

## Best- practice fisheries management associated with reduced stocks and changes in life histories

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### Abstract :

Current best-practice policy recommendations for managing fish stocks are achieved by a mixture of maintaining modest fishing mortality (restricting effort, times and gear), marine reserve networks and not subsidizing unprofitable fisheries. A seldom evaluated question is how effective these proposed approaches are for maintaining all fish stocks and biodiversity elements in marine seascapes? Both recommended and unrecommended fishing practices fragment habitats and reduce metapopulation connectivity with potentially unexpected seascape-level consequences. To better understand these outcomes, we pooled and evaluated fish community data into two seascape groupings for comparisons of biomass and life-history characteristics. These were remote baseline reefs (>9 hr from regional cities and >4 hr from human habitation, n = 584 locations) and those emulating best-practice seascapes (BPS, n = 140). BPS were a mix of high-compliance marine reserves (fishable biomass =  $892 \pm 696$  ( $\pm$ SD) kg/ha, n = 95; >5 km<sup>2</sup> and >15 years of closure) and fished seascapes ( $478 \pm 395$  kg/ha, n = 45) that had biomass near the maximum sustained yield (MSY) estimates for coral reefs. The fish communities in the BPS locations differed considerably from the remote baseline by having 49% of the median and 32% of the mean biomass, smaller community-weighted body sizes, and faster growth and mortality rates. Most of the declines were associated with high biomass taxa that included carnivorous jacks (Carangidae), snappers (Lutjanidae), groupers (Serranidae) and triggerfish (Balistidae), which were reduced to between 11% and 28% of the mean baseline. Surgeonfish (Acanthuridae) and parrotfish (Scarinae) were an exception in being reduced to only 48 and 53% of the baseline's mean biomass, respectively. As expected, community-level body sizes and age values were larger and trophic level higher, while growth and mortality were lower in baselines than BPS seascapes. After evaluating the different environmental responses between seascapes and accounting for the largest geographic factor, longitude, we evaluated the community responses to 4 possible BPS planning scenarios. Biomass responses to age and trophic level and length at maturity were similar and predictable for the two seascapes. In contrast, growth and generation time responses differed between seascapes. Baselines had peak biomass patterns at intermediate values, whereas BPS displayed a declining influence of growth and a saturating response

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for generation time. Consequently, deviations between BPS and baselines indicate that current BPS proposals do not fully emulate the ecology of remote or wilderness locations. Therefore, wilderness will be a required management designation if the global fish communities are to be fully conserved.

**Keywords** : baselines and benchmarks, fisheries and ecological indicators, fragmented populations, island biogeography, pristine or virgin biomass, seascapes, sustainability

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## 1. INTRODUCTION

Modern fisheries are, at best, managed by a combination of active marine reserve networks containing fisheries closures located within fished seascapes managed to maintain mortality at sustainable levels (Gaines et al. 2010). Therefore, many current stakeholder policies are focused on creating a patchwork of marine reserves interspersed among regulated fishing grounds (Sumaila and Pauly 2007; Roberts et al. 2017; Marshall et al. 2019; Rassweiler et al. 2020).

When fishing is not highly profitable or subsidized, economic costs will ensure fishing effort is restricted to modest travel distances from landing-sites; which, in principle, would be interspersed with modest sized marine reserve networks (Lester et al. 2013; Schuhbauer et al. 2017; Sala et al. 2018). This best-practice system is generally promoted by modelling studies as a good way to protect communities of fish and prevent their degradation and loss of resilience (O’Leary et al. 2016). While this system may be beneficial to people and sustainable fisheries, the full consequences for fish populations are less well understood. Species with large sizes, slow growth rates, large space needs, or migratory behavior are, for example, still expected to be vulnerable (Mellin et al. 2016; Hilborn et al. 2020; MacNeil et al. 2020).

Marine reserve outcomes are sensitive to a number of factors, including size, age, enforcement and isolation from human populations (Edgar et al. 2014; Cinner et al. 2020). Nevertheless, there is some evidence that permanent well-enforced small to modest-size reserves (~5 km<sup>2</sup>) in fished seascapes are sufficient for conservation and management of many important fish stocks (Rolim et al. 2019; McClanahan 2021). For example, a modelling study based on home ranges of local coral reef fish suggested that marine reserves of 10-km diameter could include the home ranges

of 70% of reef species (Krueck et al. 2018). Studies of reef fish in the Indian Ocean suggests biomass increased with closure size but was constant between 5 to 10 km<sup>2</sup> (McClanahan et al. 2009; McClanahan and Graham 2015). Additionally, life history traits of body size, age, and growth changed predictably along a biomass gradient but stabilized near 1200 kg · ha<sup>-1</sup> (McClanahan 2019a). Yet, there is increasing recognition that life spans and home ranges of many taxa, notably highly mobile migratory species and sharks (Carcharhinidae and Ginglymostomatidae) but also groupers (Serranidae), grunts (Haemulidae), and parrotfish (Scarinae), are not accommodated by typical marine reserves (Kaunda-Arara and Rose 2004; Chateau and Wantiez 2009; Sadovy de Mitcheson et al 2013; Lascelles et al. 2014; MacNeil et al. 2020). These species appear to require larger intact seascapes located far from people and seafood markets (Edgar et al. 2014; McClanahan and Graham 2015; Cinner et al. 2020; Dwyer et al. 2020; Graham et al. 2020).

How this best-practice reserve-regulated fisheries management affects the seascape and its consequences for the taxa, their life histories, stock biomass, and other trade-offs is barely understood (Lester et al. 2013; Sala et al. 2018, 2021; Cabral et al. 2019). Certainly, limited space caused by either destruction, degradation, and fragmentation of habitats are considered key threats to the persistence of many large terrestrial species and many parks and reserves function like ecological islands (Whittaker et al. 2005, 2017). Oceanic islands and isolated reefs, rivers and lakes are comparable systems, and therefore potentially influencing the local dynamics of marine species metapopulation dynamics (Crowder et al. 2001; Fuller et al. 2015). Yet, spatially disrupted metapopulations are not so clearly observed as on land, requiring other proxies to estimate their impacts (Sale et al. 2008; Jones et al. 2018). Nevertheless, some marine

ecosystems including coral reefs, naturally occur as underwater islands and support among the highest diversity of animals in the ocean (Barber and Meyer 2015). Therefore, does fragmenting the reef seascape and isolating some area-sensitive fish populations produce similar outcomes to terrestrial systems by disrupting metapopulations and source-sink processes? The answers should illuminate the consequences of best-practice policies and recommendations that have emerged to reduce the permanent long-term impacts of fishing. The ability to evaluate and answer these large-scale geographic questions is increasingly possible due to the large-scale application and coordination of underwater visual observations and sharing of fish census data (Cinner et al. 2020).

Here, the potential problem of disrupting fish metapopulations is addressed by comparing fish communities on coral reefs in locations that act as proxies for the future best-practice fisheries and a control, baseline, or wilderness condition (Fig. 1). The proposed future state or best-practice seascape (BPS) would be one where marine reserves are common and located in some balance or design between coverage by reserves, such as 20 to 30% of the area, with the larger remaining coverage occupied by sustainable fishing. While the BPS is difficult to achieve experimentally, we can develop a proxy for it by evaluating sites within current seascapes containing a mix of moderate-sized marine reserves and sustainable fishing (e.g.  $B_{msy} \sim 0.5B_0$ ). Comparing sites emulating BPS conditions with the baseline state should provide some indication of the consequences of current proposals to manage fish populations with this form of spatial organization (Sala et al. 2021). Some large-bodied species, such as sharks for example, are reported to be affected by BPS seascapes because they are less common in nearshore marine reserves than remote locations (Juhel et al. 2018; Dwyer et al. 2020; MacNeil et al. 2020).

Predictions are that fisheries and fish community metrics in BPS should reflect disrupted metapopulations, especially among species' populations that are affected by isolation and low connectivity in space (Mellin et al. 2010a). However, apart from sharks, the status of the larger community of fish in different seascape contexts has not been well evaluated, leaving a number of unanswered questions. Are some taxa of bony fish impacted by fishing and the disruption of their metapopulation structure not receiving the same scientific and societal attention? How good are the assumptions that marine reserves stop the disruption of fish metapopulations and subsequent community reorganization (Crowder et al. 2001; Ovando et al. 2021)? Could larval and adult dispersal or source-sink locations be too spatially and temporally variable to sustain natural and stable meta-populations even with reasonable reserve coverage (Figueira 2009; Botsford et al. 2009)? For example, equilibrium biomass levels in marine reserves are reported to be considerably lower than remote baselines (Chabanet et al. 2016; D'Agata et al. 2016, McClanahan et al. 2019). Therefore, to understand the population consequences of either degrading, fragmenting the seascape, and isolating populations for specific taxa, we evaluated underwater visual census data of coral reef fish across a large expanse of the Indian and Pacific oceans in different remoteness or wilderness contexts (Fig. 1). We identified fished and marine reserve sites that should act as proxies for the best-practice outcomes and baseline controls expected to have undisturbed metapopulation dynamics. While this proxy method lacks the strength of strong experimental designs, the large sample size and geographic scale should compensate for some of the weaker inferences.

The above questions ask if the patterns seen in fish communities fit the related predictions of metapopulations and island biogeographic theory (MacArthur and Wilson 1967; Hanski 1999; Sale et al. 2006; Whittaker et al. 2017)? That is, if populations inhabit discrete habitat patches and interpatch dispersal is neither so low as to negate significant demographic connectivity or so high as to produce independence of local population dynamics, then increased isolation should lead to increased local extinctions (Mellin et al. 2010a,b). Changing source-sink dynamics of fish sub-stocks will produce reef fisheries seascapes increasingly influenced by discrete populations and their colonization, extinction, and particularly survival rates (Figueira 2008; Ovando et al. 2021). Even in the presence of marine reserves, local population depletion should increasingly isolate some vulnerable populations into refuge habitats. Thus, we would expect a considerable reorganization of the community that will be variable and dependent on the sensitivity of the species to spatial disruption (Kritzer and Sale 2006). This is to be expected particularly among species living in fractured habitats with small body size, high reproduction, and short generation times, common to some types of coral reef habitats, such as isolated reef islands (McClanahan and Arthur 2001). These species are more likely to have metapopulation structures and consequences for elevated local extinction. The consequences should depend on the scale of the seascape and resilience to habitat and population disruption. Consequently, given the broad-scale reporting of a large depletion of biomass between baseline and BPS seascapes, which taxa would be most affected?

The predictions are that common life-history metrics, such as body sizes, growth rate, mortality, generation time, and diets respond in the directions predicted for habitat fragmentation and isolation of metapopulations. Predictions include less biomass, fewer taxa as high trophic levels

(i.e. carnivores), changes in the distribution of body sizes to fit the space and resources accessible in the reduced and more sparsely distributed habitats. These changes in resources and body size would be expected to increase growth and mortality or turnover in BPS compared to baseline seascapes. Species assemblages present across large geographic scales are difficult to compare; therefore, our focus was on coarse taxonomy and pooled-species life-history predictions. Given the scale of the problem and the lack of a planned data collection for the preferred manipulative experimental design, the inferences from this study should be seen as exploratory and having the common limitations of large-scale descriptive studies.

## **2. METHODS**

### **2.1 Study sites and design**

The study compiles a large data set on fish communities compiled by the NOAA Pacific Islands Fisheries Science Center's Coral Reef Ecosystem Program for Pacific Island, islands under French jurisdictions in the southwest Indian Ocean and New Caledonia, and the larger Western Indian Ocean. The full data include 724 coral reef locations and habitats located throughout the Indo-Pacific region (Fig. 1). Previous studies of fish stocks have shown that their distance from cities or human habitation is among the strongest drivers of total fish biomass (Maire et al. 2016; Cinner et al. 2019; 2020; McClanahan et al. 2020). At ~9 hours from regional cities or ~4 hours from human habitation, biomass values tend to asymptote and lie within a confidence interval with modest variability (D'Agata et al. 2016; McClanahan 2020). Consequently, these distance thresholds were used to discretely categorize our studied reefs. Sites included in the evaluation met a fished, nearshore marine reserve, or a wilderness or baseline criteria. Baselines sites had to be > 9 hours in travel time to the nearest regional market or city and >4-hours from human

habitation (Maire et al. 2016). We examined the distance to cities and human habitation and found that 584 reefs were both >9-hours from cities and >4-hours from human habitation (McClanahan 2020). The remaining sites were either in high-compliance reserves of moderate size, fished reefs near reserves (often used as controls for evaluating reserve impacts) or < 9-hours travel time to cities (n=140). To avoid small size and early closure aspects of reserves that might not reflect planned BPS, we only included reserves sites that were older than 15 years since fishing was prohibited and having total closure areas of between 5 km<sup>2</sup> and 100 km<sup>2</sup>. One large park in Mozambique was included because most of the area was not coral reefs but protected dugong habitat (Appendix 1b). Thus, we avoided including the many recent small community closures and the very large and remote marine reserves that might act more like baselines (i.e. Northwestern Hawaiian Islands; Edgar et al 2014). The intention here was to have the BPS category reflect a present or future nearshore state of moderate sized high compliance closures located among reefs fished near maximum sustained yield.

The study of these sites was unplanned but based on a compilation of selected sites using the above criteria. While a potential weakness, the large replication and diversity of locations should be seen as a strong sampling element that can uncover patterns that can be tested with stricter large-scale experimental designs, such as before and after management initiation or matched sites comparisons (Kelaher et al. 2015). Consequently, different environmental and human influence contexts could inform hypotheses for future better-controlled comparisons. Expected biases in the design are that BPS exist more frequently in inhabited and fished seascapes near continents or larger islands while baselines are more frequently offshore and on uninhabited smaller island chains. There are also difficulties when comparing different faunal regions that

exist across large scales of geography (Luiz et al. 2013). Thus, the non-random distribution of sampling and other factors is likely to produce differences and bias in evaluating factors such as isolation, physical energy, ocean productivity, and the density of reefs among other factors.

Below, we describe how we reduced these potential biases.

Island biogeographic theory predicts that critical habitat size and isolation will structure animal communities by influencing their local immigration and extinction rates within these habitats. For example, large bodied and carnivorous species or species with high resource and area requirements are predicted to have higher extinction rates and lower probability of persistence on small and isolated habitats. In contrast, species with limited larval dispersal, short larval duration, or low post-settlement survival should also have more local extinctions and not likely to colonize remote locations (Luiz et al. 2013). Therefore, given that BPS will locally deplete populations in habitats with sustainable yields and therefore isolate populations compared to baseline seascapes, we should expect changes in community-weighted life histories metrics, such as body sizes, age at reproduction, and growth and mortality variables. The emergent community should reflect both the ability to maintain viable populations in increasingly fragmented critical habitats and colonize distant habitats. Some responses are not expected to be linear but will have more asymptotic characteristics or responses within specific categories of the community metrics distributions. Addressing these problems requires examining the responses of biomass to both environmental and life history metrics in these two seascapes. This approach requires accounting for complex and non-independent responses that are best resolved through machine learning algorithms, which can integrate multiples variables, modes, and scales.



## 2.2 Fish biomass and weighted life histories

Biomass data of coral reef fish families was derived from Underwater Visual Census (UVC) in the Indo-Pacific oceans collected by Tim McClanahan, NOAA (led by Robert Schroeder), Alan Friedlander, Laurent Wantiez, Nick Graham, Pascale Chabanet, and Henrich Bruggemann. Data were collected in 845 sites between 2005 and 2018 where all fish >10 cm had to be counted in belt transects that covered  $\geq 250 \text{ m}^2$ , sized, and identified to, at minimum, the family level. This minimum transect size was used to reduce variability in sampling and the potential sampling-induced exclusion of large fishes that can be missed in smaller or stationary transects (Samoilys & Carlos 2000; McCauley et al. 2012). Individual fish were identified to 21 families and pooled by size into 10 cm size bins. Large bodied and transient members of the reef including sharks, barracuda (Sphyraenidae) and fusiliers (Caesionidae) were not frequently or accurately observed in the UVC transects hence not included in the total biomass evaluation. Nonetheless, we present the published literature summary of their life histories for context with our studied taxa.

Count and size data were converted into wet weights using either species or family-specific length–weight relationships, dependent on the specific conversion methods used by the observer. This method was used to account for site or region-specific differences in length-weight coefficients. Published life history metrics of nine variables (trophic level, annual natural mortality, growth rate, age at maturity, generation time, lifespan, maximum length, length to obtain optimum yield (suggested minimum size to capture a species) and length at maturity (first reproduction) were compiled for all available species and statistics pooled and computed at the family level (FishBase.org, September 23, 2019). The average life history characteristics of the 21 families was weighted by the family biomass to obtain the final weighted life history variable

for each fish community or site. This method may miss some of the variability and relative weighting of species level evaluations but given the wide distribution of the surveys, different studied species, and count methods, the family is the most accessible and finest resolution obtainable from these data.

### 2.3 Habitat variables

The habitat variables of depth and coral cover were evaluated by outlier analysis but not contained in the final analysis due to the focus here on environmental and geographic factors. Data providers provided their coral cover data collected at each site according to their own protocols, but 46% sites were missing these data.

### 2.4 Environmental variables

The geographic location and four environmental variables evaluated in the study were net oceanic primary productivity (NPP), wave energy, chlorophyll-*a* (Chl-*a*), and photosynthetic active radiation (PAR). NPP ( $\text{mg C m}^{-2} \text{ day}^{-1}$ ) and wave energy ( $\text{kW m}^{-1}$ ) data were obtained for each site from a 2.5 arcmin grid ( $\sim 4.6 \text{ km}$  at the equator) based on user-input latitude/longitude coordinates on the MSEC platform (Yeager 2017). NPP data were extracted from 8-day composite layers from 2003-2013 produced by NOAA Coast Watch (Yeager 2017) and should be seen as oceanic and not reef production estimates. Mean wave energy was computed from the WAVEWATCH III hindcast dataset ([http://polar.ncep.noaa.gov/waves/CFSR\\_hindcast.shtml](http://polar.ncep.noaa.gov/waves/CFSR_hindcast.shtml)) over a span of 31 years (1979-2009) (Yeager 2017). Chlorophyll-*a* (Chl-*a*,  $\text{mg m}^{-3}$ ) and PAR ( $\text{Einsteins m}^{-2} \text{ day}^{-1}$ ) data were obtained from GlobColour ([www.globcolour.info/](http://www.globcolour.info/)). Means were determined for these two variables from the beginning of the time series (1998 for Chl-*a* and 2002 for PAR) to the end of the available time series in 2018.

## 2.5 Anthropogenic influence variables

Travel time and gravity to the nearest major city and markets from coral reef sites were extracted by joining coral reef points with a 10-km resolution shapefile with estimates developed by Maire et al. (2016) and using QGIS 3.10.2-A Coruña. Travel times were estimated using a cost–distance algorithm that computes the least ‘cost’ (in minutes) of travelling between the site and the nearest major market and human habitation based on a regular raster grid. The calculation uses speeds appropriate for different types of boats, roads, and land. Gravity was calculated using the human population at these nearest major cities and dividing it by the squared travel time between the site and market human population (Maire et al. 2016).

## 2.6 Data properties

The focus here was on general patterns and therefore we were conservative in including sites with unusual characteristics that might overly-influence mean responses. Therefore, empirical coral reef fish biomass data was tested for outliers as a first step in ascertaining the variability. Multivariate outlier analysis of  $\log_e$  transformed biomass versus longitude, latitude, and depth was conducted at the family and site scale in JMP version 15.0. Mahalanobis distances of  $\log_e$  transformed biomass of coral reef fish families at various localities were evaluated whereby sites with family level outliers, defined as values with a significant distance from the mean center of all other observations, were excluded from further analysis (Mason & Young 2002). This led to the reduction in the number of total family level data entries from 13,048 to 12,286. The remaining 12,286 family biomass values were summed to give the per site fishable biomass in a total of 824 sites. Coral reef sites were also evaluated for outliers by including  $\log_e$  transformed

biomass, longitude, latitude, and depth in a multivariate Mahalanobis outlier analysis to further exclude outliers at the site level, resulting in a final sample of 751 sites. Of these coral reef sites, 584 were in remote areas referred to as baselines (>9 hours travel time to nearest market and >4 hours from human habitation) while 167 were either large and old marine reserves (n=95), small and young marine reserves (n=27), or fished sites (n= 45) and referred to as BPS (Fig.1; Table. 1). The BPS sample is weighted more towards marine reserves than fished sites and should therefore be conservative in that human impacts would be less than, for example, if 30% of the BPS sample was composed of marine reserves. This imbalance is largely driven by fish ecologists' tendency to sample marine reserves more than other types of fisheries management areas. Many of the fished reefs were selected as control sites for evaluating marine reserve impacts.

Tests of normality were conducted on biomass and environmental variables in order to ascertain suitable distributions for modelling relationships (JMP version 15). Log<sub>e</sub> transformed biomass performed better in the Kolmogorov-Smirnov tests of normality and log<sub>e</sub> data were used in modelling rather than raw values. Boosted Regression Tree (BRT) models and partial dependence plots were evaluated in R version 3.6.0 using the package 'gbm' version 2.1.5. The 'gbm.step' function was used in building models where BRT output metrics were then used in presenting overlaid partial dependence plots in ggplot2. All other statistical methods used JMP version 15.0.

## 2.7 Data analyses

The large and old marine reserves had about twice the mean biomass ( $892 \pm 696$  SD) as the fished seascapes ( $478 \pm 395$ ) (Appendix 1a). The mean values of the sites were highly variable and not significantly related to the travel time and human gravity metrics (Appendix 2). The fished seascape values were well placed within MSY estimates. The combined biomass values of the marine reserves and fished reefs, or BPS ( $759 \pm 644$ ) were well above any estimates of MSY for coral reefs in fished seascapes (McClanahan et al. 2019). Subsequently, the following analyses were conducted: 1) a summary and tests of normality of total biomass, biomass-weighted life histories, family-level biomass, environmental, and human influence variables for baselines and BPS, 2) tests of significance comparing variables between baselines and BPS using two-sample Kolmogorov-Smirnov tests for differences, and 3) evaluation of potential relationships among site-level biomass associations with geographic and physical environmental variables by both the General Additive Models (GAM) and boosted regression tree (BRT). These analyses indicated complex responses that were best evaluated and displayed by the BRT analyses (Appendices 4 and 5).

### 2.7.1 Boosted Regression Tree modelling of biomass

BRT modelling was chosen for presentation as it incorporates machine learning decision tree methods and boosting, which accounts for complex non-linear relationships and reducing predictive errors of linear or single variable models (Breiman 2001; Elith et al. 2008). BRT has also been used to quantify the relative influence of human and environmental variables in shaping reef ecosystems as well as species-seascape relationships at a range of spatial scales (Jouffray et al. 2019; Aston et al. 2019). Predictive performance was optimized by adjusting for possible combinations of the parameters bag-fraction (0.5, 0.75, 0.8), learning rate (0.01, 0.025,

0.05, 0.001, 0.0025, 0.005), and tree complexity (1-10) while maintaining a minimum of 1000 fitted trees (Aston et al. 2019). Combinations with the lowest cross validation deviance are presented as the final BRT model. The different scenarios of baseline and BPS seascapes described below were evaluated for relative influence of variables in predicting residuals of biomass from longitude, due to strong regional effects that can hide non-regional patterns (Luiz et al. 2012).

A series of possible scenarios of baseline and best practice site combinations were analyzed to evaluate the effect of BPS site selection on relative influence of studied variables using BRTs. These included baselines versus i) marine reserves of all ages and sizes and fished reefs combined, ii) old and moderate size marine reserves (>15yrs, >5km < 100km<sup>2</sup>), iii) old and moderate size marine reserves randomly selecting among sites to approximate a 30% reserves and 70% fished sites combined, and iv) all old and moderate size marine reserves, and all fished reefs. Sample sizes for fished reefs and small and young closures were n<50, which did not allow the BRT to subset sites and in turn build the necessary trees for generating the BRT models .

We evaluated the potential bias created by site selection in each scenario. This was done by randomly selecting sites from the two treatments per scenario and dividing them into a training (75%) and test (25%) subsets, while maintaining the range of minimum and maximum values. These were evaluated using optimum tuning parameters, low cross validation deviance, and trees >1000 and compared by R-square values. Below, we describe each scenario.

## 2.8 The four management planning scenarios

Below are four management scenarios that were considered as potential planning decisions. To account for data clustering and between-region variability we used the residuals from strong longitudinal association with biomass. In each case we compared the results of the longitudinal residual outputs of BPS and baselines for differences in the environment and life history variables between the baseline and the specific scenario. The final scenario is considered the most likely BPS option but the other scenarios are presented to broaden the context for the consequences of potential policy decisions.

#### 2.8.1 Best-practice seascapes as all marine reserves and fished reefs

BPS composition of sites in this scenario consisted of old and large marine reserves (n=95), young and small marine reserves (n=27), and fished reefs (n=45). The age of reserves ranged from 4-48 years of closure whereas sizes ranged between 0.28-345,000 km<sup>2</sup>. The predictive performance of cross validation of equal and random sample sizes in this scenario was high for BPS sites ( $R^2$  training=0.96, test=0.37). The size of marine reserves was not randomly located geographically, such that smaller reserves were often closer and larger further from the equator ( $R^2=0.48$ , p-value=0.0001). Therefore, this scenario potentially has more latitudinal bias in size of closures that reflect human geographical influence on closure-area decisions.

#### 2.8.2 Best-practice seascapes as only old and large marine reserves

BPS composition of sites in this scenario consisted of only older and larger marine reserve (>15 years since closure and size >5km < 100km<sup>2</sup> (n=95)). Predictive performance of cross validation in this scenario for BPS was high ( $R^2$  of 0.99 and 0.39) for training and test subsets respectively.

This scenario is a special case where there is no sustainable fishing and therefore presented as an alternative where human use is present but minimal.

### 2.8.3 Best-practice sites as 30% reserve and 70% fished seascape

To account for the unbalanced sample sizes in treatments and the proposed 30% closure policy (O’Leary et al. 2016), we randomly selected sites in each ecoregion using the ‘ssamp()’ function in the ‘sampler’ version 0.2.4 package in R version 3.6.0 to obtain a 30% marine reserve and 70% sample in the BPS category. This resulted in a total of 20 sites in old and large reserves and 45 sites in fished reefs. To account for sample-selection and small-sample biases, a total of four randomly selected sets of reserve sites were evaluated for this scenario using BRTs and the final relative influence values predicting residual biomass averaged to give a mean value per variable. The average predictive performance across models based on the four randomly selected reserve sites was high ( $R^2$  training=0.90, test=0.39). Outputs resulted in minor differences compared to the final scenario that reflect the BPS ideal and uses the most existing data.

### 2.8.4 Best practice seascapes as only old and large marine reserves and fished reefs

BPS composition of sites in this scenario consisted of the above older and larger marine reserves (n=95) and fished reefs (n=45). Predictive performance of cross validation in this scenario for BPS was high ( $R^2$  of 0.95 and 0.41) in training and test subsets respectively. This design best reflects the idealized BPS management plan and had the largest sample size.

## 3. RESULTS

### 3.1 Biomass patterns



Biomass values of means and medians, distribution statistics of kurtosis and skewness, and tests of normality indicate non-normal but highly centralized and right skewed distributions in the biomass. These distribution patterns were similar for all samples from the two simulated seascapes but with greater centralization and right skewness for the combined marine reserves and fished or BPS sites (Table 1). The distribution patterns for the baseline resulted in large differences between the mean biomass of  $2350 \text{ kg} \cdot \text{ha}^{-1}$  (CI = 2108-2593  $\text{kg} \cdot \text{ha}^{-1}$ ) and the median, being nearly half that value at  $1278 \text{ kg} \cdot \text{ha}^{-1}$  (CI = 1109-1442  $\text{kg} \cdot \text{ha}^{-1}$ ). Differences were not as marked for the BPS sites but still differed considerably in that means were  $759 \text{ kg} \cdot \text{ha}^{-1}$  (CI = 651-867  $\text{kg} \cdot \text{ha}^{-1}$ ) and medians  $627 \text{ kg} \cdot \text{ha}^{-1}$  (CI = 529-738  $\text{kg} \cdot \text{ha}^{-1}$ ). Therefore, differences in biomass between the two seascapes depended on the metric used, BPS means were 32% and medians were 49% of baseline biomass. Mean biomass and life history values differed significantly between the two seascapes (Fig. 2). Randomly-selecting sites for a balanced sample of baseline and BPS sites, found that biomass between seascapes was still different when comparing equal sample sizes ( $n=140$ ;  $p=0.0001$ ) and the baseline biomass did not change significantly with the smaller sample size. Thus, the unbalanced sample size is not the cause of the reported differences.

Biomass distribution evaluated at the family level indicated high variance, especially among baseline sites (Table 2). Sample sizes were large and therefore most tests of significance were different except for the batfish (Ehippidae), rudderfish (Kyphosidae), wrasses (Labrinae), filefish (Monacanthidae), and balloonfish (Diodontidae). There were often differences among high, moderate, and low fish biomass taxa when evaluated as the percent differences of the BPS compared to the baseline. For example, among the high biomass taxa ( $>250 \text{ kg} \cdot \text{ha}^{-1}$ ), the BPS

biomasses at the family level were a considerably smaller portion of the baselines (11 to 28%) for the jacks (Carangidae), snappers (Lutjanidae), groupers, and triggerfish (Balistidae). The surgeonfish (Acanthuridae) and parrotfish were the two high biomass families that were less reduced, with BPS sites being 48% and 53% of baseline sites, respectively. The moderate biomass families (20-250 kg · ha<sup>-1</sup>) showed BPS biomasses were generally reduced relative to the baselines (33 to 80%) but these differences were less than the high biomass groups. Among the low biomass families (<20 kg · ha<sup>-1</sup>), the grunts, sandperches (Pinguipedidae), and lizardfish (Synodontidae) were the three families with notably more biomass in BPS than in baseline sites.

### 3.2 Life histories patterns

The distribution of life histories at the family level showed similar patterns for the length-based metrics of length at first maturity, optimum length at capture, and maximum length (Fig. 3). The largest taxa by size were piscivorous families (barracuda and jacks), followed by mixed-diet families of snappers, emperors (Lethrinidae), batfish, grunts, and triggerfish and larger herbivores (parrotfish and rudderfish). All other families had moderate (<40 cm) to small maximum body sizes based on the means of commonly studied and sampled species. The metrics of age at first maturity, generation time, and life span were more variable and not closely aligned with the length metrics.

Most of the high biomass families had life spans near or in excess of 10 years. The moderate biomass families of the emperors, batfish, grunts, and rudderfish were also similarly long lived. Groupers, parrotfish, and triggerfish were the three families with more moderate (5 to 10 year) mean maximum life spans. However, groupers and surgeonfish were notable for having highly

variable life spans. The growth and mortality metrics generally show that growth rates ( $\text{cm} \cdot \text{y}^{-1}$ ) and natural mortality increase with decreasing length at optimum yield in linear relationship (growth  $R^2$  of 0.31 ( $p=0.01$ ) and natural mortality  $R^2$  of 0.33 ( $p=0.005$ )) (Fig. 3). Most of the high and moderate biomass families had similar biomass turnover rates of individuals or biomass with the exception of the parrotfish, which had the highest mean turnover for these size and biomass groups. Trophic levels were highly variable and did not follow any size or age-related metrics.

### 3.3 Environment and geographic and life history associations with biomass

Comparisons of environmental variables between baselines and the final BPS scenario (large and old closures and fished reefs) indicate statistical significance for all variables but considerable variability in the magnitude of differences (Table 1c). Differences in habitat included higher coral cover, Chl-*a*, and NPP, but lower wave energy in BPS compared to baseline sites. The difference in PAR between baselines and BPS was small. The average travel time to the baseline sites was 54 hours compared to 2.2 hours for the BPS.

Evaluating the biomass of all sites combined using BRT methods, indicated that planetocentric longitude was the strongest predictor of biomass (Relative importance (RI) = 28%) with moderate predicted biomass in the western Indian Ocean (40 to 100°E), declining to the lowest levels to 200°E, and rising to the highest values further east into the central Pacific until 240°E (Appendix 4a). Latitude was a more modest predictor (RI=12.2) and showed a peak biomass between 5-10° of the equator that declined towards temperate reefs beyond 20°. For all sites combined, environmental relationships, such as PAR, NPP, wave energy, and Chl-*a* were

generally weak ( $RI < 6.3\%$ ). Responses patterns reflect the expected rise and levelling or saturating responses of biomass beyond low to modest levels of these energy-input variables.

Life history trait influences were split between the stronger contributions of instantaneous mortality (14.3%) and length at maturity (13.1%) and weak contributions from generation time (2.9%) and the body growth coefficient (2.7%) (Appendix 4b). Consequently, for the purpose of comparing baselines and BPS systems, we evaluated and present the residuals from the longitude-biomass relationship to better account for regional clustering and variability in the data.

### 3.4 Best practice and baseline seascape differences

Residual biomass responses using BRT analysis differed between all baselines and BPS sites (Table 4). In general, life history traits were stronger predictors of biomass than environmental variables in both baselines and BPS. For example, length at maturity was the strongest predictor for both baselines ( $RI=53.7\%$ ) and BPS sites ( $RI=21.1\%$ ). Relative latitude was the environmental variable with the highest relative influence for baselines ( $RI=6.4\%$ ) and BPS sites ( $RI=10.6\%$ ). Generation time had more influence in the BPS (11.4%) than the baselines (2%). Wave energy and NPP had similar small influences on both seascapes. Differences in the relative influence among traits indicates the largest deviances for baselines and BPS comparisons was length at maturity (-33%) and generation time (9.4%) but with smaller differences (<3%) for trophic level and natural mortality.

All mean values of the biomass-weighted life histories variables were statistically different for comparisons of baselines and BPS (Fig. 4). As predicted, the variables of trophic level, body lengths, generation time, life span, and age were all lower in the BPS than baseline sites.

Additionally, BPS sites had higher growth and mortality rates but lower length at maturity than baselines. These differences were smaller or between 89 and 109% of the baselines compared to the BPS biomass being 32% of the baselines suggesting some conservation of life history metrics with declining biomass.

Responses to environmental variables for the longitudinal residual biomass relative to the biomass in each seascape indicated a flat response and rapid rise in biomass in both seascapes above 20° for latitude (Fig. 5a). This suggests that longitude was the cause of the high biomass seen between 5-10° of the equator in the data with longitude included (Supplementary Figure 4a). The responses of biomass in BPS for PAR, NPP, and Chl-a were saturating as these energy inputs increased. For baselines, the responses were flatter except for Chl-a and wave energy, which largely followed the saturating pattern observed in BPS. Biomass responses to life history variables indicated similar patterns for length at maturity, trophic level, and instantaneous mortality but more deviation between seascapes for growth and generation time variables (Fig. 5b). Body lengths increased while trophic levels and mortality declined predictably in both seascapes. In contrast, in the baselines, body growth and generation time influence on biomass was hump-shaped but the generation time pattern was flatter than the growth pattern. Growth peaked between 0.4 and 0.5 K y<sup>-1</sup> while generation time peaked at 2.75 to 3.25 years. In the BPS sites, growth rates declined sinusoidally but with a large dip at 0.5 K y<sup>-1</sup>. Generation time rose

and its influence on biomass saturated above 2.5 years. Therefore, growth and age differed the most between seascapes by their influences on biomass.

### 3.5 Comparing scenarios

Comparing the relative influence among the four scenarios by BRT analyses produced consistent differences in the variables with most life history variables being more influential than environmental variables for both seascapes (Fig. 6). Length at maturity was the strongest variable while estimates of production, PAR and NPP, were the weakest influences on biomass.

Comparing baseline with the four BPS scenarios indicated that baseline biomass was most distinguished by the large strength of the length at maturity variable. The BPS was distinguished from the baseline by the higher influences of the growth coefficient and generation time variables. Scenario 4 is the most similar to proposed BPS management and, among scenarios, the most different from the baseline. Particularly, large differences in the influences of the length at maturity, body growth, and generation time were evident and indicate different fisheries management needs in baselines than BPS.

## 4.0 DISCUSSION

The state of fish communities reflects a number of population and ecological organization attributes that have consequences for fisheries management, stock size, and yield estimates (Cinner et al. 2020). In particular, making accurate estimates of yields requires a clear understanding of the variability in unfisher biomass, growth, and mortality metrics (McClanahan and Azali 2020). Here, we found that human influences in reef fish communities living in nearshore sites acting as proxies for fisheries best-practices conditions, had community biomass and life history attributes that differed significantly from sites in remote wilderness baseline

sites. Many of the differences reflect the patterns predicted by disturbances to habitats and isolation of populations and possibly ecological generalization or homogenization of the fish community's life histories (Stuart-Smith et al. 2021). It is likely that previous studies of marine reserves that found exponential increases in biomass with the number of MPA features of age, area, enforcement, and isolation arose because many of the most successful reserves were located in wilderness or baseline-like conditions rather than nearshore seascapes (Edgar et al. 2014). While knowing what creates positive responses to marine reserves is useful for planning, the conditions of very large and isolated closure sizes are seldom what are being proposed or achievable by current policies for the governance of nearshore BPS management systems. Geographic context matters greatly and findings must distinguish the larger seascape context prior to making management recommendations and predictions.

Predictions supported here were that fragmented seascapes would experience a decline in maximum potential biomass, trophic levels, large-bodied taxa and an increase in the turnover of the biomass. While most hypotheses were supported by the findings, the turnover metric suggest a more complicated pattern than a simple linear increase in turnover in BPS reefs. BPS had greater relative biomass at low growth rates and longer generation times while mortality rates had a smaller declining influence than observed in baselines. In contrast, the overall higher biomass in baselines showed a hump-shaped pattern with growth rates rather than the more sinusoidal decline in BPS sites. This suggest that BPS seascapes, while having overall higher turnover, maintain their biomass at low growth rates and longer generation times with smaller influences attributable to the community's natural mortality increases compared to baselines. The baselines pattern is different with peak biomass at intermediate growth and generation time with

large biomass declines when mortality is high ( $M > 1.0$ ). This suggests variable food web responses in these seascapes that might be mediated by predation and marine reserves selecting for specific life histories.

Seascapes organized in novel and complex ways when the large-scale geographic contexts differed. In baselines, mortality and length at maturity appeared more influential and directional factors than growth and generation time. While the BPS responses of increasing biomass turnover is an expected response, high turnover reduces the maximum achievable biomass. Higher biomass in the baselines was being driven more by low natural mortality rates and larger sizes at maturity, rather than growth and generation time. The lower biomass among fractured BPS populations is associated with smaller sizes at reproduction and higher body growth. Therefore, the two seascapes maximize biomass by different life-history mechanisms with consequences for the maximum achievable levels. The BPS seascape is more likely to increase population turnover and therefore maximum potential yields. This may be a benefit to fisheries management but at a cost of unique fish life-histories that persist in the absence of human use. The ecological and evolutionary outcomes will be quite different, particularly when viewed through the long-term lens of sustainability goals. Life history attributes like carnivory, large body sizes, low mortality, and associated spatial needs may be an evolutionary advantage in wilderness but not in sustainably fished seascapes (Mellin et al. 2016b). It behooves fisheries scientists to consider ways to protect species that fail to maintain their populations even in BPS seascapes with marine reserves.



We propose that the patterns observed here will emerge and potentially be further accentuated in less well-managed BPS than those studied here. This should occur because fished seascapes will be near to shore and people increasingly contribute to habitat changes, fracturing of habitats through ecological degradation, isolation of fish populations, and lower and unsustainable biomass levels (Cinner et al. 2018, 2020). Moreover, low and intermittent compliance and small sizes of reserve areas are common and increasingly suggested as a solution for unsustainable use in human-influenced seascapes (Wood et al. 2008; Jupiter et al. 2014; McClanahan et al. 2021). While it might be possible to plan BPS management systems that do not produce these unintended effects, most fisheries management is reactive and restorative rather than proactive and planned. An unknown aspect of this research is what effect proactive versus reactive management might have had on the outcomes? Many of the marine reserves studied here were closed to fishing between the 1970s and 1990s as reactive response to high fishing. Might the restored fish differ from the original community? The long history of fishing in most reefs would make this question difficult to address. Nevertheless, regardless of the options among our scenarios, there was a consistent and directional reorganization of fish communities relative to a baseline.

#### 4.1 Two seascapes?

The implication of this study is that fragmentation and increased isolation of fish populations of nearshore seascapes is expected to create a unique system-level biomass and life history equilibriums that differs from wilderness baselines. Thus, there may be two or more potential seascape biomass and turnover equilibrium states with consequences for stock levels and sustainable production levels. Baselines having high stocks but lower sustainable yields and BPS

the opposite; but, often modified considerably between studied regions as reflected by the strong effect of longitude on biomass levels. Moreover, the usage of mean versus medians metrics will further accentuate the differences in the seascapes' distribution of stocks, production estimates, and variability (Britten et al. 2021). This variability can influence the short and long-term production estimates as seascapes transition between these two states. Furthermore, at the large scale of global geography, maximum biomass and associated life histories varies with longitude and other regional scales (Luiz et al. 2013; McClanahan et al. 2019). Less understood patterns are the geographic location, such as the high biomass in isolated eastern Pacific Island reef fishes. This needs further investigation but could result from the benefit of greater schooling and larger body sizes shown to be advantageous for colonizing isolated islands (Luiz et al. 2015). Luiz et al. (2013) found that region was the strongest predictor of geographic range and normalizing for the region's size produced stronger effects among the life history metrics. This is a similar finding to our longitudinal effect and subsequent use of residuals for evaluating other variables. Latitudinal patterns were notably changed by accounting for longitudinal effects. Nevertheless, from the seascape equilibrium view suggested here, fragmentation and isolation of populations was among the largest influences and needs to be considered when estimating stocks and production potentials but also conservation status.

BPS fish communities appeared unable to achieve the biomass levels obtained in baselines. Rather, BPS sites contained smaller bodied taxa, more relative storage of biomass in lower trophic taxa with moderate-size and life spans. Consequently, even if BPS support high biomass as in the greater reserve and less fished scenario, maximum biomass and life history distributions were still not expected to reach baseline values. Biomass in the reserves of BPS should

subsequently support fisheries through resilience of some disturbance-sensitive taxa and increasing production in the broader seascape (Mellin et al. 2016a; McClanahan 2021). However, the maximum potential stock biomass level will still be unattainable. This appears to be the case for the better studied shark taxa (MacNeil et al. 2020) but our findings suggest it is more general to other taxa of bony fish. Lower abundances of small-bodied taxa have been observed in many isolated locations, including various oceanic islands (Mellin et al. 2010; Luiz et al. 2013; Chabanet et al. 2016), even as large as Madagascar (McClanahan and Jadot 2017).

From a fisheries point of view, differences between seascapes should be most observable through changes in size and taxonomic composition because fishing mortality should promote the persistence of smaller and faster turnover taxa that feed lower in the food web (Zgliczynski and Sandin 2017; Houk et al. 2018; Robinson et al. 2019). Thus, more relative biomass was contained in BPS among taxa with moderate sizes and life spans. It should, therefore, be possible to overfish some large-bodied taxa while maintaining or increasing production in small-to-moderate bodied taxa. This may be especially common in stable environments like coral reefs where large size, long-life and slow growth may be evolutionarily advantageous but only when production is high, habitats are well connected, and natural and fishing disturbances low (Mumby et al. 2004; Mellin et al. 2016a). In fisheries with diverse species and life-histories, declines in stocks but a compensatory maintenance of yields may be a key reason why overfishing is infrequently detected without examining taxonomic changes over historical time (McClanahan et al. 2012).

#### 4.2 Implications for fisheries models

Maximizing or optimizing yields is often the primary goal of fisheries management rather than the maintenance or protection of biomass or taxa. Very few tropical fisheries have stock biomass data and frequently depend on national-level yield information to evaluate yields and fisheries status in tropical countries (Pauly and Zeller 2016; Hilborn et al. 2020). National statistical methodologies also underestimate actual yields, which leads to the false impression that fishing effort can be increased to achieve MSY. This problem is exacerbated by the use of yield models calibrated with short-term catch data and equilibrium assumptions (Dalzell 1996). Stock-based models of coral reefs have shown, for example, that using yields instead of stock biomass frequently overestimates potential yields (McClanahan and Azali 2020). Stock-based models indicate that population growth and maximum achievable biomass values are likely to be inversely related. The inappropriate selection of catch rates, stock biomass, or population growth rate values from either baselines or BPS applied to the opposite or inappropriate context should result in poor estimates of MSY. Consequently, it would be prudent to have no less than two gross level estimates of population growth and maximum biomass when stock-based fisheries models are applied to either baselines or BPS conditions. These may be further modified by local or regional differences in productivity and other geographic and environmental and fish community factors.

The degree of centrality, skewness, and aggregations of fish can also be influenced by the scale of sampling and therefore stock estimates (Britten et al. 2021). Consequently, estimated stocks measured by underwater census on the scale of 100s of meters, but captured and recorded at landing sites on the scale of kilometers, may not match well. The spatial and aggregations needs of fish will vary by taxa and location and some sensitive taxa will increasingly be at an

ecological disadvantage as metapopulation structure changes with differential foci on source or sink populations for both fishing effort and reserve placement (Cooper and Mangel 1999; Crowder et al. 2000; Wilen et al. 2002). Marine reserves have been shown to create population resilience in many reef fish species and fisheries production (Mellin et al. 2016a; McClanahan 2021). Nevertheless, disruption of fish metapopulation dynamics by fishing and other human impacts make it unlikely that, even under the best conditions of high marine reserve coverage and effectiveness, that reserve networks will protect all taxa and behaviors. Many of these taxa have migrations and aggregating behaviors that are considered wildlife spectacles. Declines in the populations of these species should have negative consequences for ecotourism.

#### 4.3 Possible mechanisms

Differential responses of high biomass carnivores and herbivores to seascape patterns should reflect the mechanisms of biomass depletion. Variable energetic requirements of these taxa and the distribution of these resources are the most likely explanation for carnivore-herbivore differences. On average, herbivores will require less space than carnivores because their resources are more concentrated and productive. Consequently, the larger declines in carnivores relative to herbivore biomasses from baselines to BPS indicate the greater resilience of herbivores to seascape disturbances. The consequences of this biomass depletion at the finer taxonomic levels is likely to be considerably more nuanced. For example, among sit-and-wait or sedentary meso-carnivorous families, such as sandperches, balloonfish, and lizardfish, we observed smaller differences or even small increases in their biomass in BPS compared with baselines. These findings generally support the hypothesis that anthropogenic disturbances promote smaller bodies and space-restricted life cycles. Some these species have a considerable

capacity for high turnover, even in reefs not disturbed by humans. For example, a study of a remote Pacific lizardfish populations found they replaced their disturbed populations 20 times in four years (Schroeder and Parrish 2005). Moreover, predator replacement could be caused by prey release or reduced competition.

Despite large biomass losses among some high biomass taxa; the changed spatial distribution of resources is less likely to explain some observed changes in the moderate and low biomass groups. Grunts are one example, as they are a more vagile family than surgeonfish and parrotfish but were considerably more abundant in BPS than baselines. Carnivorous grunts often feed over large shallow sand and seagrass areas and aggregate at night. How BPS conditions promote this reversed prediction is speculative because their life histories are not well understood. Possibly, population response among grunts is linked to their feeding close to shore, in lagoons, or shallow-water environments – that were more extensive in BPS. In East Africa the extent of shallow water around coral reefs was one of the best predictors of increasing fish biomass and nocturnally migrating and feeding groups, such as grunts and cardinalfish (Apogonidae) (McClanahan 2019b).

Among alternative explanations is that these taxa are occupying niches vacated by the high biomass carnivores, such as snappers. Higher abundance of low-space requiring lizardfish and sandperches could be due to ecological compensation for the losses of carnivorous jacks, groupers, and snappers in BPS. Similarly, higher biomass of rabbitfish (Siganidae) in BPS could be due to ecological release from predators in disturbed seascapes. Rabbitfish, like grunts, may also benefit from the closeness to continents and shores, which might increase macroalgae and

seagrass, their main food, and therefore their abundance in BPS. Rabbitfish and grunts are key fisheries resource that appear highly resilient to fishing and habitat shifts and part of the maintenance of fisheries yields in much of the African coastline (Hicks and McClanahan 2012; Samoilys et al. 2017; Robinson et al. 2019). The findings here offer a new set of investigations into human impacts by providing a unique human-impact seascape treatment for future comparison. This contrast with the well-studied comparisons between marine reserve and fishing grounds (Mellin et al. 2016a; Sala and Giakoumi 2018; Cheng et al. 2019). Consequently, like most unnuanced predictions, there are taxa with life histories that will fit poorly to predictions from the simple effects predicted by habitat fragmentation and population isolation.

#### 4.4 Consequences of change

Populations of a number of species of grunt and groupers appear sensitive to fishing (Sadovy et al. 2013; Luiz et al. 2016; Buckley et al. 2018). Because their populations aggregate and disperse, it is challenging to study and evaluate the causes and consequences of their population trends. Rather, more accessible study topics, such as the losses of herbivores between reserves and heavily fished reefs, has received considerable attention (Adam et al. 2015). Studies of herbivore loss have uncovered many ecological effects of both declines in abundance or species but also compensating factors that create resilience to these declines (Thibaut et al. 2012; Lefcheck et al. 2019; Ruttenberg et al. 2019; Humphries et al. 2020). Yet, less considered is the major loss of carnivorous biomass that occurs once human activities disturb the seascape even when reserve networks are created to diminish fishing impacts. For example, there are clear broad-scale changes in reef ecology once key triggerfish species, often caught as bycatch, decline in fishing grounds (McClanahan and Muthiga 2016a,b). This study should make it clear

that there are unexpected consequences when disrupting populations and seascapes that are poorly investigated and understood in marine environments.

Dissimilarities in the locations and environments of baselines and BPS were likely to play some role in the contrasting patterns. However, apart from longitude, the influences were generally small relative to the life history metrics - the main focus on this study. The nearshore location and greater adjacency to humans meant that Chl-a and net ocean primary productivity were higher in BPS, while wave energy was lower in these sites. Nearshore BPS areas also had 5% higher coral cover, but overall the differences were not large, nor were the above associations particularly strong in predicting fish biomass. Geographic locations seemed to be quite important and might be driven by isolation and connectivity that selects for certain life history characteristics, such as larger body size, increased schooling, and nocturnal behaviors (Luiz et al. 2013). Body size and trophic level were, however, among the dominant variables influencing biomass in all locations. Comparing sites among adjacent islands and similar environments, such as the Line Islands in the Pacific, has shown similar patterns to the size differences reported here (Zgliczynski and Sandin 2017). Consequently, while the large-scale of this study resulted in some problems in direct and unconfounded comparisons, the use of large samples and non-linear machine-learning BRT models should have reduced covariance problems. One positive aspect of this study is the high replication and spread of sites across a very large geographic scale. Thus, the observed strong and divergent patterns in the two seascapes are not likely to result from limited spatial and sample-size replication. Studies of more evenly distributed sampling and at finer or more restricted geographies is likely to uncover a number of poorly articulated aspects of this macro-study.



The findings here support the modelling results that marine reserve networks can potentially increase yields and services to people (O’Leary et al. 2016). However, this comes at the cost of declines in biomass of some taxa, changes in life histories, and failing to support the full complement of taxa or ecological processes. The accumulation of biomass into moderate body sizes and lifespans in BPS sites is an indication of both the contribution of these taxa to yields but also the limits to the sustainable fisheries management and conservation of larger taxa. Thus, moderate-sized taxa that are productive are likely to benefit from marine reserves networks and support the stability of yields outside reserves (Hopf et al. 2016; McClanahan 2021). For example, one empirical study of fishing in a heavily fished seascape of Kenya found that a small reserve was able to maintain yields by preventing recruitment limitations of species with small optimum capture lengths of ~22-25 cm (McClanahan and Kosgei 2019). These same fishing grounds had lost a number of taxa of larger bodied fish among the shark, groupers, and grunt families (Buckley et al. 2018). Archeological studies of fishing bone middens in Kenya indicate that jacks, barracuda, spadefish, and sharks were more commonly fished in these seascapes between 750 and 1400 BCE (McClanahan and Omukoto 2011). Therefore, these taxa did exist in fishable numbers in these nearshore areas but have declined over the many centuries of fishing. Consequently, these nearshore environments have the ability to support these taxa but not under modern conditions. Therefore, many large-bodied and space-requiring taxa will require more than reserve networks to support their populations.

#### 4.4 Conclusions

Marine reserve networks in fished seascapes have their own seascape properties for maintaining fish populations and communities that do not emulate undisturbed populations in fully intact seascapes. Most prior studies have focused on local ecological site factors such as depth, habitat, coral cover, taxonomic composition, and reef complexity (Darling et al. 2017; Komyakova et al. 2018). Yet, these local ecological factors are nested within larger seascapes with consequences for the persistence of key species (Gilby et al. 2016; Richardson et al. 2017). Baselines are clearly protecting populations of some large-bodied species, such as sharks (Juhel et al. 2018; Dwyer et al. 2020; MacNeil et al. 2020). But, we see here the importance of other changes in taxa within broadly fished seascapes that are not receiving the same scientific attention, conservation concern, and management policies. Clearly, the findings here indicate that habitat fragmentation, population isolation, and faunal relaxation are occurring in fished seascapes and the consequences are only poorly understood. Fully embracing the reserve network system of management without considering the consequences illuminated here and elsewhere could lead to an impoverished marine fauna. Our findings indicate the importance, quantification, and integration of marine wilderness into environmental and fisheries planning policies (McClanahan 2020).

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## **DATA AVAILABILITY STATEMENT**

The NOAA Pacific Islands Fisheries Science Center's Coral Reef Ecosystem Program data are freely available online at ([https://www1.usgs.gov/obis-usa/ipt/resource?r=ncrmp\\_nspc\\_fish\\_pacific](https://www1.usgs.gov/obis-usa/ipt/resource?r=ncrmp_nspc_fish_pacific)). All other data are personal to the Principal Investigators and requires submitting a formal request and review to each separate author.

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## Tables

Table 1. Summary statistics of biomass and environmental variables in a. Remote baseline sites b. Best practice seascape BPS c. Tests of differences between baseline and BPS sites. SD: Standard deviation, CV: Coefficient of variation, CI: Confidence interval, K-S: Kolmogorov Smirnov tests of normality. Chl-a = chlorophyll-a concentrations, PAR = photosynthetic active radiation, and NPP = net primary productivity.

a) Remote baseline sites									
Variable	n	Mean $\pm$ SD	CV	Mean 95% CI (Lower; Upper)	Media n	Median 95% CI (Lower; Upper)	Kurtosis	Skewness	K-S test P- value
Fishable biomass (kg ha <sup>-1</sup> )	584	2350.3 $\pm$ 2986.7	127.1	2107.5; 2593.0	1277.8	1108.7; 1442.0	9.8	2.8	0.0001
Hard coral (%)	298	25.6 $\pm$ 13.5	53.0	24.0; 27.1	22.9	22.2; 23.9	2.9	1.5	0.0001
Chl-a (mg m <sup>-3</sup> )	584	0.3 $\pm$ 0.2	73.6	0.30; 0.34	0.27	0.29; 0.25	11.8	2.8	0.0001
PAR (E m <sup>-2</sup> day <sup>-1</sup> )	584	42.7 $\pm$ 3.2	7.5	42.4; 42.9	42.8	42.5; 43.2	-0.2	-0.1	0.0001
NPP (C (m <sup>2</sup> day) <sup>-1</sup> )	584	657.2 $\pm$ 267.0	40.6	635.5; 678.9	633.6	611.4; 675.1	10.4	2.2	0.0001
Wave energy (kW m <sup>-1</sup> )	584	32.9 $\pm$ 34.7	105.4	30.1; 35.7	29.8	29.7; 30.4	317.9	15.3	0.0001
Travel time to the nearest market (hrs)	584	54.2 $\pm$ 32.5	59.9	51.5; 56.8	47.1	43.2; 60.9	-1.5	0.1	0.0001
Total gravity (population traveltime <sup>-2</sup> )	584	0.19 $\pm$ 0.46	245.8	0.15; 0.22	0	0; 0	5.5	2.5	0.0001

b) Best practice seascape BPS

Variable	n	Mean $\pm$ SD	CV	Mean 95% CI (Lower; Upper)	Media n	Median 95% CI (Lower; Upper)	Kurtosis	Skewness	K-S test P- value
Fishable biomass (kg ha <sup>-1</sup> )	140	758.9 $\pm$ 643.7	84.8	651.3; 866.5	627.1	529.2; 738.2	25.4	3.9	0.0001
Hard coral (%)	109	29.3 $\pm$ 15.0	51.2	26.4;32.1	29.0	25.8; 34.6	-0.8	0.1	0.0001
Chl-a (mg m <sup>-3</sup> )	140	0.90 $\pm$ 0.45	50.2	0.83; 0.96	0.84	0.84;0.91	-0.4	0.4	0.0001
PAR (E m <sup>-2</sup> day <sup>-1</sup> )	140	43.8 $\pm$ 3.5	8.1	43.3; 44.4	42.4	42.0; 45.0	-1.6	0.1	0.0001
NPP, C (m <sup>2</sup> day) <sup>-1</sup>	140	1003.3 $\pm$ 343.7	34.3	945.9;1060.7	956.9	956.9; 972.1	4.2	1.6	0.0001
Wave energy (kW m <sup>-1</sup> )	140	5.6 $\pm$ 8.2	145.3	4.3;7.0	0.9	0.9; 3.8	8.9	2.7	0.0001
Travel time to the nearest market (hrs)	140	2.2 $\pm$ 1.5	65.5	2.0;2.5	2.2	2.0; 2.4	0.2	0.8	0.0001
Total gravity (population traveltime <sup>-2</sup> )	140	736.4 $\pm$ 1279.8	173.8	522.7; 950.3	43	20; 227	5.1	2.3	0.0001

c. Two sample Kolmogorov-Smirnov tests of significant difference between environmental variables in remote baseline sites and best practice seascapes (BPS)

Variable	Baseline		BPS		BPS as percent of baseline	K-S test P-value
	n	Mean $\pm$ SD	n	Mean $\pm$ SD		
Fishable biomass (kg ha <sup>-1</sup> )	584	2350.3 $\pm$ 2986.7	140	758.9 $\pm$ 643.7	32.3	0.0001
Hard coral (%)	298	25.6 $\pm$ 13.5	109	29.3 $\pm$ 15.0	114.5	0.0001
Chl-a (mg m <sup>-3</sup> )	584	0.3 $\pm$ 0.2	140	0.9 $\pm$ 0.5	300.0	0.0001
PAR (E m <sup>-2</sup> day <sup>-1</sup> )	584	42.7 $\pm$ 3.2	140	43.8 $\pm$ 3.5	102.6	0.0001
NPP (mg C (m <sup>2</sup> day) <sup>-1</sup> )	584	657.2 $\pm$ 267.0	140	1003.3 $\pm$ 343.7	152.7	0.0001
Wave energy (kW m <sup>-1</sup> )	584	32.9 $\pm$ 34.7	140	5.6 $\pm$ 8.2	17.0	0.0001
Travel time to the nearest market (hrs)	584	54.2 $\pm$ 32.5	140	2.2 $\pm$ 1.5	4.1	0.0001
Total gravity (population traveltime <sup>2</sup> )	584	0.19 $\pm$ 0.46	140	736.4 $\pm$ 1279.8	3875.8	0.0001

Table 2. Mean ( $\pm$  SD) biomass of the studied families and two-sample Kolmogorov-Smirnov tests for differences between remote baseline sites (n=584) and reefs that compose the BPS (n=140). NS = Not significant.

Fish family	Baselines	BPS	BPS as percent of baseline	K-S test P-value
	Mean $\pm$ SD	Mean $\pm$ SD		
<b>High biomass &gt;250 kg/ha</b>				
Jacks (Carangidae)	540.2 $\pm$ 1417.9	56.7 $\pm$ 142.4	10.5	0.0001
Surgeonfish (Acanthuridae)	400.5 $\pm$ 612.1	192.6 $\pm$ 273.9	48.1	0.0001
Snappers (Lutjanidae)	364.4 $\pm$ 660	86.6 $\pm$ 151.9	23.8	0.0001
Parrotfish (Scarinae)	325.2 $\pm$ 610.5	171.9 $\pm$ 174.5	52.9	0.0002
Groupers (Serranidae)	307.1 $\pm$ 664	85.8 $\pm$ 100.8	27.9	0.0001
Triggerfish (Balistidae)	277.9 $\pm$ 911.1	60.3 $\pm$ 121.3	21.7	0.0001
<b>Moderate biomass 20-250 kg/ha</b>				
Batfish (Ephippidae)	245.7 $\pm$ 157.5	171.6 $\pm$ 56.9	69.8	NS
Rudderfish (Kyphosidae)	97.3 $\pm$ 236.3	9.3 $\pm$ 10.6	9.6	NS
Wrasses (Labrinae)	91.8 $\pm$ 111.6	73 $\pm$ 78.8	79.5	NS
Emperors (Lethrinidae)	64.3 $\pm$ 169.1	30.1 $\pm$ 102	46.8	0.0132
Rabbitfish (Siganidae)	45.7 $\pm$ 40.6	21.9 $\pm$ 28	47.9	0.0008
Goatfish (Mullidae)	39.5 $\pm$ 65.2	12.9 $\pm$ 15.2	32.7	0.0001
<b>Low biomass &lt;20 kg/ha</b>				
Angelfish (Pomacanthidae)	19 $\pm$ 49.4	14.3 $\pm$ 15.6	75.3	0.0001
Moorish Idol (Zanclidae)	16.3 $\pm$ 41.5	3.2 $\pm$ 2.2	19.6	0.0001
Puffers (Tetraodontidae)	12.9 $\pm$ 32.7	2.2 $\pm$ 4.2	17.1	0.0001
Filefish (Monacanthidae)	12.4 $\pm$ 24.4	5.8 $\pm$ 10.6	46.8	NS
Grunts (Haemulidae)	9.6 $\pm$ 36	61.6 $\pm$ 65.9	641.7	0.0001
Sandperches (Pinguipedidae)	1.2 $\pm$ 0.7	1.6 $\pm$ 0.7	133.3	0.0001
Balloonfish (Diodontidae)	1 $\pm$ 0.4	2.2 $\pm$ 3.6	220	NS
Lizardfish (Synodontidae)	1 $\pm$ 0.2	1.2 $\pm$ 0.2	120	0.0001

Table 3. Summary statistics of weighted life history traits in a. Remote baseline sites and b. Best practice seascape BPS sites. c. Tests of differences in weighted life histories between baseline and BPS sites. SD: Standard deviation, CV: Coefficient of variation, CI: Confidence interval, K-S: Kolmogorov Smirnov tests of normality.

a. Remote baseline sites (n=584)

Life history trait	Mean $\pm$ SD	CV	Mean 95% CI (Lower; Upper)	Median	Median 95% CI (Lower; Upper)	Kurtosis	Skewness	K-S test P-value
Trophic level	3.05 $\pm$ 0.36	11.96	3.02; 3.08	3.07	3.04; 3.13	-0.8	-0.21	0.0001
Length at maturity (cm)	24.74 $\pm$ 3.63	16.19	24.44; 25.03	24.63	24.24; 24.93	0.87	-0.17	0.0001
Length at optimum yield (cm)	27.98 $\pm$ 4.73	16.91	27.59; 28.36	27.81	27.27; 28.21	0.67	-0.06	0.0001
Maximum length (cm)	47.06 $\pm$ 7.98	16.96	46.41; 47.71	46.69	46.03; 47.40	0.89	-0.13	0.0001
Asymptotic length (cm)	44.35 $\pm$ 7.18	16.19	43.76; 44.93	44.11	43.31; 44.73	0.73	-0.09	0.0001
von Bertalanffy growth coefficient (K; 1 yr <sup>-1</sup> )	0.46 $\pm$ 0.05	9.89	0.46; 0.47	0.46	0.45; 0.46	-0.33	0.12	0.0001
Instantaneous rate of natural mortality (M; 1 yr <sup>-1</sup> )	0.87 $\pm$ 0.10	11.14	0.86; 0.88	0.87	0.86; 0.88	-0.52	0.09	0.0001
Generation time (years)	2.78 $\pm$ 0.29	10.35	2.76; 2.80	2.79	2.76; 2.82	-0.39	-0.17	0.0001
Lifespan (years)	8.98 $\pm$ 0.93	10.38	8.91; 9.06	9.02	8.91; 9.11	-0.45	-0.15	0.0001
Age at first maturity (years)	2.15 $\pm$ 0.18	8.57	2.13; 2.16	2.16	2.14; 2.17	-0.08	-0.24	0.0001

b. Best practice seascape (BPS) site summary (n=140)

Life history trait	Mean $\pm$ SD	CV	Mean 95% CI (Lower; Upper)	Median	Median 95% CI (Lower; Upper)	Kurtosis	Skewness	K-S test P-value
Trophic level	2.91 $\pm$ 0.32	11.1	2.85; 2.96	2.90	2.85; 2.96	-0.60	0.08	0.0001
Length at maturity (cm)	22.37 $\pm$ 2.13	9.51	22.02; 22.73	21.88	21.65; 22.16	1.48	0.98	0.0001
Length at optimum yield (cm)	24.86 $\pm$ 2.77	11.16	24.39; 25.32	24.23	23.86; 24.58	1.70	1.08	0.0001
Maximum length (cm)	41.83 $\pm$ 4.69	11.21	41.06; 42.62	40.52	40.02; 41.59	1.56	1.01	0.0001
Asymptotic length (cm)	39.61 $\pm$ 4.21	10.64	38.9; 40.2	38.70	38.14; 39.23	1.63	1.04	0.0001
von Bertalanffy growth coefficient (K; 1 yr <sup>-1</sup> )	0.50 $\pm$ 0.05	10.32	0.49; 0.50	0.50	0.48; 0.52	-0.72	-0.08	0.0001
Instantaneous rate of natural mortality (M; 1 yr <sup>-1</sup> )	0.94 $\pm$ 0.09	9.42	0.93; 0.96	0.96	0.94; 0.98	-0.16	-0.50	0.0001
Generation time (years)	2.60 $\pm$ 0.26	9.88	2.55; 2.64	2.60	2.52; 2.65	0.17	0.35	0.0001
Lifespan (years)	8.39 $\pm$ 0.81	9.69	8.25; 8.52	8.37	8.19; 8.52	0.18	0.40	0.0001
Age at first maturity (years)	2.03 $\pm$ 0.19	9.35	2.0; 2.06	2.04	2.00; 2.07	0.65	-0.17	0.0001

Table 4. Boosted regression tree model settings and results for residuals of  $\log_e$  transformed biomass and planetocentric longitude versus environmental variables and life history traits. CV deviance = cross validation deviance. Chl-a = chlorophyll-a concentrations, PAR = photosynthetic active radiation, and NPP = net primary productivity.  $\Delta$  relative influence, % = BPS - Baseline

Variable	<i>Baseline sites</i>	<i>Best practice sites</i>	
n	584	140	
<i>Model Parameters</i>			
Tree complexity	2	10	
Learning rate	0.005	0.005	
Bag fraction	0.8	0.75	
Number of trees	1800	1300	
Mean total deviance	0.5	0.2	
Mean residual deviance	0.3	0.04	
CV deviance $\pm$ se	0.35 $\pm$ 0.03	0.19 $\pm$ 0.03	
<i>Relative Influence, %</i>			<i>Difference in relative influence, %</i>
Length at maturity (cm)	53.7	21.1	-32.6
Trophic level	12.5	14.6	2.1
von Bertalanffy growth coefficient, K (year <sup>-1</sup> )	9.5	19.3	9.8
Instantaneous rate of natural mortality, M (year <sup>-1</sup> )	8.8	8.3	-0.5
Relative latitude (degrees)	6.4	10.6	4.2
Chl-a (mg m <sup>-3</sup> )	2.3	5	2.7
Wave energy (kW m <sup>-1</sup> )	2.1	2.1	0
Generation time (years)	2	11.4	9.4
NPP (mg C (m <sup>2</sup> day) <sup>-1</sup> )	1.5	2.9	1.4
PAR (E m <sup>-2</sup> day <sup>-1</sup> )	1.1	4.7	3.6



## Figures

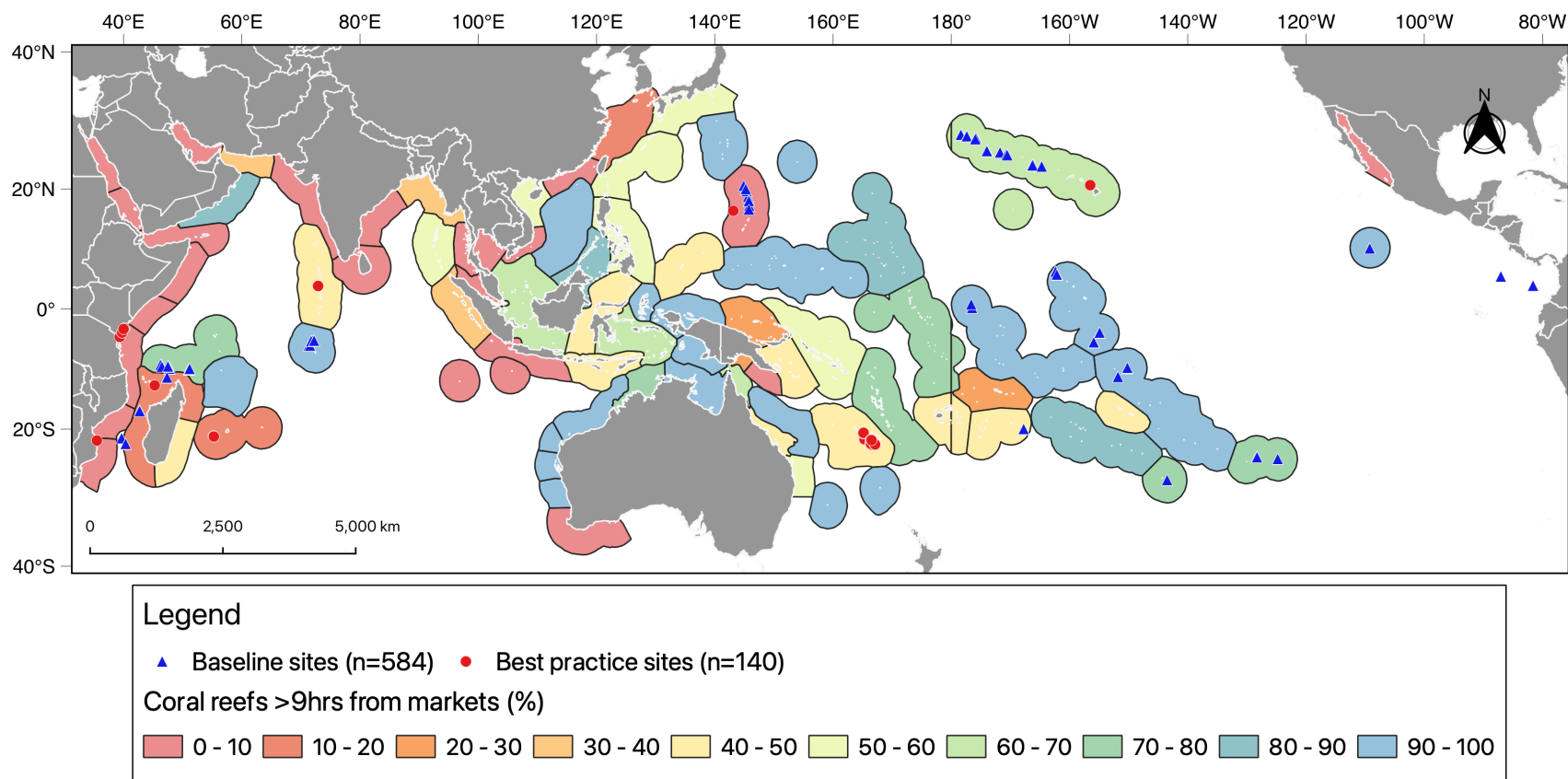


Figure 1. Geographic distribution of the study sites distinguished as baseline (sites >9 hours from cities and >4 hours from human habitation) and best practice sites (high compliance and old marine reserves and fished reefs < 9 hours from cities and <4 hours from human habitation). The percentage of reefs that can be classified as wilderness (>9 hours from cities) at the ecoregional level (outlined and colored by % of reefs) is taken from McClanahan (2020).

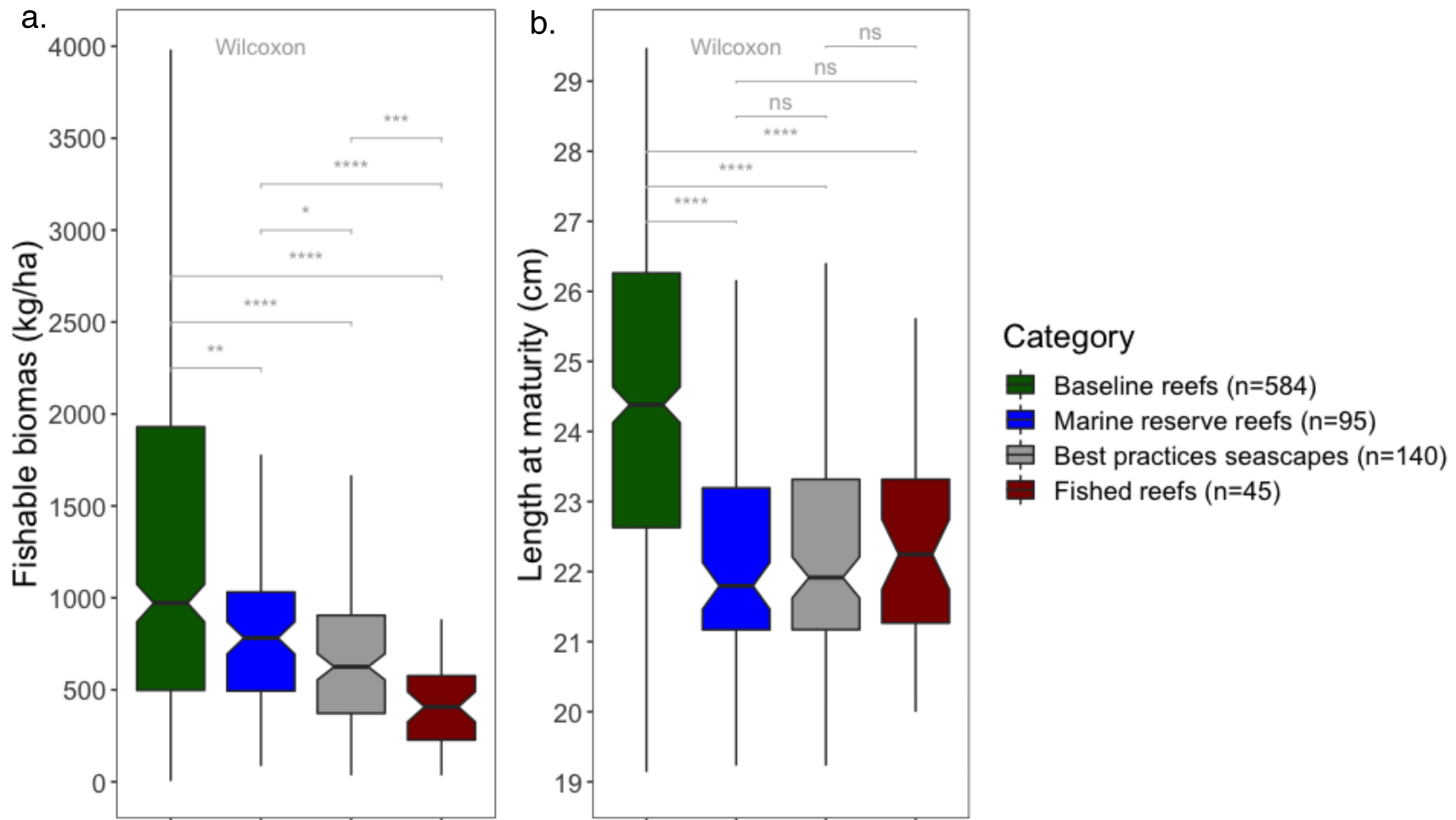


Figure 2. (a) Biomass and (b) length at maturity distributions in four management categories 1) baselines, 2) marine reserves, and 3) best-practice seascapes (or the combination of offshore or fished and marine reserves sites), and 4) fished reefs. Upper and lower boundaries of boxes indicate interquartile ranges (IQR), midlines are medians, notches show confidence intervals around the median and whiskers add 1.5 times the IQR to the 75th percentile and subtracts 1.5 times the IQR from the 25th percentile, with values outside the minimum and maximum whisker points considered as outliers.

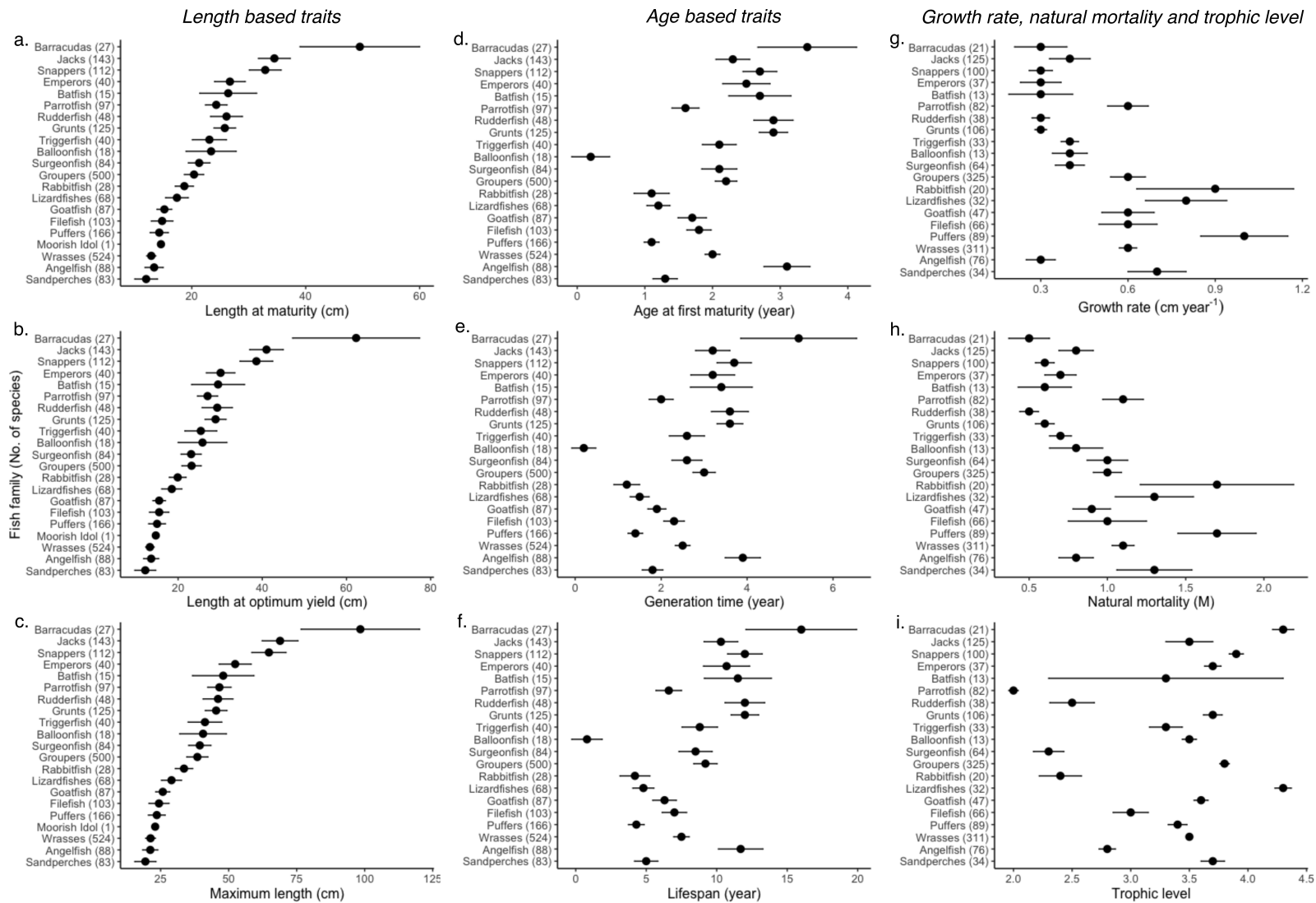


Figure 3. The distribution of coral reef fish families in terms of the 9 studied life history traits. Presented as (left) length-based variables, (middle) age-based variables, and (right) growth, natural mortality, and trophic level variables. Taxa ordered from (top) largest to (bottom) smallest sized families. Mean ( $\pm$  2SEM) of the common species (n) presented from data compiled from FishBase. See methods for Latin family names.

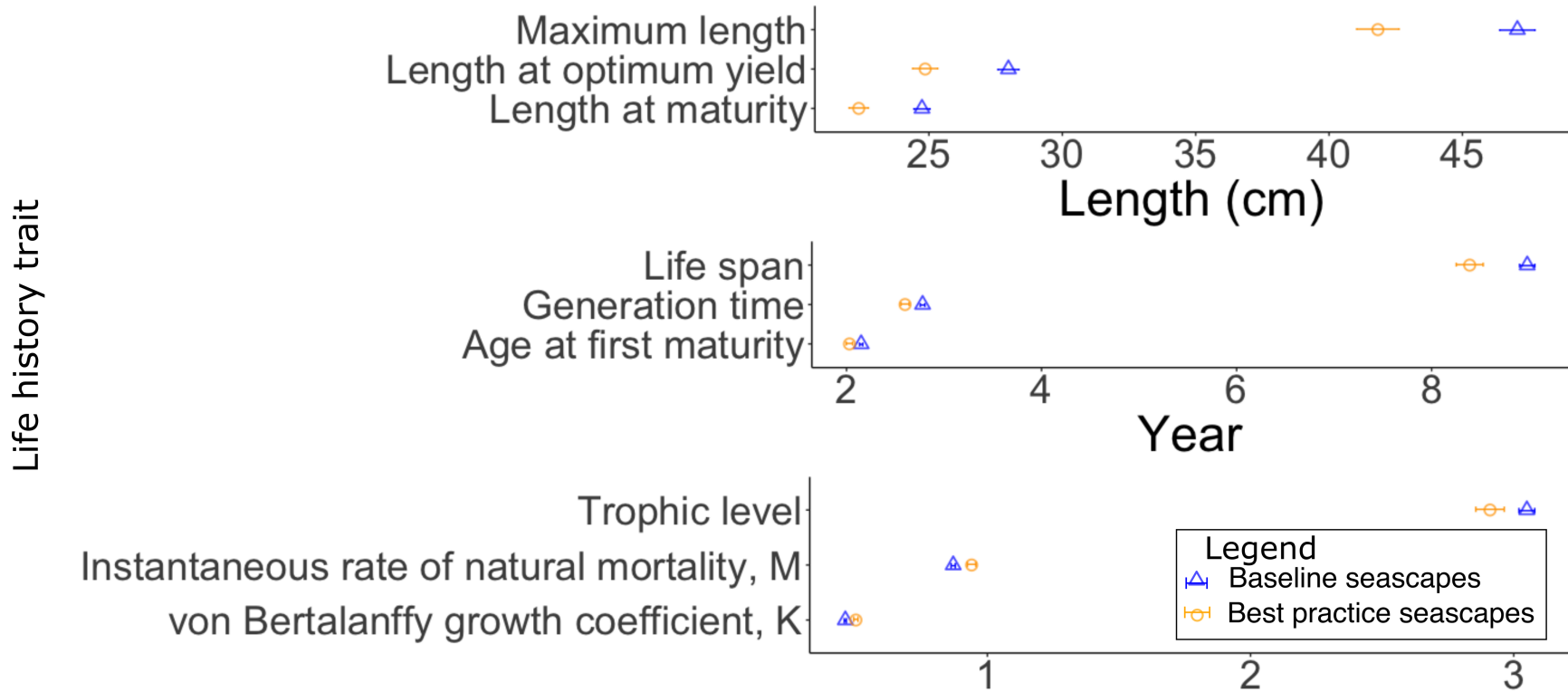
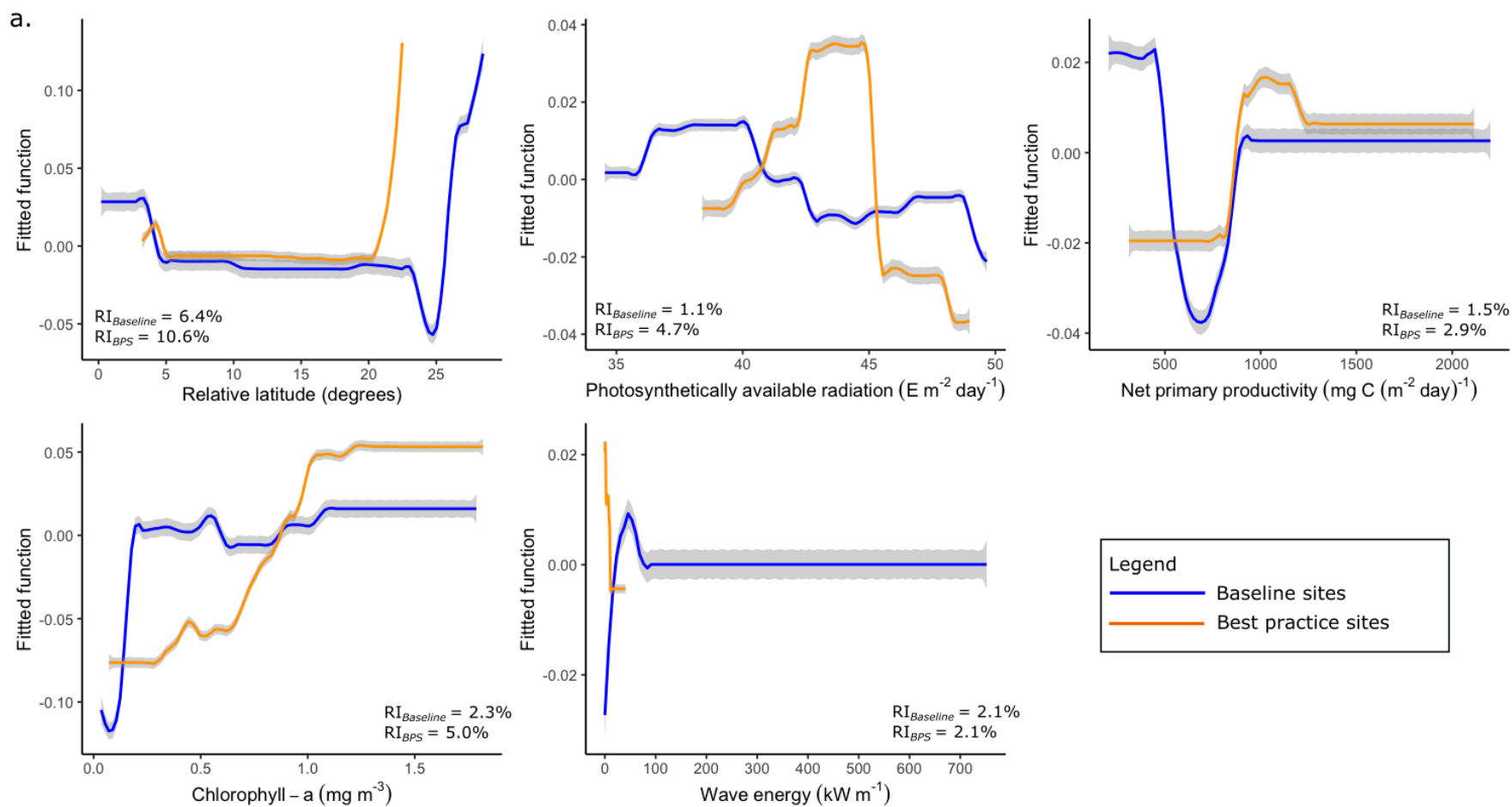


Figure 4. Comparison of the nine fish life history metrics (mean  $\pm$  2SEM) in baselines and best-practice seascapes. Life histories were evaluated for differences using two sample Kolmogorov-Smirnov tests and found to be significantly different between baseline and BPS sites for all traits ( $P < 0.001$ ).



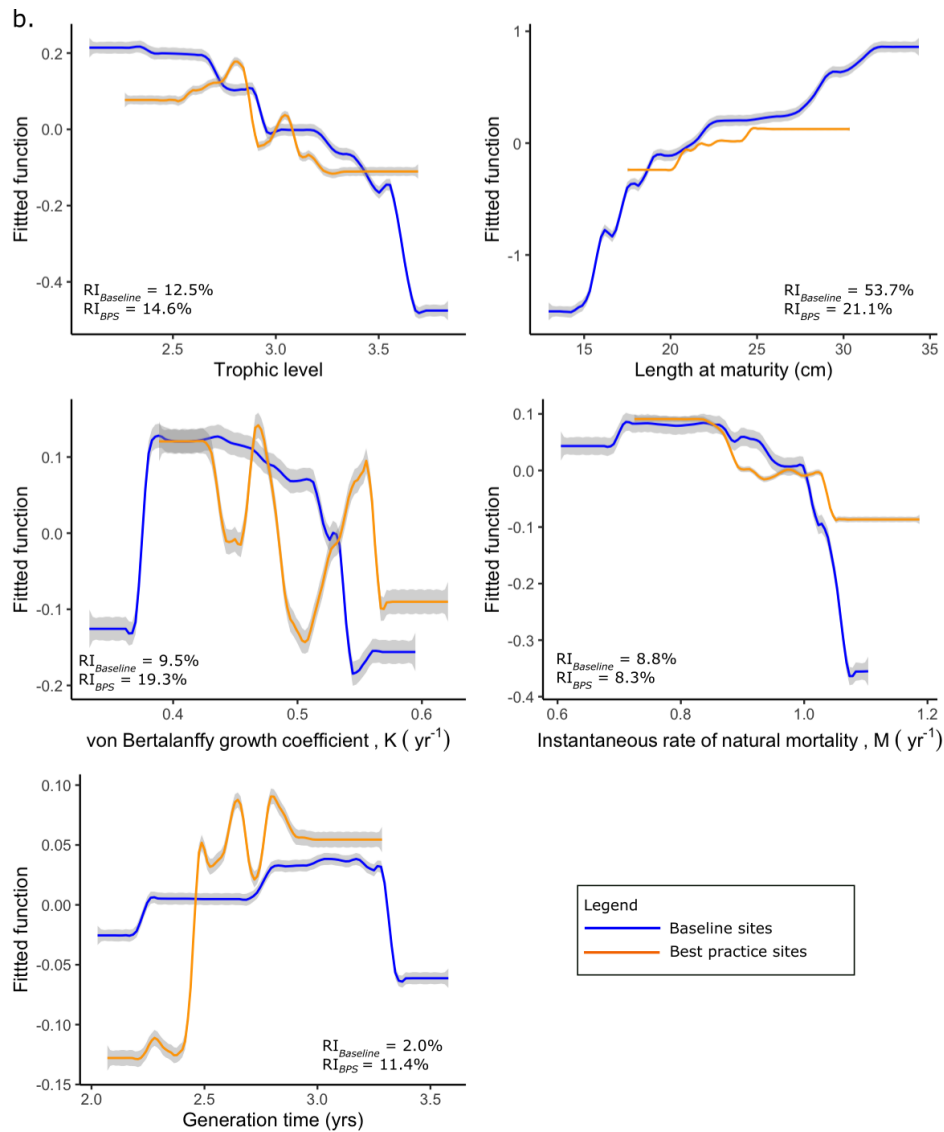


Fig. 5. Overlays of Boosted Regression Tree (BRT) partial dependence plots of biomass residuals from longitude versus (a) environmental variables and (b) weighted life history traits in baseline and BPS sites. Note that biomass scale (y) is relative to the seascape with baselines having higher values than BPS.

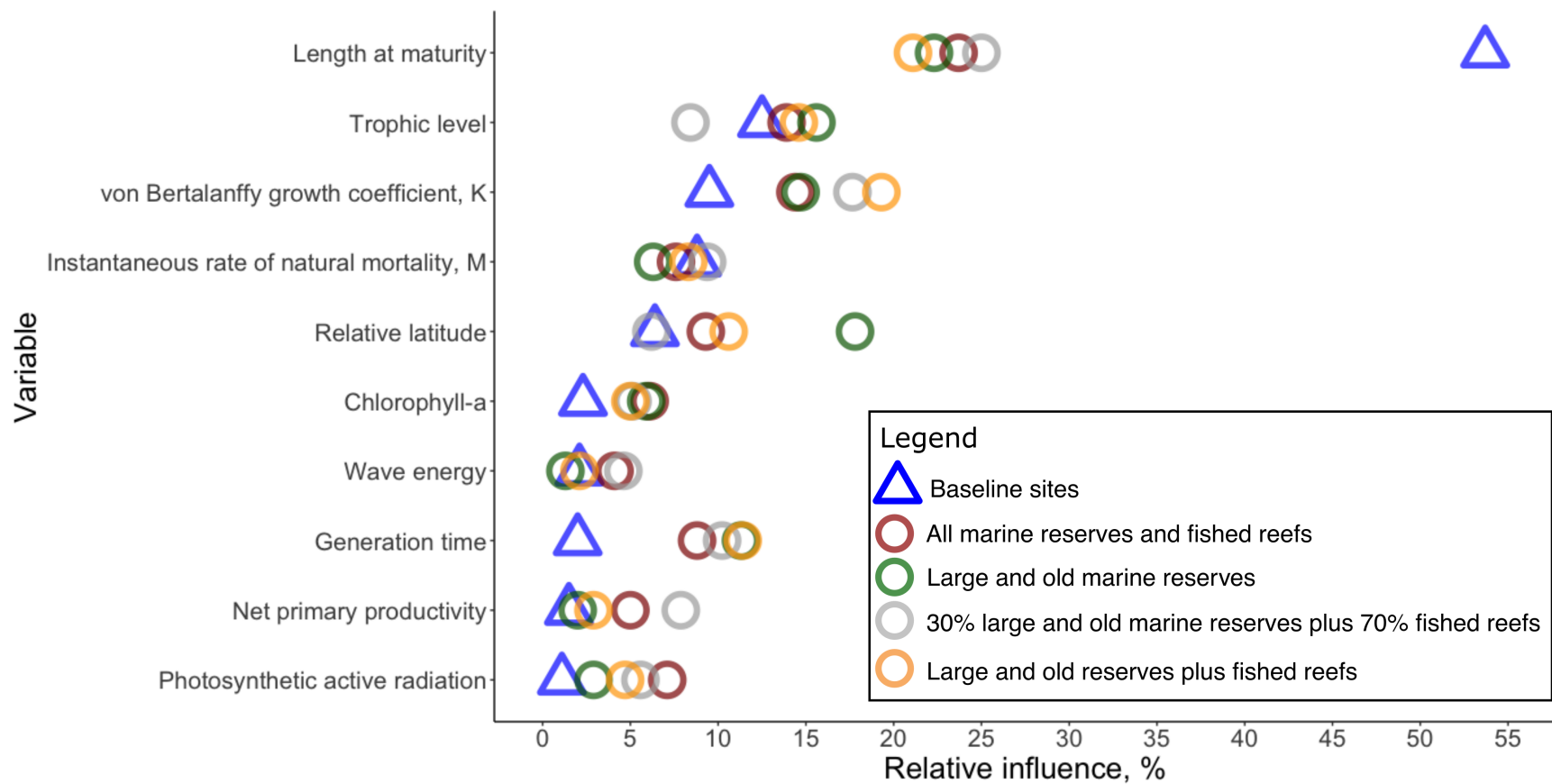


Figure 6. Boosted regression tree relative influence of variables predicting biomass residuals in different site scenarios for baseline and best practice seascapes.