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Trait groups as management entities in a complex, multispecies reef fishery

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Article Impact Statement

Groups of species that share similar traits respond differentially to fishing pressure, which can be used to structure management actions.

Abstract

Localized stressors compound the ongoing climate-driven decline of coral reefs, requiring natural resource managers to work with rapidly shifting paradigms. Trait-based adaptive management (TBAM) is a new framework to help address changing conditions by choosing and implementing management actions specific to species groups that share key traits, vulnerabilities, and management responses. In TBAM maintenance of functioning ecosystems is balanced with provisioning for human subsistence and livelihoods. We first identified trait-based groups of food fish in a Pacific coral reef with hierarchical clustering. Positing that trait-based groups performing comparable functions respond similarly to both stressors and management actions, we ascertained biophysical and socioeconomic drivers of trait-group biomass and evaluated their vulnerabilities with generalized additive models. Clustering identified 7 trait groups from 131 species. Groups responded to different drivers and displayed divergent vulnerabilities; human activities emerged as important predictors of community structuring. Biomass of small, solitary reef-associated species increased with distance from key fishing ports, and large, solitary piscivores exhibited a decline in biomass with distance from a port. Group biomass also varied in response to different habitat types, the presence or absence of reported dynamite fishing activity, and exposure to wave energy. The differential vulnerabilities of trait groups revealed how the community structure of food fishes is driven by different aspects of resource use and habitat. This inherent variability in the responses of trait-based groups presents opportunities to apply selective trait-based adaptive management strategies for complex, multi-species fisheries. This approach can be widely adjusted to suit local contexts and priorities.

Introduction

Climate change and local stressors have caused a global deterioration of coral reef ecosystems despite attempts to reduce human impacts and manage for resilience (McLeod et al., 2021). These impacts are reorganizing species assemblages and altering ecosystem function, requiring a shift in management approaches (Bellwood et al., 2019). This need has been acknowledged by researchers and the conservation community, where efforts have pivoted from protecting species and contemporary community types toward maintaining the long-term functioning of rapidly changing environments and species assemblages (Bellwood, Pratchett, et al., 2019; McLeod et al., 2019).

The functions performed by species in an ecosystem are determined by their traits (Mouillot et al., 2013; Kraft et al., 2015). Because the types and abundances of traits are influenced by the environment, a trait-based lens provides an important tool for understanding ecosystem change (Sommer et al., 2014; Henriques et al., 2017; Kim et al., 2019) and for responding to these changes through management (Laughlin et al., 2017). Biotic, abiotic, and anthropogenic processes shape the trait combinations present in a community (Villéger et al., 2017); hence, species with similar trait combinations and functional roles share potential vulnerability and recovery responses (Dee et al., 2016). Classifying groups of species from their traits can glean new insights into community structuring (Darling et al., 2012), and we argue that they provide a hitherto underutilized opportunity to inform management in marine systems.

Functioning reefs and fisheries that maintain human food security and livelihoods are not mutually exclusive (Martin et al., 2017), and management that accounts for species traits and functions can help meet these goals. Building on principles of resilience-based and adaptive management (Anthony et al., 2015; McLeod et al., 2019), we devised trait-based adaptive management (TBAM), a practical framework for incorporating emerging trait-based principles in management of diverse species assemblages in changing ecosystems.

A trait-based adaptive management framework for coral reefs

Species with similar traits, and by extension, functioning, respond similarly to both disturbances and management. Indeed, disturbances ranging from localized fishing to climate change have the potential to remove entire functional groups from some fish assemblages (Micheli & Halpern, 2005). Functions are thus increasingly used as an avenue to inform management (McLeod et al., 2019), ranging from the impacts of reef degradation (Plass-Johnson et al., 2016), to fisheries (McClanahan et al., 2015; Mbaru et al., 2019), to the role of herbivory (Roff & Mumby, 2012). Consequently, the concept of using functional groups as a management tool is well established (Bellwood et al., 2004). However, many previously defined functional groups are in fact trophic groups (McClanahan et al., 2015), which are not necessarily consistent between studies (Parravicini et al., 2021). Trophic group is a single trait and when used alone presents a limited view of functionality.

We went beyond use of trophic groups to exclusively define functionality and considered (SSG, tense) how additional traits mediate responses to fishing disturbance. Body size, for example, determines vulnerability to fishing pressure (Stuart-Smith et al., 2013), and aggregation behaviour affects vulnerability to different fishing methods (Plass-Johnson et al., 2016). This information is useful for formulating management strategies and underpins the reasoning behind our proposed trait-based adaptive management framework.

The TBAM framework suggests using functional groups, derived from a wide range of traits, as broad management units in species-rich fisheries (Figure 1). Using traits in management has been advocated previously, and we outlined a practical approach to implementing those insights. This approach assumes that species in each functional group respond similarly to disturbance impacts and management actions, and so we tested that first assumption.

Provided one can accurately assess the vulnerabilities of different groups of species, managing fisheries in this way allows controlled exploitation of more robust groups and

places limits on fishing for more vulnerable groups. This selectivity and flexibility in how fisheries are exploited lends itself well to actions such as gear-based management, additionally informed by species traits (Mbaru et al., 2019). In applying this framework to other systems or contexts, trait choices can conceivably vary depending on management goals, relevant taxa, and available trait information. Trait selection aims to capture a range of traits denoting different aspects of likely function, and so the framework is flexible to including different traits.

Using a coral reef fishery in Chuuk Lagoon, Federated States of Micronesia (FSM), as a case study (Appendix S1), we explored whether TBAM is a viable strategy. First, we used species traits to identify key functional groups of food fish (species targeted for sustenance and market sales). We then tested how those groups respond to proxies of fishing disturbance and environmental drivers. Finally, we examined how groups' divergent responses to these drivers can inform targeted management strategies, according to their specific vulnerabilities and the needs and priorities of local communities. We considered potential management actions, but did not test their efficacy.

Methods

Fish and coral surveys

Food-fish biomass data and coral diversity and cover data were collected from 61 sites throughout Chuuk Lagoon in 2016, representing a variety of reef types, management regimes, geographic areas, and levels of wave exposure. Fish size and abundance data were collected using 12 stationary point counts (5-m radius, 3 minutes) per site, and food-fish families identified through landings data on target species (Appendix S2). Habitat types covered outer reefs (outside the lagoon), channel reefs, patch and back reefs (inside the lagoon), and inner reefs (adjacent to islands). Detailed survey methods (Houk et al., 2015; Cuetos-Bueno &

Hernandez-Ortiz, 2017) are in Appendix S3. Data available at

<https://micronesiareefmonitoring.com/>.

Reef fisheries activity

Approximate locations of dynamite fishing were obtained from the Chuuk Department of Marine Resources; staff shared experiential knowledge. Nine survey sites were in these areas and were classified as having had dynamite fishing within the last few years. These sites were all located in patch and back reef and inner reef types.

Total annual landings and the number of fishing trips were derived from landings data based on market surveys conducted by Cuetos-Bueno et al. (2018) during 12 consecutive months. These estimates relate to specific fishing areas and are attributed to the nearest ecological survey sites (Appendix S4).

Survey sites were allocated estimates of human population size of the nearest municipality derived from the most recent census (FSM Census, 2010). We assumed that proximity to larger populations implies greater fishing pressure (Cinner et al., 2018). Fishing pressure associated with both local consumption and international export was linked to two locations: Weno, where the state capital and airport are located, and Faichuuk, where most commercial fishers live (Appendix S1) (Cuetos-Bueno et al., 2018). Proximity to these places was interpreted specifically as greater commercial fishing pressure (Cinner et al., 2018). Distance to these markets (kilometers) was calculated with `spDistsN1` from the `sp` package (Pebesma & Bivand, 2005). Mean wave energy (joules per square meter) for each survey site were derived from wind speed, wind direction, and fetch length (Jenness & Houk, 2014).

Fish traits and functional groupings

Trait information was compiled from Fishbase (Froese & Pauly, 2019) and the literature, and data gaps were imputed for phylogenetically related species based on expert opinion. We

selected five traits relating to species' ecological responses to disturbances and fishing sensitivity that had good coverage for the species in the study area and were a combination of continuous and categorical traits (Weiher et al., 1999): maximum length (centimeters), mean pelagic larval duration (PLD) (days), trophic mode, aggregation type, and position in the water column (Table 1). These traits deal with facets of reproductive capacity, life history, feeding ecology, and behaviour that link to several ecosystem functions, vulnerability to fishing, habitat preferences, recovery from disturbance, and requirements for protection (Table 1).

To identify clusters of similar species based on shared traits, we used average-method hierarchical clustering of a species by traits, cailliez corrected Gower dissimilarity matrix (100 runs) (Hennig, 2018). Seven groups were identified by assessing the relative cluster stabilities of 6-10 groupings (Appendix S5). We also used a generalized boosted regression model in which group was modeled as a function of each of the traits. Sequentially improving model fit based on a subset of the traits provided, identifies which trait best predicts the groupings (1000 iterations) (Darling et al., 2012; Greenwell et al., 2019). Community trait space was visualized with a principal coordinate analysis (PCoA) of the dissimilarity matrix, retaining the first four axes as a reasonable assessment of diversity (Maire et al., 2015). The third and fourth PCoA axes are visualized in Appendix S8.

We assessed whether our results were robust to trait choice by comparing our original dissimilarity matrix against matrices with all possible combinations of four out of five of the chosen traits (Mbaru et al., 2019; Mouillot et al., 2021). We used mantel tests to determine that all were strongly correlated with the original distance matrix. We ran separate PCoAs for each trait combination and found they explained similar amounts of variation along their first 4 axes, except when maximum length was excluded (Appendix S9). However, there was strong ecological justification for retaining this trait in the analyses (Table 1).

Relationships of trait groups to the environment and fishing pressure proxies

Separate models were constructed for the square-root-transformed mean biomass (kilograms) of each trait group at each site. Generalized additive models (GAMs), with landings (kilograms), percent coral cover, wave energy (log joules per square meter), nearest human population size (log), and distance to fish markets (kilometers) at each site as smooth terms (thin plate regression splines) and reef habitat type (patch or back, inner, channel, and outer) and method (spear and dynamite fishing) at each site as categorical terms, were constructed (mgcv package) (Appendix S10) (Wood, 2011). The GAMs were selected to avoid assumptions of linearity in relationships and because they cope well with potential concavity issues in spatial data. The number of fishing trips was discarded from the models due to high correlation with landings ($r= 0.985$). Transformations of biomass to the square root were applied to satisfy normality, and all continuous variables were standardized by subtracting the mean and dividing by the standard deviation to aid interpreting the models. We applied interaction terms between coral cover and reef type and wave energy and reef type. Inclusion of interaction terms was determined by whether they better fit the data than the smooth term alone, based on Akaike Information Criterion (AIC) values and visual inspection of residual plots.

Results

Food-fish trait groups and characterization

We identified seven groups from the 131 recorded fish species that encompassed different taxa and trait combinations (Table 2, Figure 2, Appendix S6). Water column position was the best predictor of the groupings (71.36%), followed by trophic mode (10.24%), mean pelagic larval duration (8.77%), maximum length (7.16%), and aggregation type (2.47%). Trait group six contained one species and one observation for the giant moray (*Gymnothorax javanicus*)

and was excluded from further analyses. We also excluded trait group seven. This was the least stable cluster with the largest number of times dissolved, implying that it was not a true grouping, and it contained just three *Myripristis* species (Hennig, 2018). The remaining five groups represented 127 species overall. Group size ranged from 75 to 7 species (Table 2).

Group one contained mostly small fishes with shorter PLDs that prefer swimming above the reef (upper benthic habitat association) and are largely solitary or in small groups (Table 4). It is the largest group and contained several trophic modes, mainly herbivores and predators.

Group two contained 29 species of primarily solitary predators, sharing similar PLDs and body sizes with group one. They were distinguished from similar trophic modes in group one because they occupied a benthic position in the water column. Group three had seven species. They were mainly schooling or grouping, reef pelagic species with the longest PLDs of any of the trait groups. Except for the brassy trevally (*Caranx papuensis*), all were planktivorous or herbivorous Acanthurids. Group four was characterized by large-bodied, upper benthic, solitary piscivores with short or no PLD and included several shark species. Group five also was composed of high trophic level fish, made up of large, pelagic, and schooling species, such as *Grammatorcynus bilineatus* (Figure 2).

Drivers of trait group biomass

Trait group biomass was affected by environmental characteristics and proxy fishing activity measures, and groups responded to different drivers (Table 3, Figure 3). Fishing pressure proxies affected biomass of several groups. Human population had a possible positive relationship with biomass for small, solitary benthic predators (group two; $p=0.058$), but otherwise did not predict biomass. Distance to key markets emerged as having significant relationships with biomass in groups one and four. For example, the farther large, solitary, upper benthic predators were from Faichuuk the lower their biomass (group four; $p=0.006$),

whereas the farther small reef-associated species were from Weno and Faichuuk the higher their biomass (group one; $p=0.006$, $p=0.038$). Wave energy affected biomass when interacting with reef type. Mean annual landings did not affect biomass of these trait groups (Table 3). The presence or absence of spearfishing (versus dynamite) activity at a site strongly affected biomass of small, solitary, benthic predators (group two, $p=0.006$) and large upper benthic predators (group four, $p<0.001$). Both tended to have lower biomass at sites where only spearfishing occurred (no reported dynamite fishing) (Appendix S13, S15). Reef habitat types emerged as important predictors of biomass for group two ($p=0.003$) and four ($p=0.041$) in their own right. They also interacted with coral cover and wave energy for group two and with wave energy for group three. Wave energy had a roughly unimodal relationship with biomass at outer reefs for group two's small, solitary, benthic predators ($p=0.028$) and a positive relationship with biomass at inner reefs for group three's schooling planktivores ($p=0.008$). At patch and back reefs, biomass of group three declined as wave energy increased ($p=0.023$). Biomass of small reef-associated species in group one increased as coral cover increased ($p=0.031$) (Table 3).

Discussion

Effective use of the TBAM framework requires that groups of species with similar traits respond similarly to disturbances and management. For a case study of marine food fishes on a Pacific atoll, we demonstrated that trait-based groups indeed showed group-specific or variable magnitudes of responses to environmental and human drivers, such as proximity to ports and dominant fishing methods. By extension, trait groups were also likely to respond comparably to group-specific management actions. The TBAM framework thus breaks down a diverse fishery into convenient units that can be prioritized for different management actions, enabling fishing of some groups and protection of others.

Functional implications of trait group responses to biophysical and socioeconomic variables

Chuuk's food-fish community comprised five stable groups that captured functional roles and exhibited different relationships with key environmental and socioeconomic drivers. A multitude of traits characterized these groups, highlighting that traits that relate to a range of ecological function and susceptibility to threats are most appropriate for TBAM, despite the frequent use of trophic mode as a proxy for function in the coral reef literature (McClanahan et al., 2015; Nash et al., 2016; Richardson et al., 2020). Groups were further distinguishable in terms of desirability within the fishery. Larger species tended to be targeted for commercial export, and many of the species in group one represented important targets for subsistence fisheries in Micronesia. Fishing methods, habitat types, coral cover, wave energy, and distance to key markets all emerged as important predictors of group biomass. Indeed, many of these also drive total biomass (McClanahan et al., 2015; Cinner et al., 2018), so as subsets of the total assemblage we would expect to see these responses among the trait groups.

Small, solitary, benthic predators (group two) and large upper benthic predators (group four) both had higher biomasses at sites where dynamite fishing had occurred. Similar to this finding, greater biomass of high trophic level fish has been associated with fishing disturbance (Graham et al., 2017). Group four contained several shark species, including the grey reef shark (*Carcharhinus amblyrhynchos*), which has a notably high biomass relative to the broader fish community. The higher numbers of sharks at dynamited versus spear-fished sites may suppress herbivory and alter ecosystem functioning (Rizzari et al., 2014). Our study design did not allow us to parse whether these patterns were an effect of changing behaviour, altered biomass because of disturbance, or an effect of site selection by fishers. The relationship between these species and destructive fishing activity requires further investigation.

Reef-associated, short PLD species (group one) increased in biomass as distance from the Weno market increased and are desirable catch. Of the 20 species that collectively make up 75% of the landings in Chuuk (Cuetos-Bueno et al., 2018), 70% were represented by this group and a further 25% were represented in group two. Body size, more than trophic level, is a key driver of exploitation in other Micronesian fisheries, such as Guam, where smaller species and individuals are making increasing contributions to the overall catch (Houk et al., 2018). Species in groups one and two had smaller maximum body sizes (median 47cm and 50 cm respectively) than all the other groups, and the proportion of these fish in landings suggested they were fished because other, larger species had been depleted.

Estimates of annual landings help identify unsustainable exploitation, areas of vulnerability, and apparent stability (Cinner et al., 2016; Mbaru et al., 2019). However, mean annual landings do not predict biomass of our trait groups, and landings data at the national level can be unreliable (Pauly & Zeller, 2016). In most island regions, landings already outstrip sustainable levels, and the FSM is considered fully exploited. Landings are thus not necessarily a useful indicator of community dynamics in the context of fisheries that are fully or overexploited (Harborne et al., 2018).

Applying trait-based adaptive management

Insights from our case study have potential to inform management strategies. The TBAM framework is an objective-driven management approach that considers trade-offs in species requirements against the needs and adaptability of fishers. Actions that have been identified as contextually appropriate because they work within existing management structures and traditional strategies include MPA networks with designated areas for commercial versus subsistence fishing, gear, and species-based restrictions (Houk et al., 2016). Trait-based, functional groupings fit particularly well with gear and species- and trait-group restrictions (Mbaru et al., 2019), and the cumulative effects of different actions can be positive for

biomass overall (Melnychuk et al., 2021). Spatial features of human activity (i.e., proximity to key markets) and an understanding of how they interact with the biomass of different trait groups can inform spatial management, such as temporary closures (Appendix S17).

For example, our findings indicated that current fishing effort was focused on group one, which contained species that are valued for local consumption in Micronesia (Cuetos-Bueno et al., 2018). Group one was also the largest trait group derived from our clustering. A limitation of our study is that the food-fish community is subset of the entire assemblage of reef fishes. Because these species will inherently share several traits, it is unsurprising that the clustering produced one much larger group, which may also arise when applied to other datasets of only fished species. Larger groups also imply species occupying a broader functional niche compared with specialists in smaller trait groups.

To manage this group with the TBAM framework, actions such as prioritizing local subsistence exploitation over commercial export or placing size restrictions on catches could help maintain biomass and key functions (i.e., herbivory) while enabling some fishing of an important group of species. It may also be practical to have some more targeted management within large trait groups, such as widely employed restrictions on parrotfish (Pinheiro et al., 2021) or on morphologically similar species (to facilitate communication and enforcement of any restrictions) and species-specific actions, such as bans for *Bolbometopon muricatum* (Roff et al., 2017). The TBAM approach also offers a way to prioritize. In contexts where management resources are limited, focusing on one or two large, stable groups with particular importance to the fishery may yield maximum benefits. In contrast, less stable trait groups, and the species within them, will have to be evaluated by managers on a case-by-case basis as to their utility for inclusion in the framework.

We did not capture intraspecific trait variability (Villéger et al., 2017). This had implications on our interpretation of results, such as the role of body size in size-selective fisheries, where

targeting of smaller species or earlier life history stages can imply overexploitation of other trait groups. Management decision-making based on the TBAM framework needs to consider this limitation. The exact systems that link different traits to ecosystem function are unknown for reef fishes (Bellwood, Streit, et al., 2019), but managing for specific functions could certainly be incorporated in this framework. Including additional traits as data on them become available would strengthen the groupings. Trait choice invariably influences the outcomes and interpretations of trait-based work (Mouillot et al., 2021), which is why here we tried to include traits that encompassed several possible functional roles and responses to disturbance. Traits that capture productivity, such as size at maturity or generation time, would be good candidates for inclusion in future TBAM frameworks where that information exists (Taylor et al., 2014). Fisheries with reduced biomass can still have relatively high productivity, and the relationship between the two is important for understanding how fisheries are responding to exploitation (Morais et al., 2019).

Ultimately, a balance must be found that minimizes impacts to fishers while recognizing that environmental change may require yield reductions. Decisions must be made in full consultation with affected communities to accommodate local priorities, requiring robust links between local people and management bodies (Jupiter et al., 2014). There is a strong precedent for the trait-based management proposed here in traditional marine resource governance. Such practices, including adaptive temporary closures and gear and species restrictions, have a long and successful history throughout the Pacific (Cinner & Aswani, 2007), and areas with traditional management remain “bright spots” with high fish biomass (Cinner et al., 2016). Partitioning of resources to restrict fishing of certain species or groups while exploiting others is thus an established concept in coral reef fisheries (Johannes, 1982; Cinner & Aswani, 2007). Trait groupings could therefore empirically support the ecological component of decision-making processes in traditional governance, government, or

nongovernmental-organization-led efforts. How well trait groups work for fisheries management within the wider context of protecting biodiversity and ecosystem functioning needs to be tested. This includes understanding the interactions between groups and how focusing fishing effort on perceived resilient groups could have repercussions for others. Whether or not the fisheries management proposed under the TBAM approach enables people to meet their subsistence and livelihood needs will also need to be addressed.

Implications for conservation practitioners and managers

Effective conservation of functioning coral reefs, or indeed any ecosystem near dependent human populations, requires informed decisions that enable some level of exploitation to meet local subsistence and livelihood needs. Growing human pressures combined with escalating climate impacts heap additional urgency on balancing these trade-offs between human and biodiversity requirements. We used a Pacific coral reef fishery as proof of concept, but the trait-based methods and accompanying TBAM framework are applicable in other coral reef areas, or indeed across marine systems. By reducing some of the complexity that comes with managing multispecies fisheries (McClanahan et al., 2015), it provides opportunities for managers to meet both conservation goals and local needs under an adaptive framework.

We identified key trait groups for food fish in Chuuk and illustrated how patterns of human resource use are influential drivers of trait structure and function on coral reefs. We found that groups were affected differentially by gradients in habitat and fishing proxy measures. The TBAM framework outlined here is a suggestion for how the growing understanding of traits and functions could support management decision-making by incorporating flexibility for different local contexts and by providing the scope to use existing management actions and to design new ones. These outcomes provide a catalyst to further explore targeted, trait-

based adaptive management of key groups of species that transcends biodiversity-based management of coral reefs.

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Supporting Information

Additional supporting information may be found in the online version of the article at the publisher's website.

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Table 1. Selected species traits and justification for inclusion in hierarchical clustering analysis to derive trait-based groups of food fish. .

| Type | Trait | Definition | Justification |
|----------------------------|---|--|---|
| Morphological/Life history | Maximum length (Numeric) | Maximum tail length (cm) recorded in the species core range. | Important for species sensitivity to predation, thermal resistance, fecundity, extinction risk, and metabolic rates (Graham et al., 2011; Beauchard et al., 2017). Related to vulnerability to size selective fishing (Stuart-Smith et al., 2013; Bellwood, Streit, et al., 2019). |
| Reproductive | Mean pelagic larval duration (PLD) (Numeric) | Theoretical time (days) that a larval fish remains viable in the water column, measured from hatching or spawning. | Associated with range size, recovery following disturbance and dispersal connectivity (Álvarez-Romero et al., 2017; Wilson et al., 2018). |
| Trophic ecology | Trophic mode (Factor) | Broad diet categories. (Piscivore, predator, planktivore, | Linked to food acquisition, growth requirements, demographics (predator-prey interactions), vulnerability to |

| | | | |
|-----------|---|---|---|
| | | omnivore, corallivore, herbivore) | climate change and nutrient cycling (Graham et al., 2011; Beauchard et al., 2017). |
| Behaviour | Position in water column (Factor) | Location on reef where species spend the most time. (pelagic, reef pelagic, upper benthic, benthic, demersal, subbenthic, sand associated, cnidarian associated, echinoderm associated and algae) | Ties in with motility, foraging, migratory requirements, and dispersal (Stuart-Smith et al., 2013; Beauchard et al., 2017). |
| Behaviour | Aggregation (Factor, ordered) | Grouping behaviour (schools, groups, harems, pairs, solitary) | Linked to foraging strategy, vulnerability to predation and different fishing methods (Plass-Johnson et al., 2016). |

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Table 2. Food-fish trait groups derived from hierarchical clustering, with number of species (n=131), broad characterization of defining traits, example species and functional implications of each group modelled against habitat and fishing pressure. Cluster stability and number of times resolved derived from the clusterboot function (Hennig, 2018), which runs bootstrap iterations to test stability. Clusters are more stable when stability is closer to 1, and those that have been dissolved (do not appear in new bootstrapped iterations) more are less stable.

| Group | Cluster stability | no. times dissolved | no. species | Broad characterization | Example species | Functional implications |
|-------|-------------------|---------------------|-------------|--|--|--|
| 1 | 0.839 | 8 | 75 | Small body size, mid-range PLD, reef-associated fishes. Mostly upper benthic, some cnidarian associated. Combination of trophic modes and aggregation types (majority are solitary). | <i>Acanthurus blochii</i> , <i>Balistoides viridescens</i> , <i>Chlororus bleekeri</i> . | Largest, broadest group. Would likely require further classification for management. Comparatively small body size, association with the reef and shorter PLD characterizes them as site attached species that may be vulnerable to localized disturbances. Species in this group perform functions as grazing herbivores and predators of smaller fish and invertebrates. |

TRAIT GROUPS FOR FISHERIES MANAGEMENT

| | | | | | | |
|---|-------|----|----|--|--|--|
| 2 | 0.684 | 33 | 29 | Solitary benthic predators, with similar PLD and body size ranges to group 1. | <i>Epinephelus howlandi</i> , <i>Parupeneus barberinus</i> , <i>Sargocentron tiere</i> | This group has smaller body sizes than the other predator or piscivore groups. This is an important functional distinction between predators that consume a range of fish and invertebrates, versus piscivores targeting other fishes. |
| 3 | 0.910 | 7 | 7 | Reef pelagic, primarily schooling or grouping planktivores with long PLDs. Contains one reef pelagic predator. | <i>Acanthurus mata</i> , <i>Naso annulatus</i> , <i>Caranx papuensis</i> . | Reef pelagic species. From a functional perspective this is important for nutrient cycling between reefs and pelagic systems. Mainly planktivores or algal browsers (Fox & Bellwood, 2013). <i>Caranx papuensis</i> is an incongruous inclusion, but because it shares habitat-uses is potentially vulnerable to the kinds of disturbances that affect the rest of this group. |

TRAIT GROUPS FOR FISHERIES MANAGEMENT

| | | | | | | |
|---|-------|----|---|---|---|--|
| 4 | 0.721 | 17 | 9 | Large, mainly solitary piscivores with short or no PLD. Mostly upper benthic. | <i>Aphareus furca</i> , <i>Carcharhinus melanopterus</i> , <i>Syphraena barracuda</i> | Most reef sharks occupy a similar functional role to other large piscivores (Frisch et al., 2016), and so are included in this group. |
| 5 | 0.925 | 4 | 7 | Large, pelagic, schooling or grouping predators or piscivores. | <i>Caranx sexfasciatus</i> , <i>Elagatis bipinnulata</i> , <i>Seriola lalandi</i> | Distinguished from group 4 by pelagic rather than reef association and therefore play different roles in nutrient cycling (Roff et al., 2016). |
| 6 | 0.640 | 38 | 1 | Giant moray eel. Large, demersal, solitary predator with a long PLD | <i>Gymnothorax javanicus</i> | Excluded from further analysis. |
| 7 | 0.470 | 64 | 3 | Small, solitary planktivores with longer PLDs. Either subbenthic or cnidarian associated. | <i>Myripristis adusta</i> , <i>Myripristis berndti</i> , <i>Myripristis kuntee</i> | Excluded from further analysis. |

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Table 3. Degrees of freedom (df) for parametric terms, effective degrees of freedom (edf) for smooth terms, and *p* values for generalized additive models (GAMs) with smooth, parametric, and interaction terms for biomass of each fish trait group (1-5) at each site (*n* = 61).

| Terms | | 1 (df or edf, <i>p</i>) | 2 | 3 | 4 | 5 |
|-------------------|--|--------------------------|--------------|--------------|--------------|----------|
| Parametric | Reef Type (RT) | 3, 0.693 | 3, 0.003** | 3, 0.132 | 3, 0.041* | 3, 0.466 |
| | Spear | 1, 0.132 | 1, 0.006** | 1, 0.076 | 1, <0.001*** | 1, 0.547 |
| | Dynamite | 1, - | 1, - | 1, - | 1, - | 1, - |
| Smooth | Mean annual landings (kg) | 1, 0.158 | 1, 0.592 | 1, 0.388 | 1, 0.661 | 1, 0.560 |
| | (log) Wave energy (joules/m ²) | 1, 0.531 | - | - | 1, 0.146 | 1, 0.376 |
| | (log) Population | 1, 0.220 | 1.755, 0.058 | 1, 0.541 | 1, 0.670 | 1, 0.866 |
| | Coral cover (%) | 1, 0.031* | - | 1, 0.573 | 1, 0.867 | 1, 0.945 |
| | Distance from Weno (km) | 1, 0.006** | 1, 0.393 | 1.533, 0.161 | 1, 0.265 | 1, 0.775 |
| | Distance from Faichuuk (km) | 1.857, 0.038* | 1, 0.819 | 1, 0.911 | 1, 0.006** | 1, 0.396 |
| | Interaction | energy:RT channel | - | 1, 0.060 | 1.375, 0.668 | - |
| energy:RT inner | | - | 1.375, 0.740 | 1, 0.008** | - | - |

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| | | | | | | |
|--|--------------------------|---|------------------|------------------|---|---|
| | energy:RT outer | - | 1.822, 0.030* | 1, 0.910 | - | - |
| | energy:RT patch, back | - | 1.508, 0.051 | 1.515, 0.023* | - | - |
| | cover:RT channel | - | 1, 0.261 | - | - | - |
| | cover:RT inner | - | 1, 0.028* | - | - | - |
| | cover:RT outer | - | 1, 0.188 | - | - | - |
| | cover:RT patch, back | - | 1, 0.812 | - | - | - |

* $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$.

TRAIT GROUPS FOR FISHERIES MANAGEMENT

Figure 1. Generalized schematic of the trait-based adaptive management framework, using theoretical trait groups, threats, and management actions.

Figure 2. Characteristics of trait groups of food fishes in Chuuk: (a) 7 trait-group clusters based on hierarchical average clustering of the dissimilarity matrix (branch length truncated), (b) principal coordinates analysis representation of food fish community trait space (point size weighted by overall biomass observed during 2016 surveys and points colored by trait group; first two axes, 17% of variation; first four axes, 28% of variation) (Equivalent figure with species labels in Appendix S7, and plot of axes 3 and 4 in Appendix S8.), (c) trait variability for mean pelagic larval duration (days), maximum length (cm), trophic mode, aggregation behavior, and position in the water column for each of the 8 food-fish trait groupings.

Figure 3. Partial effects plots for continuous variables (smooth terms) in Generalized Additive Models (GAMs) of trait group biomass at each site in group 2-4 in which $p < 0.05$ for that term. Significant terms are coral cover, wave energy and distance to ports (colors, groupings in Fig. 2). Partial effects plots for all terms in each GAM are in Appendices S11 – S16.

Food fish community

Groups derived from species traits

Small-bodied, reef-associated predators



Schooling planktivores



Large pelagic piscivores



Threats

Vulnerable to overharvest during spawning

Increasingly targeted for commercial export

Economically important for commercial export (existing fishery)

Blanket management actions

No Take Zones, Marine Protected Areas
Ecosystem-based fisheries management

Group-level management actions (TBAM)

Spatial and or temporal protection for key spawning areas or habitat types

Regulate exports but allow fishing for subsistence livelihoods

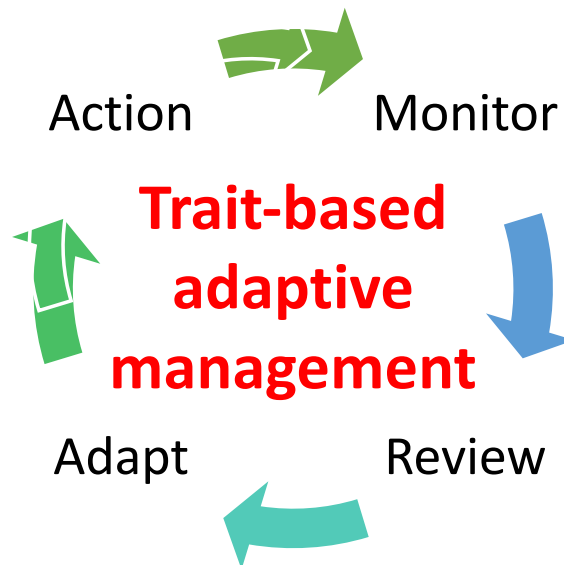
Enable some sustainable commercial export

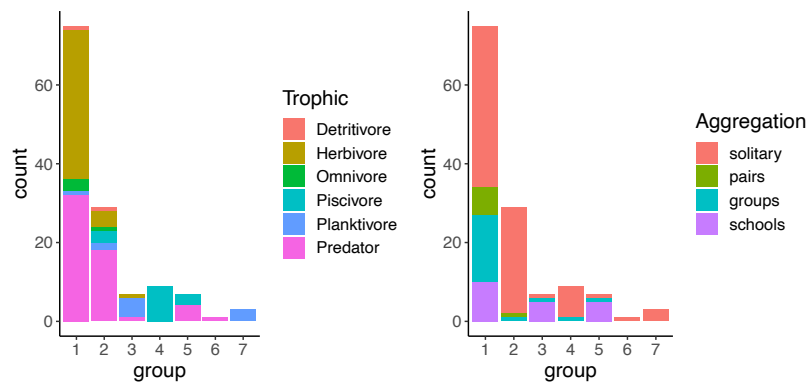
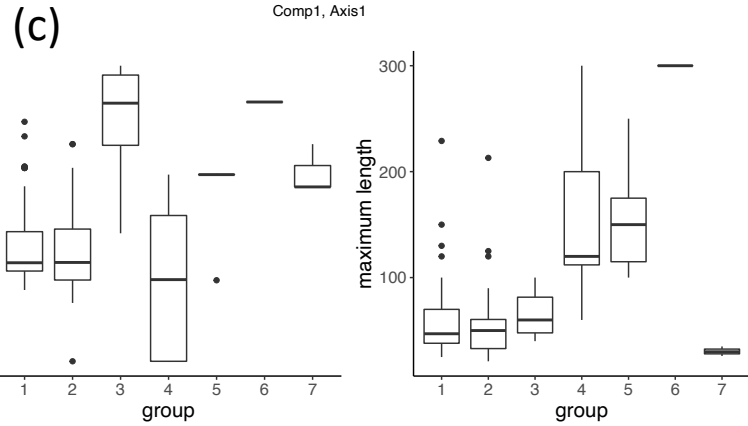
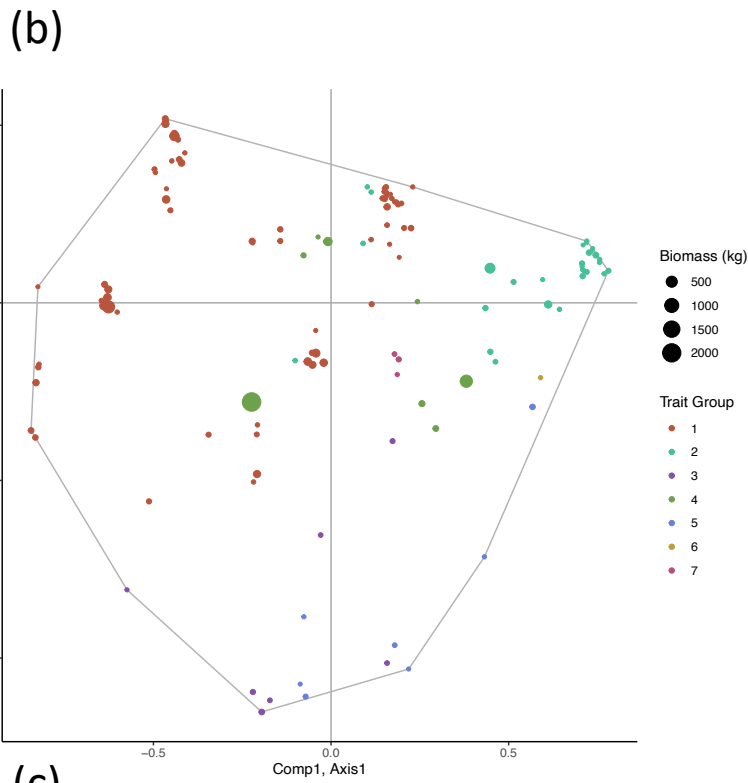
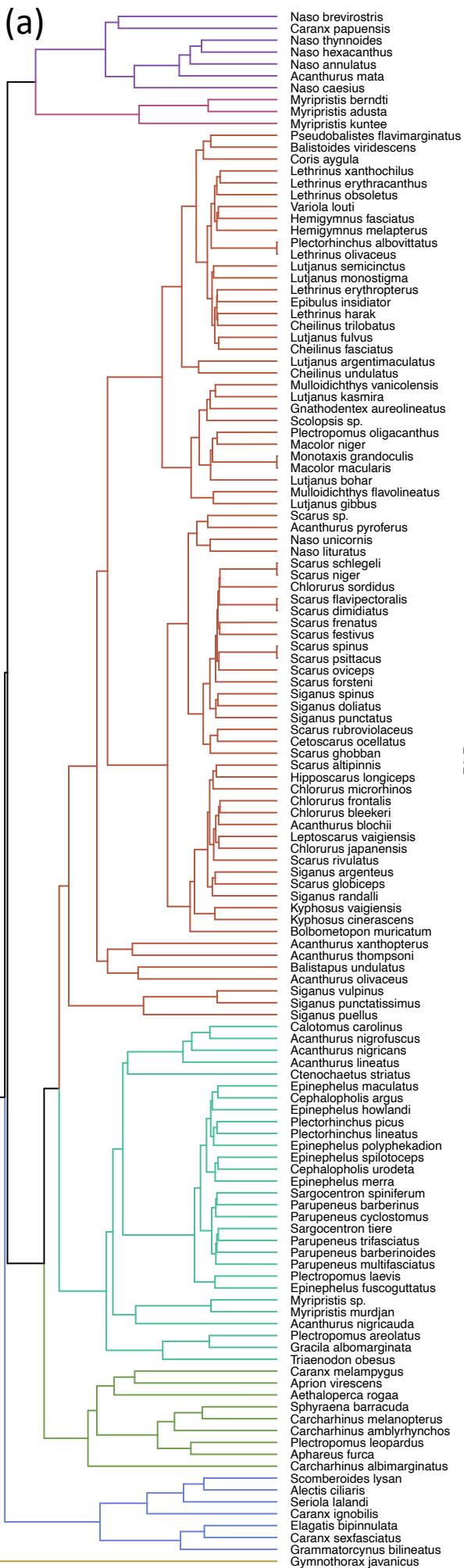
Species or community-level management actions

Allow controlled exploitation of a locally significant species

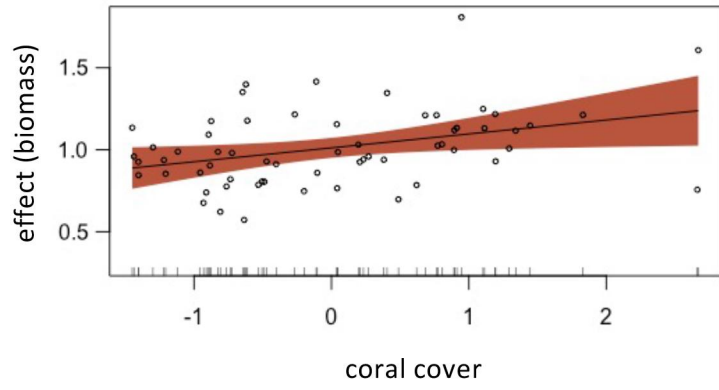
Species-specific catch limit or export ban for species with slow reproductive life history

Catch limits on specific, vulnerable species

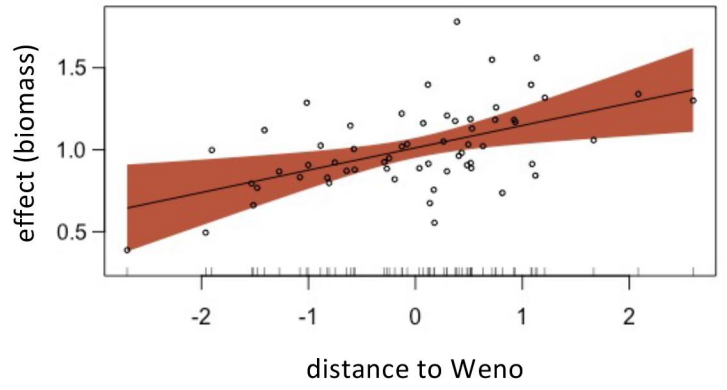




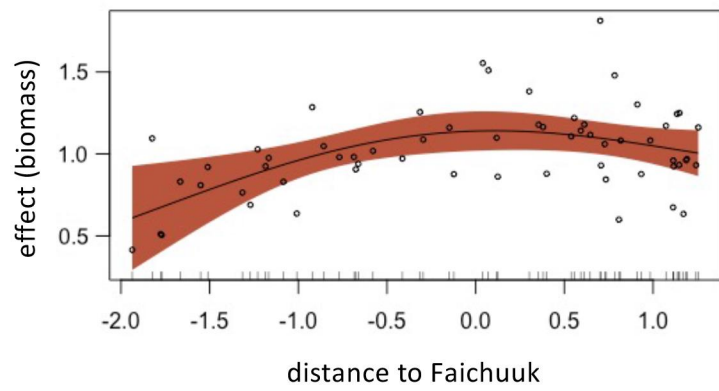
Group 1



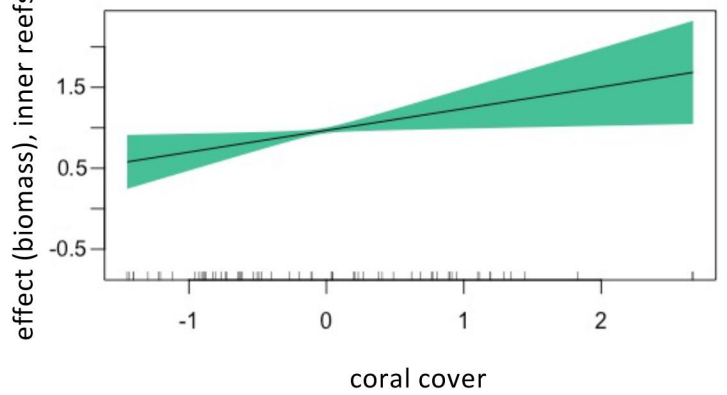
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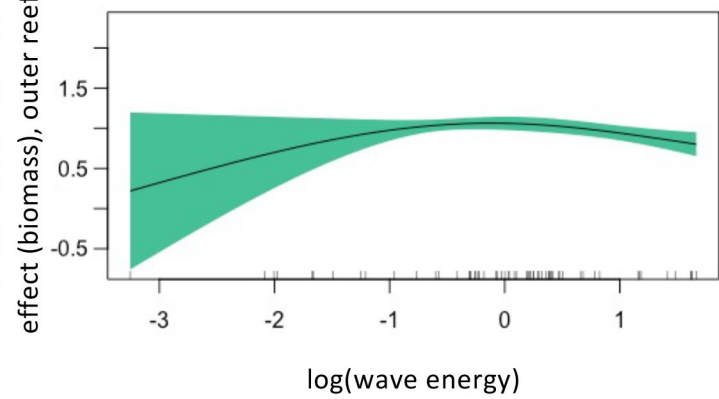
Group 1



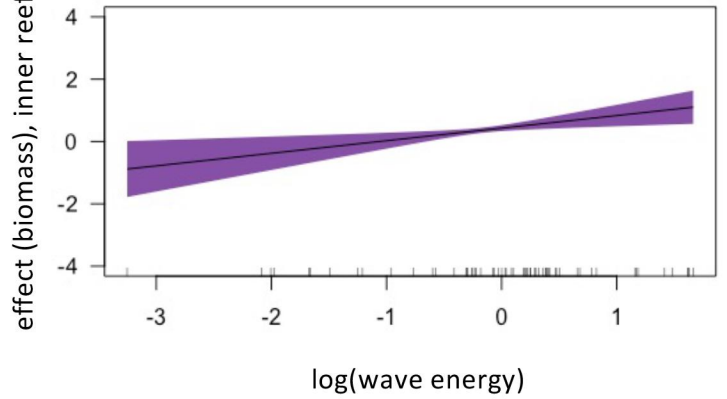
Group 2



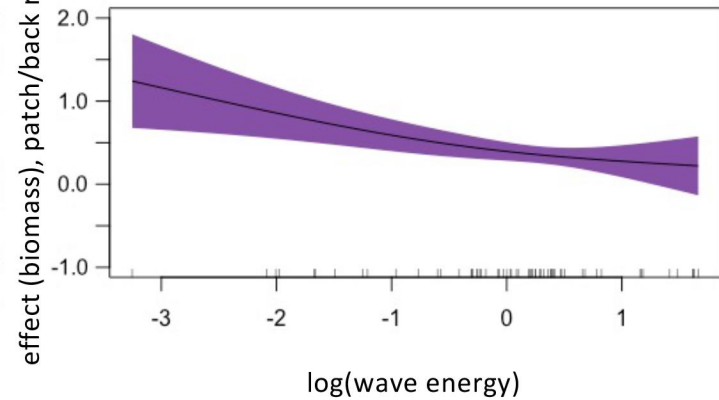
Group 2



Group 3



Group 3



Group 4

