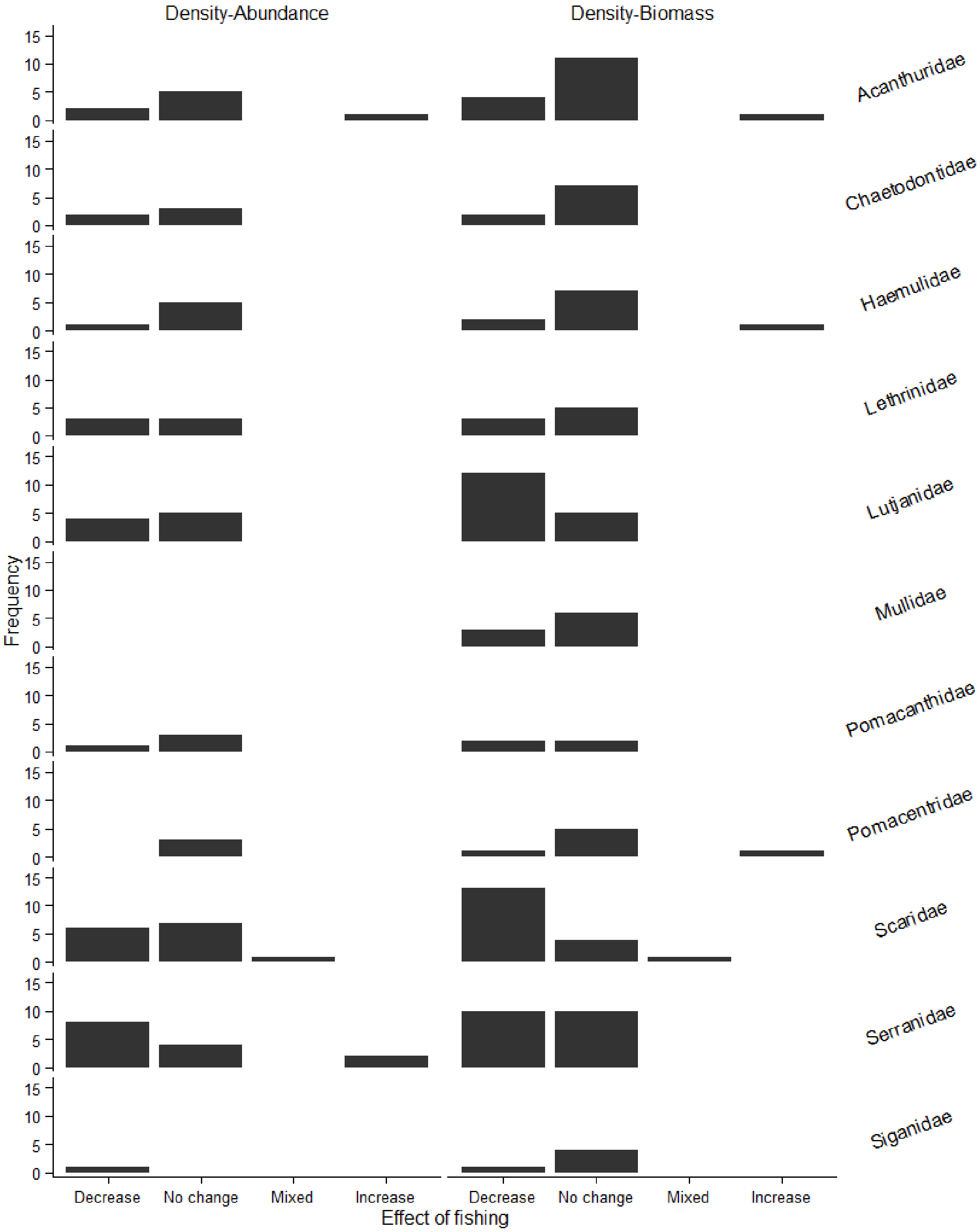


1136

FIGURE 4


A
Density-Abundance
Density-Biomass
Frequency
0
10
20
30
Decrease
No change
Mixed
Increase
B
Diversity
Species Richness
Frequency
0
5
10
15
20
Decrease
No change
Mixed
Increase
C
Mean Size
Size Distribution
Size Spectra Slope
Frequency
0
3
6
9
Decrease
No change
Mixed
Increase
Effect of fishing

1140 **FIGURE 5**



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1143 **FIGURE 6**

1144

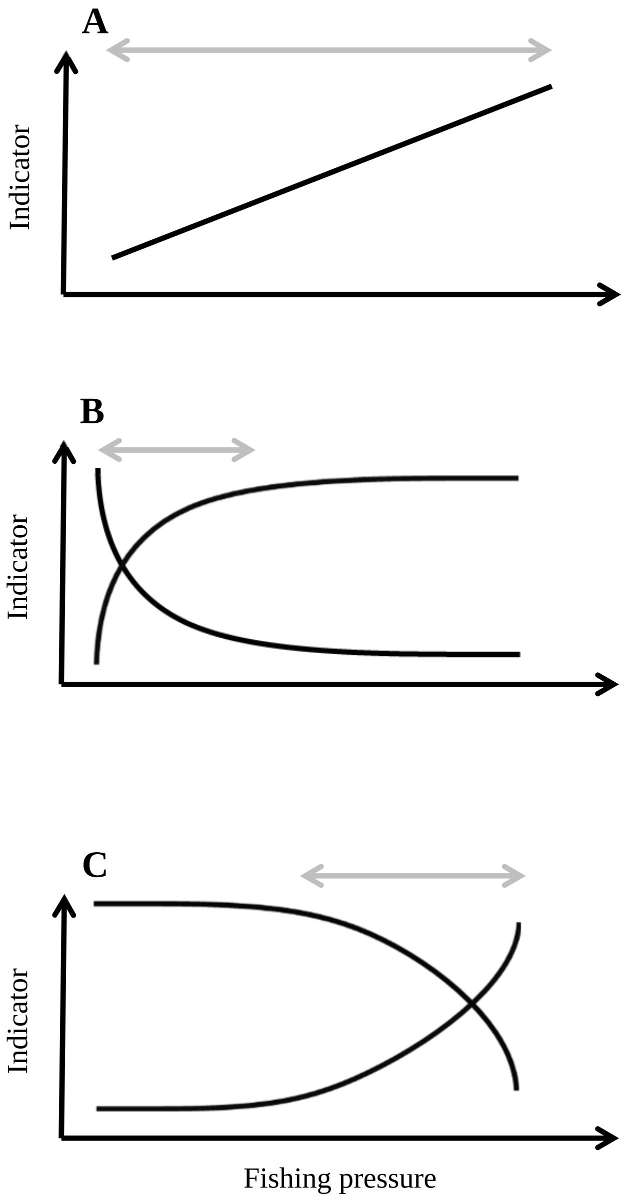


FIGURE 7

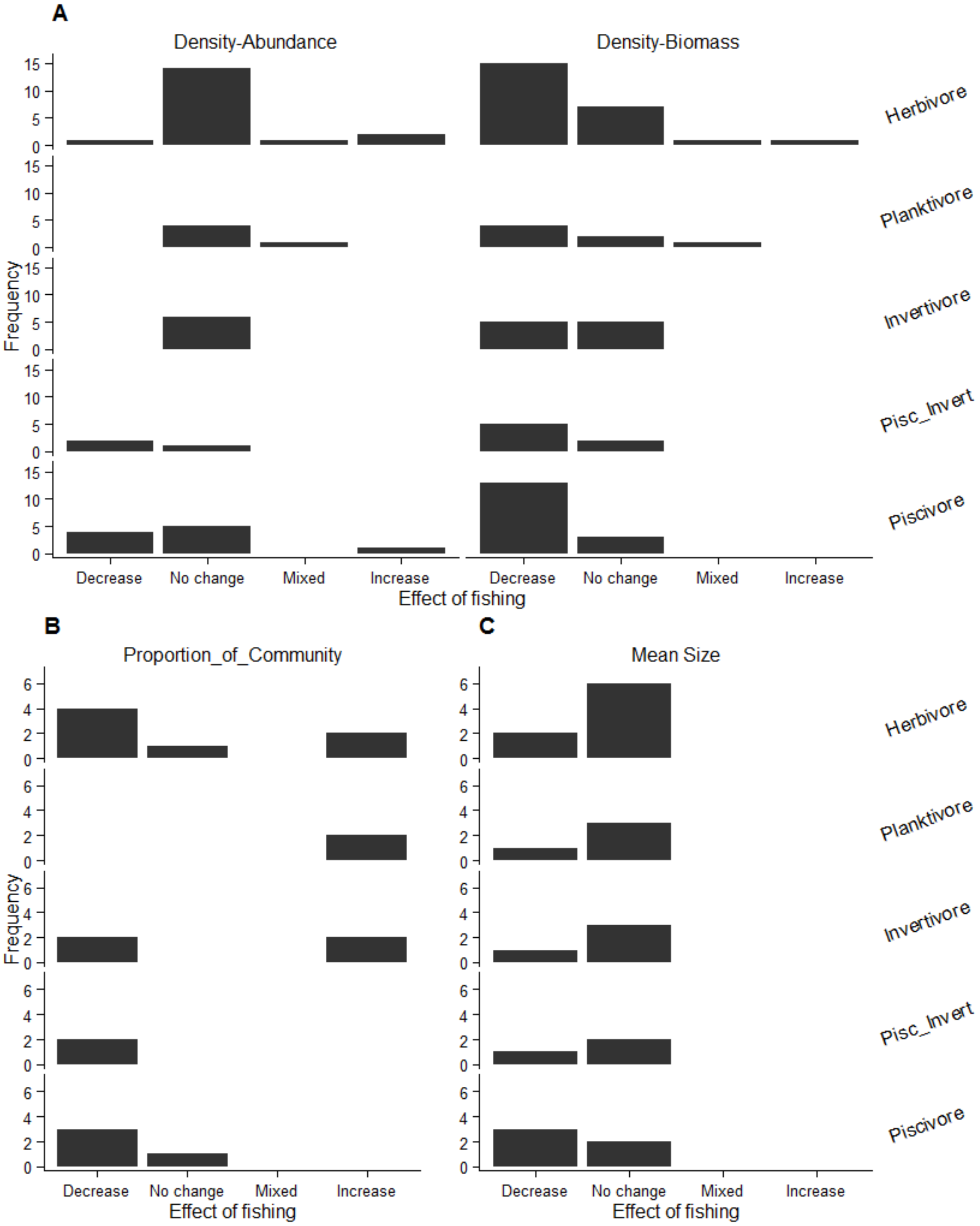
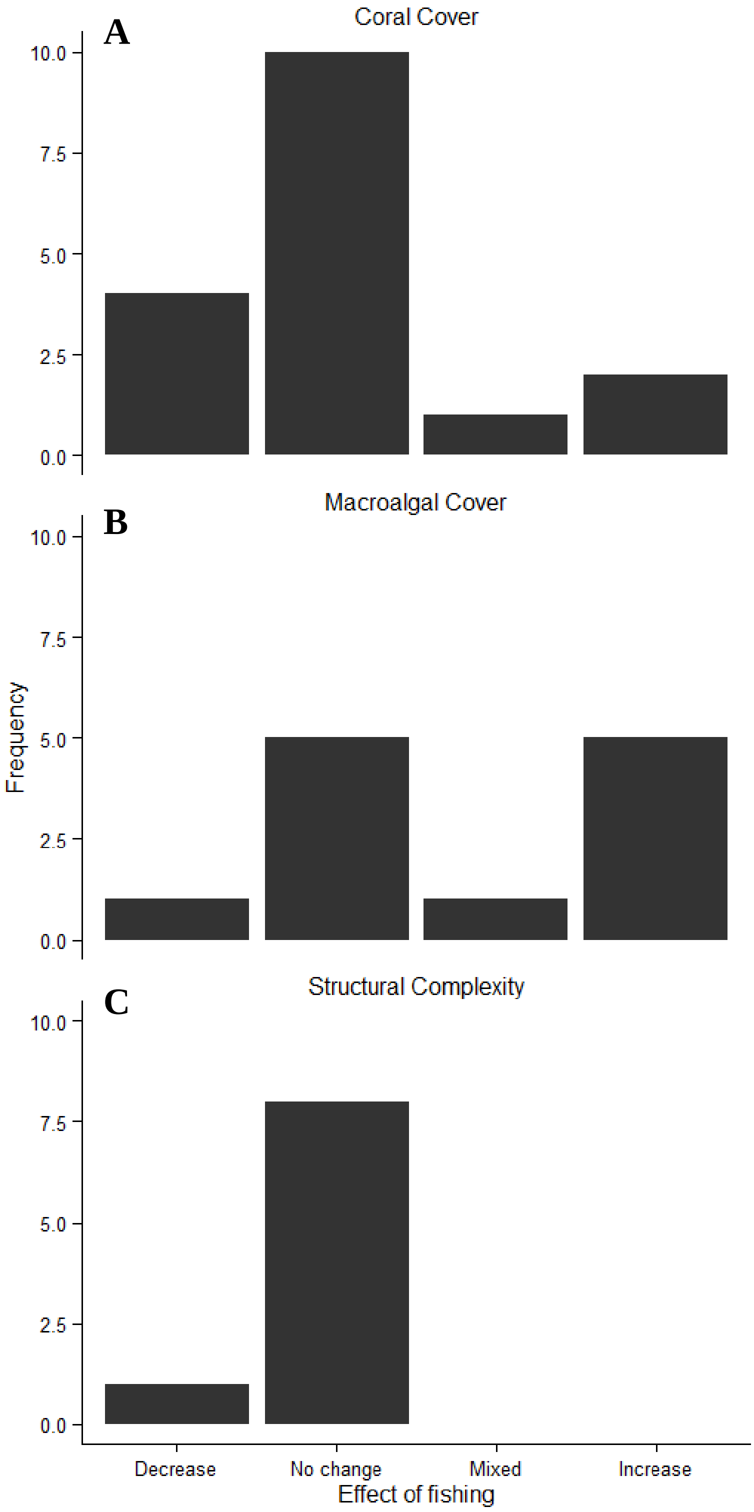

A
Density-Abundance
Density-Biomass
B
Proportion_of_Community
C
Mean Size
Frequency
15
10
5
0
6
4
2
Herbivore
Planktivore
Invertivore
Pisc_Invert
Piscivore
Decrease
No change
Mixed
Increase
Effect of fishing

FIGURE 8


A
Coral Cover
B
Macroalgal Cover
C
Structural Complexity
Frequency
10.0
7.5
5.0
2.5
0.0
Decrease
No change
Mixed
Increase
Effect of fishing