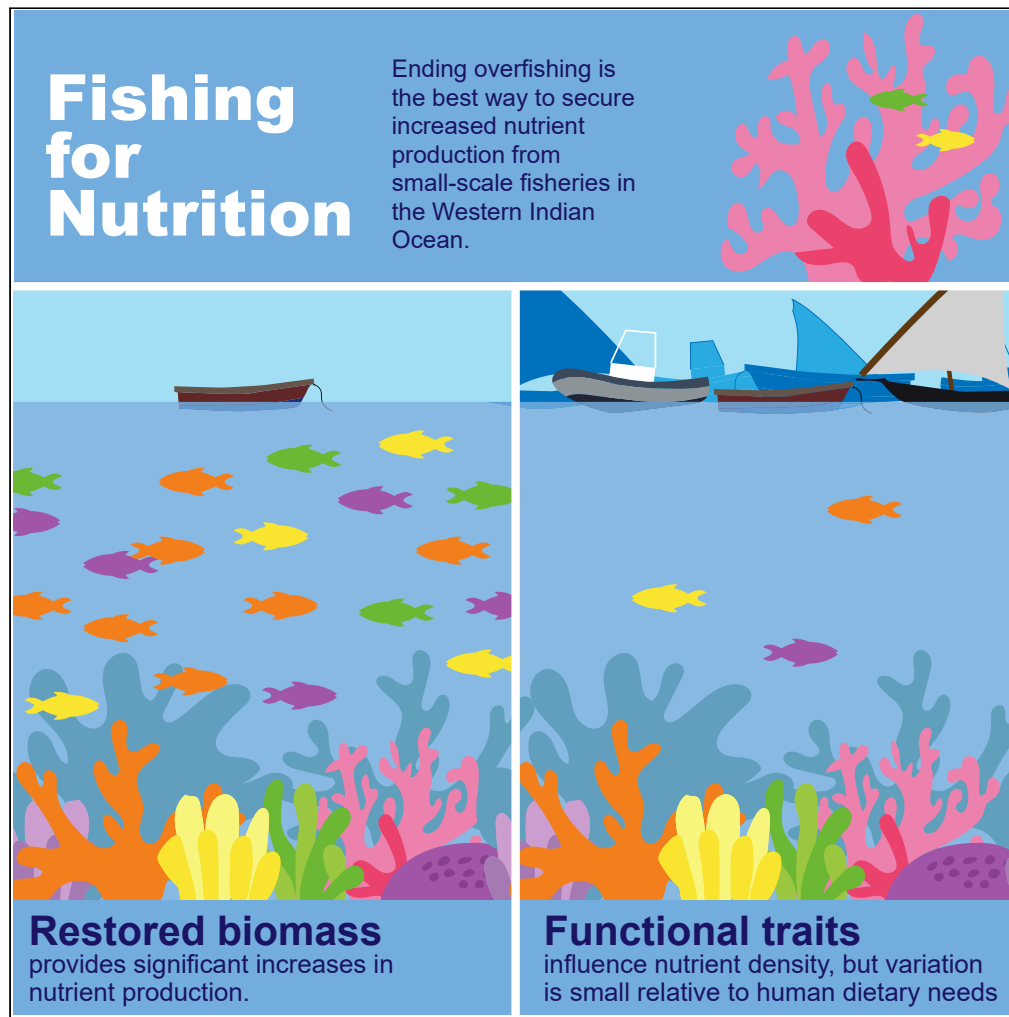**Article**

Tropical fishery nutrient production depends on biomass-based management

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Highlights

Overfishing drives lost
nutrient production in WIO
artisanal fisheries

Enhancing nutrient
production depends on
restoring biomass to
sustainable levels

Modest increases in
nutrient density are
associated with fish
functional traits

Fishing for Nutrition

Ending overfishing is the best way to secure increased nutrient production from small-scale fisheries in the Western Indian Ocean.

Restored biomass provides significant increases in nutrient production.

Functional traits influence nutrient density, but variation is small relative to human dietary needs

Article

Tropical fishery nutrient production depends on biomass-based management

Bryan P. Galligan[1,2,4,*] and Timothy R. McClanahan[3,*]

SUMMARY

The need to enhance nutrient production from tropical ecosystems to feed the poor could potentially create a new framework for fisheries science and management. Early recommendations have included targeting small fishes and increasing the species richness of fish catches, which could represent a departure from more traditional approaches such as biomass-based management. To test these recommendations, we compared the outcomes of biomass-based management with hypothesized factors influencing nutrient density in nearshore artisanal fish catches in the Western Indian Ocean. We found that enhancing nutrient production depends primarily on achieving biomass-based targets. Catches dominated by low- and mid-trophic level species with smaller body sizes and faster turnover were associated with modest increases in nutrient densities, but the variability in nutrient density was small relative to human nutritional requirements. Therefore, tropical fishery management should focus on restoring biomass to achieve maximum yields and sustainability, particularly for herbivorous fishes.

INTRODUCTION

Nearshore tropical ecosystems provide food, income, and other services to over one billion residents of tropical countries.[1,2] However, climate change and overfishing degrade tropical ecosystems and threaten their ability to provide food security and nutrition to nearby populations.[3,4] The fish harvested in these ecosystems are highly nutritious, but malnutrition often remains high, in part due to lost production as a result of overfishing.[5–8] In spite of this, existing approaches to fishery management have largely failed to consider the value of fish as a nutritional resource, particularly in food insecure regions where this approach is most warranted.[7,9] There is thus an urgent need to safeguard the nutritional benefits currently derived from tropical fisheries and sustainably increase nutrient production where possible.[3]

Nutrition-sensitive governance (NSG) offers one approach to safeguarding and enhancing the nutritional benefits of tropical fisheries.[10] NSG leverages governance interventions at all levels through a distributive justice lens to provide dietary nutrients to those who most need them.[10] In so doing, it addresses all six dimensions of food security: availability, access, utilization, stability, agency, and sustainability.[11] Within the NSG framework, fisheries management plays an important supporting role by seeking to achieve sustainable production of plentiful dietary nutrients in coastal communities. This is normally accomplished by estimating the relationship between fish biomass and surplus production, which is mediated by the recovery rate of fish communities, reef locations, and histories of disturbance, among a variety of other ecological and environmental factors.[12–16] By maintaining fish biomass at or near a locally specific management reference point, usually around 50% of the unfished biomass, sustainable yields of ~5–6 tons km^{-2} year^{-1} can be achieved, although this value is highly variable depending on the estimation methods and locations reported.[15–18] Managing nearshore tropical ecosystems with biomass-based targets achieves a number of goals, such as maintaining biodiversity and ecosystem functioning to the extent possible within fished seascapes, increasing microbial diversity, and enhancing reefs' resilience to climate change and other sources of stress.[19–22] These targets are usually met by implementing fishing restrictions such as spatial closures and gear restrictions that protect sensitive habitat and sexually immature fishes.[23] However, even the best managed nearshore fisheries do not represent the diversity, trophic structure, or biomass present at pristine wilderness locations.[24]

Biomass-based management has not yet considered the nutritional quality of fish catches.[3] Doing so could lead to alternative strategies. Preliminary suggestions to enhance nutrient production from fisheries have included the preferential targeting of small fish species,[25–27] increasing the species richness of fish catches,[8,28,29] and moving away from biomass-based targets in favor of nutrient density (concentration expressed per human nutritional requirement) or yield (total nutrient production) metrics.[3,30] These suggestions build on a premise that nutrient production might peak under different circumstances than maximum yield.[30] However, initial investigations in tropical ecosystems have not found stark tradeoffs between biomass and nutrition, nor have they been consistent with preliminary management suggestions based mostly on global studies. In Kenya, for example, fish traps modified to release small fishes generated modest increases in nutrient

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yields, suggesting that traditional length- and biomass-based management approaches might also enhance nutrition.[31] In the Seychelles, macroalgal regime-shifted reefs with low species richness supported higher densities of iron and zinc among and within fished species, suggesting that diversity does not necessarily increase nutrition.[5] Unlike land-based systems, aquatic foods and their production systems can be highly diverse.[32] As a result, blanket recommendations may fail in some contexts. Instead, local and regional solutions should be sought based on the unique characteristics of particular social-ecological systems.[33]

Options for enhancing nutrient production in tropical artisanal fisheries have not yet been evaluated on a large scale despite their crucial role as nutrient banks in the poorer Global South.[3] In this study, we explore options for nutrient production from fisheries in the food insecure faunal province of the Western Indian Ocean (WIO). The WIO includes larger countries that tend to have an increased prevalence of moderate or severe food insecurity (59–75%), such as Mozambique, Madagascar, Tanzania, and Kenya, as well as small island jurisdictions with comparatively lower rates of food insecurity, such as Maldives (13%), Seychelles (15%), and Mauritius (32%).[34] The small island jurisdictions also have comparatively better childhood nutritional outcomes, with lower rates of stunting among children aged five and younger (7–14%) than in the larger, more food insecure countries (18–39%).[34]

There is wide variation in aquatic food consumption in this region, accounting for only 7% of animal-source protein consumption in Kenya but 66% in Maldives.[35] However, these national statistics often obscure significant differences within countries.[36] For instance, artisanal fisheries in Kenya play a very important role in local subsistence despite low consumption at the national level.[36] Along the Kenyan coast, fishing households are more food secure and consume more fish than their neighbors, but micronutrient intakes remain low among children across households, including for vitamin A, iron, and zinc.[37–39] In Seychelles, insufficient intakes of iron, zinc, and selenium are common among pregnant women, but increased fish consumption, which is more common among low-income individuals, is associated with sufficient intakes.[40,41] Across the WIO, however, data on fish consumption, nutrient intakes, and nutritional status are scarce.

Here, we use large datasets and a machine learning algorithm to evaluate dietary nutrient production in the nearshore artisanal fisheries of the Western Indian Ocean. Specifically, we ask (1) what the nutritional quality of the nearshore artisanal catch is, (2) how achieving biomass-based management targets will influence nutrient yields, and (3) what factors influence nutrient densities in these fisheries. First, we reconstructed the taxonomic and nutritional composition of artisanal fishery catches in 10 jurisdictions. Second, the biomass and production of these fisheries were estimated in ~6.25 km^2 cells using a strongly predictive multivariate environment model (training-testing R^2 = 85%) developed to evaluate the factors that influence stock biomass on coral reefs.[42] We were thus able to estimate daily nutrient production for all mapped cells in our 10 jurisdictions. Finally, for 41 landing sites distributed in Kenya, Mozambique, and Madagascar, we compiled 20 environmental variables (e.g., water, temperature, current velocity), 10 catch variables (e.g., length, species richness), and 7 management variables (e.g., gear restrictions, area closures) suspected to influence catch nutrient densities (Table S1).

Data were derived from remote sensing and *in situ* measurements, catch monitoring data, and predictive models of tropical fisheries. Using a variable selection procedure and the Random Forest Model (RFM) algorithm, we evaluated the potential influences of these variables on the catch's nutrient density. Nutrient densities are presented as the percent daily recommended intake for a child 1–3 years old available in 100 g of fish.[43,44] It is unlikely that children will eat 100 g of fish in one day, but using this value allows for more direct comparison with previous studies on nutrient yields from fisheries.[5,8,45] We found that selenium, omega-3, and zinc were abundant in the WIO artisanal catch. We also found significant potential nutrient gains from restoring fishable biomass and modest increases in nutrient density associated with catches dominated by comparatively smaller and lower trophic level species.

RESULTS AND DISCUSSION

Nearshore artisanal fisheries in the WIO produce significant amounts of selenium, omega-3, and zinc, and achieving biomass-based management targets would significantly increase their overall nutrient production (Figure 1; Table 1). In the WIO region, much of the potential production has been lost due to a widespread failure to achieve biomass targets (Figures 2 and 3).[20,42] We found modest variation in nutrient densities in the WIO artisanal catch, amounting to a range of approximately 10% of the total daily requirement of a child 1–3 years old (Figure 4). Increased nutrient densities were associated with catches made up of predominantly low- and mid-trophic level species with smaller body sizes and higher growth coefficients, but that were still above the threshold for sexual maturity (Figure 4). While existing approaches to nutrition-sensitive fisheries management sometimes advocate maximizing nutrient densities (quality) rather than yields (quantity), we find that both aspects of nutrient production are important, and that restoring biomass will be a key management strategy to support NSG.[8,10,28,30]

Tropical fisheries provide key dietary nutrients

Selenium, omega-3, and zinc were abundant in the WIO artisanal catch (Figure 1). Fish catches in all 10 jurisdictions were an excellent source of selenium, providing >100% of a child's recommended daily intake in a 100 g daily portion. Catches were also a good source of omega-3, providing ≥38% recommended intake in 100 g (Figure 1). Catches from all jurisdictions except Reunion had a high density of zinc, providing ≥31% of the recommended daily allowance (Figure 1). Catches from Maldives, Comoros, and Reunion were also good sources of iron with ≥30% of the recommended daily allowance in a daily portion (Figure 1). Nutrient densities were largely similar across these jurisdictions, ranging from ~210% in Seychelles to ~260% in Maldives. A total of 600% would indicate the full recommended daily intake for all six nutrients (calcium, iron, omega-3, selenium, vitamin A, and zinc). For more data-rich jurisdictions where subnational variations in nutrient composition could be observed, there were only small variations among catches as indicated by low standard errors. In Kenya and Madagascar, the mean nutrient density was 202% (±0.6 SE), and in Mozambique, the mean nutrient density was 210% (±1.0 SE). Nutrient densities for catches in all three jurisdictions ranged from 73% to 394%.
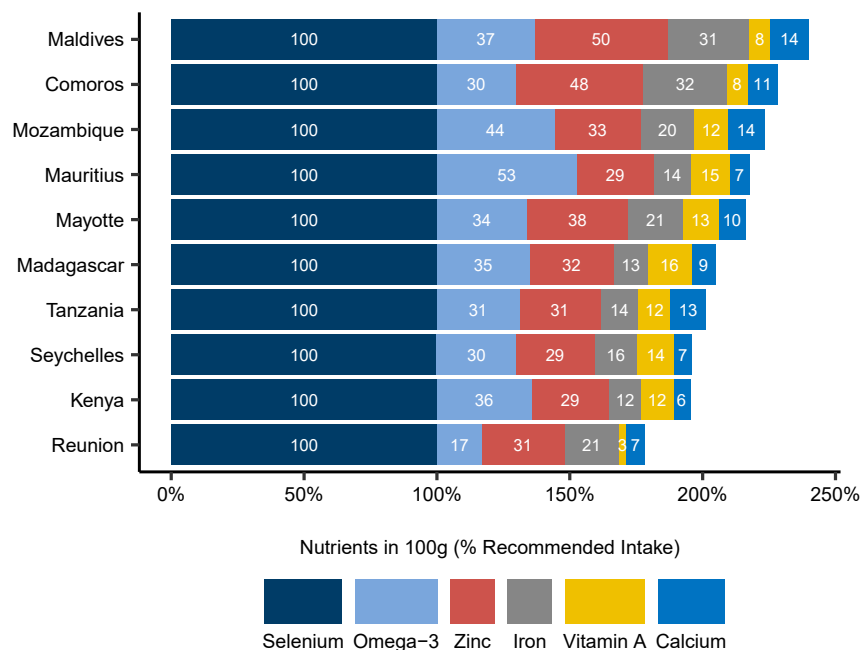
Figure 1. Nutrient density of artisanal fish catches in 10 Western Indian Ocean jurisdictions

Density of six nutrients in fish muscle tissue as percentage of the recommended dietary reference intake for a child 1–3 years old based on a 100 g daily consumption. Nutrient densities were derived from an estimated standard catch composition for each jurisdiction based on reconstructed small-scale catches from the Sea Around Us database and, where available, national catch statistics and landing site monitoring data (Table S1). Some variation is expected to exist within each jurisdiction.

Nutrient yields are limited by overfishing and biomass depletion

All fisheries jurisdictions were losing yields and nutrients to overfishing. Overfished sites, which account for ~37% of studied nearshore fishing grounds, lose on average 2.78 kg km^{-2} day^{-1} ($\pm$0.01 SE) in fish yields relative to estimated maximum sustained yield, with sites in many jurisdictions frequently losing more. These lost yields significantly limit nutrient production from tropical fisheries by several portions of the six nutrients km^{-2} day^{-1} (Table 1).

Overfishing displayed spatial patterns both within and among jurisdictions. Within jurisdictions, overfished reefs were often located near population centers and other overfished reefs, while reefs with high biomass were often remote from markets or highly protected (Figures 2 and S1–S10).[42] Among jurisdictions, overfishing was most prevalent in coastal nations with high populations and more accessible reefs, while it was less common in small island and archipelagic jurisdictions (Figures 2 and S1–S10).[42] In the most overfished jurisdictions, such as Kenya, Reunion, Mozambique, and Madagascar, overfished reefs were losing many daily portions of selenium (30–38), omega-3 (12–21), and zinc (7–15) per square kilometer per day (Figure 3).

Restoring fishable biomass on coral reefs would greatly increase nutrient production (Figure 2; Table 1). Ending overfishing in Reunion, for example, would produce enough additional selenium to meet the daily requirement of nearly 30% of children 1–3 years old (Table 1). In Seychelles, recovering lost yields would provide more than enough additional selenium, omega-3, and zinc to meet the daily requirements of all children aged 1–3 assuming the species composition of the catch does not change greatly (Table 1). In jurisdictions with larger and more widely distributed populations, such as Kenya, Tanzania, Mozambique, and Madagascar, the increase in nutrient production is smaller when compared with total child nutrient demand, but still amounts to thousands of daily requirements of all six nutrients (Table 1). These larger jurisdictions have significant inland populations that often have little or no access to marine fisheries production.[36] As such, the production figures in Table 1 should be interpreted as assets available for national food system governance, not benefits that will be automatically accrued upon ending overfishing. In general, additional production does not directly translate to food security or public health outcomes, but it can serve as a resource for more holistic interventions through governance or other means.[10,46]

Small body sizes and lower trophic levels are associated with modest increases in nutrient densities

Nutrient densities in artisanal fish catches observed at 41 landing sites in three WIO countries displayed modest variability attributed to catch characteristics. Densities clustered between 210% and 260% (out of a potential 600%) of a child's total dietary requirement for all six nutrients in a 100 g daily portion. The variables that influenced nutrient density were the habitat of fished species, trophic level, somatic growth coefficient (K), the ratio of the length of captured fish to their estimated length at sexual maturity (L/L_{mat}), and length at capture (Figure 4). Catches of fish <25 cm in length had ~20% higher nutrient densities (Figure 4F). Modeled nutrient densities also peaked at or slightly above the sexual

Table 1. Daily lost nutrients due to overfishing as proportion of national child population

	Child Population	Selenium Daily Portions	Omega-3 Daily Portions	Zinc Daily Portions	Iron Daily Portions	Vitamin A Daily Portions	Calcium Daily Portions
Reunion	42,090	12,463 (29.6%)	3,150 (7.5%)	1,059 (2.5%)	1,508 (3.6%)	153 (0.4%)	451 (1.1%)
Mozambique	3,274,842	373,589 (11.4%)	73,089 (2.2%)	64,518 (2.0%)	30,439 (0.9%)	17,562 (0.5%)	25,618 (0.8%)
Kenya	4,207,317	146,890 (3.5%)	31,858 (0.8%)	27,431 (0.7%)	11,449 (0.3%)	8,830 (0.2%)	5,767 (0.1%)
Tanzania	5,624,229	439,851 (7.8%)	75,180 (1.3%)	63,923 (1.1%)	31,425 (0.6%)	22,503 (0.4%)	23,927 (0.4%)
Mauritius	39,560	69,276 (175%)	13,040 (33.0%)	17,747 (44.9%)	6,146 (15.5%)	5,216 (13.2%)	2,796 (7.1%)
Madagascar	2,562,401	460,518 (18.0%)	95,251 (3.7%)	78,873 (3.1%)	34,168 (1.3%)	34,500 (1.3%)	21,180 (0.8%)
Seychelles	4,915	65,508 (>100%)	14,607 (>100%)	11,759 (>100%)	6,444 (>100%)	6,419 (>100%)	2,815 (57.2%)
Mayotte	32,023	18,305 (57.2%)	3,036 (9.5%)	2,045 (6.4%)	1,277 (4.0%)	941 (2.9%)	627 (2.0%)
Comoros	68,660	32,235 (46.9%)	5,060 (7.4%)	2,473 (3.6%)	2,791 (4.1%)	805 (1.2%)	935 (1.4%)
Maldives	21,821	124,562 (>100%)	18,581 (85.2%)	10,855 (49.7%)	9,043 (41.4%)	3,036 (13.9%)	4,121 (18.9%)

Legend: Total nutrient yields lost daily due to biomass overfishing of coral reefs within each fishery jurisdiction. Lost nutrients are presented as number of daily portions and percent of child population. One daily portion of each nutrient is the recommended dietary reference intake for a child 1–3 years old. Child population is the estimated number of children 1–3 years old in each jurisdiction in 2023.[36] Fishing jurisdictions are presented in decreasing order of prevalence of overfishing. Although national populations are presented here, marine artisanal fisheries primarily support coastal populations, particularly in the jurisdictions with larger land areas, such as Kenya, Tanzania, Mozambique, and Madagascar.[36]

maturity reference point of L/L_{mat} = 1 (Figure 4E). Catches dominated by herbivorous and mid-trophic species with high intrinsic growth rates (K > 1) were associated with ~10% higher nutrient densities (Figures 4C and 4D). Effect sizes were modest relative to human nutritional requirements, amounting to ~10% of the recommended intake for a child 1–3 years old in a daily portion of fish.

The RFM performed well, explaining 85% of the variance in nutrient densities for the training data and 67% for testing data. Most of the initially tested variables, including all management and environmental variables, had no relationship to nutrient densities in the daily catch (Figure S11). Climate and other anthropogenic pressures did not greatly affect the nutritional composition of these fish catches (Figure S11), although it has been suggested these factors might be related.[3] Results for individual nutrients were not always consistent with the trends in overall density, either in variable importance or the sign and shape of the relationship, which suggests that policies targeting specific nutrient deficits will differ from those seeking to maximize the overall density of the catch (Figures S13–S18).

The relationship between nutrient density and trophic level, growth coefficient, and body size is consistent with recent literature on the value of low-trophic level species with high turnover and productivity. As in Seychelles, Belize, Fiji, and Solomon Islands, the artisanal fisheries of Kenya, Mozambique, and Madagascar experience a modest nutritional benefit when catches are dominated by lower trophic levels (≤3.5) (Figure 4C).[5,47] Such fisheries are potentially problematic from a conservation perspective as they can be associated with decreased diversity, trophic downgrading, and changes in life histories in unselective tropical fisheries.[24] However, they are also sometimes associated with persistent yields and increased productivity despite often high levels of exploitation.[13,14] As a result, there may be significant potential to protect and enhance nutrient production where trophic downgrading has already occurred.

Our findings suggest a nuanced approach to the role of small fish in nutrient production. Most of the literature advocating for the increased capture and consumption of small fishes refer to specific species and families (e.g., Clupeidae).[6,26] Sustainable targeted fisheries for such species are quite valuable for nutrient production.[6,27,48] However, the WIO nearshore artisanal fisheries studied here are unselective, and catches with small body sizes contain a mix of mature individuals of small-bodied species alongside immature individuals of large-bodied species.[49] In these fisheries, targeting small fishes decreases yields and contributes to overfishing, which we connect to significant losses in overall nutrient production (Figures 2 and 3).[23,49–52] Furthermore, the nutrient gains associated with small body sizes in this study were quite modest relative to human nutritional requirements (Figure 4F). As a result, unselective targeting of small fishes from coral reefs and associated nearshore tropical habitats is expected to significantly reduce nutrient yield and overall production while only garnering small benefits for nutrient density.[49]

Catches from our 41 landing sites did not display the same positive relationship between species richness and nutrient density found in other systems and at the global level.[8,28,29] Although species richness is an important management concern for other reasons, we found no evidence it was related to nutrient production in nearshore marine tropical fisheries.[19,22] Achieving increased species richness in artisanal fish catches would likely mean restoring fishable biomass to a level higher than that required for maximum sustained yield and incurring lost yields due to underfishing.[19] Our findings suggest that high species richness is a conservation objective, not an objective for maximizing nutrient production from small-scale tropical fisheries.

Our model does not consider the potential effects of diverse recovery trajectories on coral reef fish communities. As fish biomass recovers to sustainable levels, the species, functional, and nutritional composition of restored fish communities may not be uniform across habitats or perturbations. This could cause recovered fish communities to support varying levels of nutrient production. Coral reef fish communities that have recovered from overfishing have usually regained key ecosystem functions, but they do not reflect the composition of unfished seascapes.[18,24,53] Marine heat waves and coral bleaching also drive changes in fish community composition post-recovery, often leading to
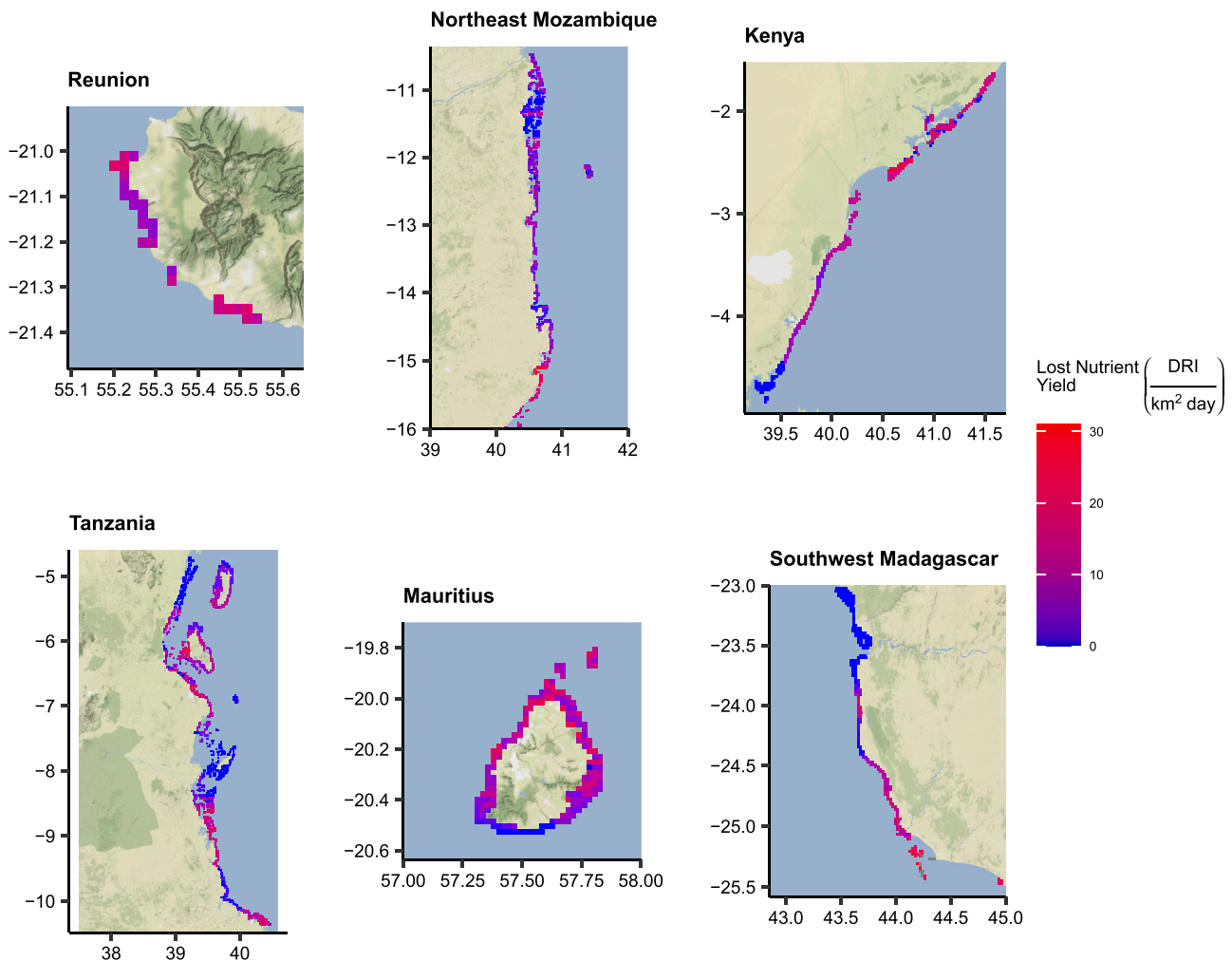
Figure 2. Lost nearshore nutrient yields due to overfishing in the Western Indian Ocean
Heat maps of lost nutrient yields due to overfishing in six jurisdictions. Lost yields are presented as a factor of the combined dietary reference intake (i.e., the complete daily requirement of six nutrients) and yield per square kilometer per day. Jurisdictions are presented left to right by row in decreasing order of prevalence of overfishing, with overfished reefs being most frequent in Reunion and less frequent in Madagascar. Detailed maps of all 10 jurisdictions can be found in Figures S1–S10.

lost species and functional richness.[54–58] Any such change in fish community functional traits can be expected to impact the nutrient composition of fish catches.[7,59] This relationship has been observed in the Seychelles, where post-bleaching reef habitats supported different fish assemblages and nutrient compositions depending on whether coral cover returned or reefs transitioned to a macroalgal dominated state.[5]

Limitations of the study

Our use of large datasets and modeling made it possible to estimate nutrient production and the variables influencing it at a regional scale. However, this approach is also vulnerable to the highly variable spatial, taxonomic, and temporal resolutions of the underlying datasets. For example, the fish biomass model that estimates production and lost yields is based on 6.25 km^2 cells that include various habitat types.[42] It had high predictive skill and provides an acceptable spatial scale considering the operating behaviors of small-scale fishers in the WIO, but it is subject to higher uncertainty at lower spatial scales.[42,60] Similarly, our jurisdiction-level catch reconstructions are based on the best data available, but they mask interannual and spatial variability in catch composition for WIO fisheries.[23] Furthermore, as fish assemblages recover from overfishing and biomass is restored, species composition is expected to change.[23] Our study of artisanal catches in Kenya, Mozambique, and Madagascar include this concern through life history parameters such as trophic level and growth coefficient. However, our broader WIO estimates assume that catch composition will stay the same as assemblages recover. Although this assumption is incorrect, we still expect our nutrient production estimates to be reasonably accurate, especially given the relatively low variability in nutrient density among landing sites
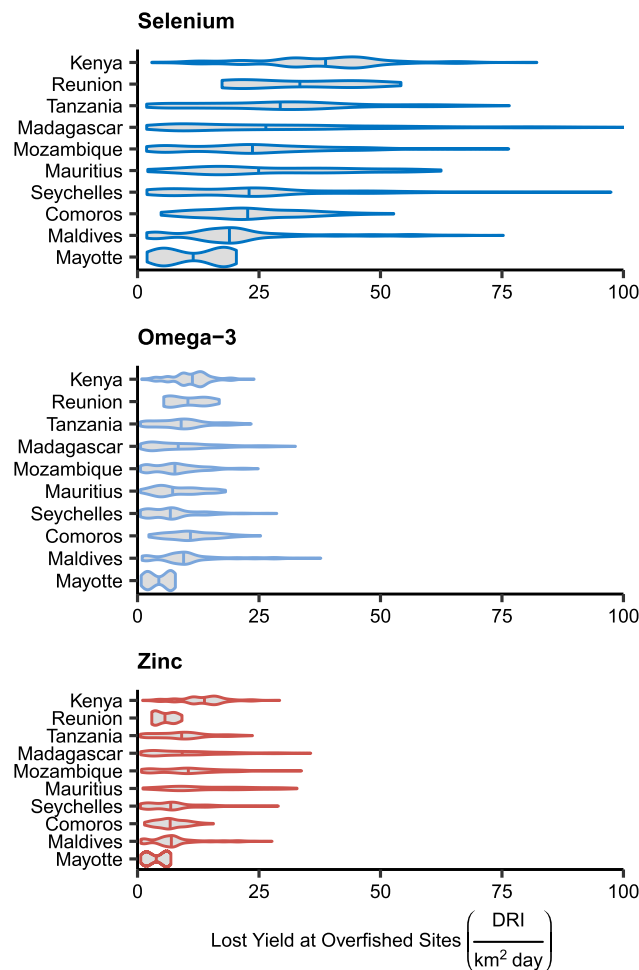
Figure 3. Lost nutrient yields at overfished sites

Violin plots of the median value and distribution density of nutrient yields lost due to overfishing. Lost yields are expressed as the expected increase in yield associated with restoring fishable biomass to sustainable levels, reported as number of daily portions of each nutrient per reef area.

and countries. Nonetheless, we consider our fish production and nutrient composition estimates to be open to revision as more data are collected across nearshore tropical systems.

STAR★METHODS

Detailed methods are provided in the online version of this paper and include the following:

- KEY RESOURCES TABLE
- RESOURCE AVAILABILITY
  - ○ Lead contact
  - ○ Materials availability
  - ○ Data and code availability
- METHOD DETAILS
  - ○ Nutrient density for 10 fishery jurisdictions
  - ○ Overfishing-induced nutrient losses
- QUANTIFICATION AND STATISTICAL ANALYSIS
  - ○ Modeling drivers of nutrient density

SUPPLEMENTAL INFORMATION

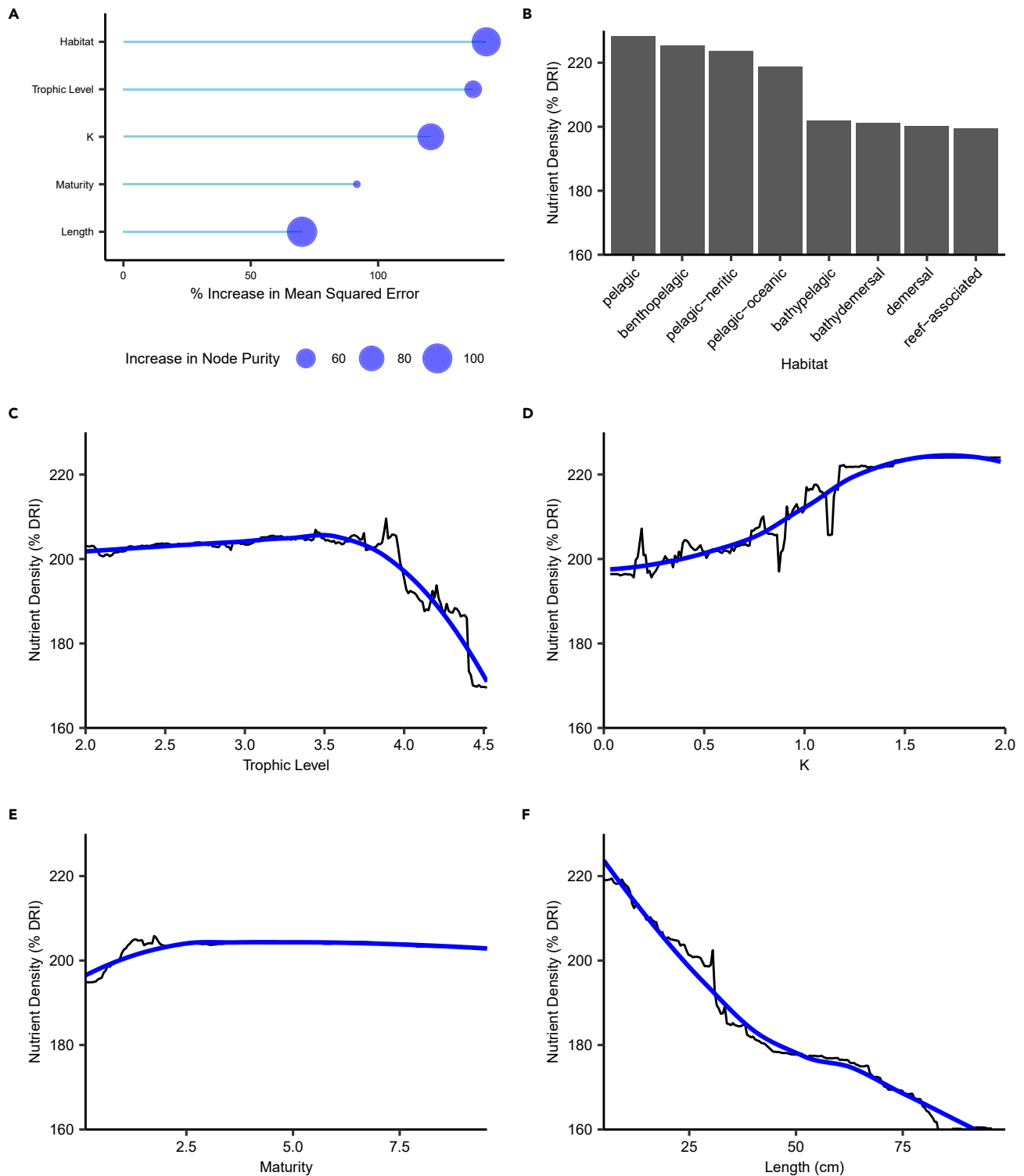Supplemental information can be found online at https://doi.org/10.1016/j.isci.2024.109420.

Figure 4. Factors influencing nutrient densities

Variables associated with nutrient densities in artisanal fish catches from 41 nearshore coral and seagrass-based landing sites in Kenya, Mozambique, and Madagascar. (A) Random Forest Model (RFM) results showing two measures of variable importance. (B–F) RFM estimates (black) and locally weighted smoothing (blue) for partial dependence of nutrient concentration on informative variables: the most frequent habitat of the captured species (B), trophic level (C), growth coefficient (K) (D), the ratio of length at capture to length at maturity (L/L_{mat}) (E), and length at capture (F). See also Figures S11–18.

AUTHOR CONTRIBUTIONS

Conceptualization, B.P.G. and T.R.M.; Methodology, B.P.G. and T.R.M.; Software, B.P.G.; Validation, B.P.G.; Formal Analysis, B.P.G. and T.R.M.; Data Curation, B.P.G.; Writing–Original Draft, B.P.G.; Writing–Review and Editing, B.P.G. and T.R.M.; Visualization, B.P.G.; Supervision, T.R.M.

DECLARATION OF INTERESTS

The authors declare no competing interests.

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STAR★METHODS

KEY RESOURCES TABLE

REAGENT or RESOURCE	SOURCE	IDENTIFIER
Deposited data		
Multivariate environment-fish biomass model informs sustainability and lost income in Indian Ocean coral reefs	McClanahan et al.[42]	https://doi.org/10.1016/j.marpol.2023.105590
FishBase	Froese & Pauly[61]	https://www.fishbase.org
Sea Around Us concepts, design, and data	Pauly et al.[62]	https://seaaroundus.org
Characterisation of artisanal catches in selected fishing areas of the Lower Tana Delta and Malindi-Ungwana Bay, Kenya	Dzoga et al.[63]	https://doi.org/10.4314/wiojms.v19i1.4
Species composition, abundance, and fishing methods of small-scale fisheries in the seagrass meadows of Gazi Bay, Kenya	Musembi et al.[64]	https://doi.org/10.1080/19480881.2019.1603608
Catch monitoring data	Wildlife Conservation Society[65]	NA
Catch monitoring data	Blue Ventures[66]	NA
An investigation into fisheries trends and a critical analysis of fisheries management within the Bay of Ranobe, Madagascar	Tiliouine[67]	NA
Fisheries co-management: Ecological and social impacts. A case study of Northern Mozambique	da Silva[68]	NA
La pêche locale aux abords de la Réunion	Biais & Taquet[69]	https://archimer.ifremer.fr/doc/00000/1455/
Unpublished data	Seychelles Fishing Authority[70]	NA
The annual fisheries statistics report	Tanzania Ministry of Livestock and Fisheries[71]	NA
World population prospects: The 2022 revision	UNDESA[72]	https://population.un.org/dataportal/
Bio-ORACLE v2.0: Extending marine data layers for bioclimatic modeling	Assis et al.[73]	https://doi.org/10.1111/geb.12693
NOAA Coral reef watch: Daily global 5km satellite sea surface temperature product	NOAA[74]	https://coralreefwatch.noaa.gov/
Global gradients of coral exposure to environmental stresses and implications for local management	Maina et al.[75]	https://doi.org/10.1371/journal.pone.0023064
Marine socio-environmental covariates: Queryable global layers of environmental and anthropogenic variables for marine ecosystem studies	Yeager et al.[76]	https://doi.org/10.1002/ecy.1884
How accessible are coral reefs to people? A global assessment based on travel time	Maire et al.[77]	https://doi.org/10.1111/ele.12577
Software and algorithms		
Original code associated with this paper	This paper	Zenodo: https://doi.org/10.5281/zenodo.8258102
rfishbase v4.1.2 [R Package]	Boettiger et al.[78]	https://doi.org/10.1111/j.1095-8649.2012.03464.x
R v4.2.2	R Core Team[79]	https://www.R-project.org/
FishLife v3.0.0 [R Package]	Thorson et al.[80]	https://doi.org/10.1111/2041-210X.14076

RESOURCE AVAILABILITY

Lead contact

Further information and requests for resources and reagents should be directed to, and will be fulfilled by, the lead contact, Bryan P. Galligan, S.J. (bgalligan@jesuits.org).

Materials availability

This study did not generate new unique materials.

Data and code availability

- This paper analyzes existing, publicly available data. These datasets and DOIs are listed in the key resources table. Some of the catch monitoring data reported in this study cannot be deposited in a public repository because access to it is governed by the original authors and/or organizations. To request access, contact the original authors via email. In addition, processed datasets derived from these data have been deposited at Zenodo and are publicly available as of the date of publication. DOIs are listed in the key resources table.
- All original code has been deposited at Zenodo and is publicly available as of the date of publication. The DOI is listed in the key resources table.
- Any additional information required to reanalyze the data reported in this paper is available from the lead contact upon request.

METHOD DETAILS

Nutrient density for 10 fishery jurisdictions

The nutrient density of fish catches was based on the relative biomass of captured species, but most jurisdictions do not report catch data with sufficient taxonomic precision to obtain precise nutrient estimates. We thus reconstructed the taxonomic composition of fish catches in 10 Western Indian Ocean (WIO) jurisdictions with available data. We began by using the catch compositions in the Sea Around Us (SAU) catch reconstruction database.[62,81] We extracted the SAU estimates for artisanal and subsistence landings in the most recent year available as this was the most convenient way of accessing SAU catch composition estimates. For WIO artisanal catches, SAU reconstructions estimate a stable catch composition that is applied to several years at a time.[62] For example, the Kenya catch reconstruction features one taxonomic breakdown applied to the small-scale catch from 1950 to 2010 and a second version for 2011–2018.[82,83] The Madagascar catch reconstruction includes one taxonomic breakdown for the entire period 1950–2018.[84,85] We removed unidentified species and non-fish species. The majority of SAU catch data were reported to the family level. For example, SAU reports artisanal landings in Kenya in 40 taxa, 38 of which (87% by mass) are families, genera, or species.[83] For Maldives, SAU reports artisanal landings in 42 taxa: 7 families, 3 genera, and 32 species.[86] For Mayotte, SAU reports artisanal landings in 95 taxa, including 31 families, 13 genera, and 46 species.[85] By mass, 98% of Mayotte's landings are reported to the family level or better. For four jurisdictions—Comoros, Maldives, Mauritius, and Mayotte—we used the SAU data as provided.[85,86] For the remaining six jurisdictions—Kenya, Madagascar, Mozambique, Reunion, Seychelles, and Tanzania—we compiled data from various contributors and published datasets to increase the taxonomic precision of the SAU reconstructions.[63–71,83,85,87–89] We did this by taking the original proportion of the catch assigned to each taxon in the SAU reconstructions and further partitioning it into finer taxonomic categories based on the proportions found in our supplementary sources of catch data. These data sources are summarized in Table S1.

By-species estimates of nutrient concentrations were extracted from FishBase using the *rfishbase* package in R, including calcium, iron, vitamin A, omega-3 polyunsaturated fatty acids, selenium, and zinc.[61,78,79] The nutrient concentrations in FishBase are estimates derived from a series of hierarchical Bayesian models that predict nutrient concentrations in finfish species based on functional traits and phylogeny and are updated annually to account for new data and model improvements. In 7% of instances, nutrient concentrations were not available for an observed species, and in 1%, catch data listed fishes under imprecise taxonomic categories, such as genera or families. Where these problems occurred, we assigned a genus- or family-level mean nutrient concentration to the taxon in question. Nutrient densities were based on the percent daily recommended intake for a child 1–3 years old in a 100 g portion of fish.[43,44] This portion size is unrealistically high for a young child, even as a daily consumption, but it is a convenient denominator and allows for more direct comparison with previous studies.[5,8] There is a need for more data on fish consumption in the WIO and elsewhere. Daily consumption of marine fish has been estimated at approximately 76 g for adult women in the Seychelles,[40] and 390 g per capita among coastal indigenous communities in East Africa.[45]

Overfishing-induced nutrient losses

We estimated nutrient yields relative to maximum sustained yield by combining our nutrient densities for each jurisdiction with estimates of actual and maximum production from a fish biomass model. Model estimates of fish biomass and lost yield were derived from a multivariate environment—fish biomass model that evaluated 15 environmental and management characteristics and used 7 variables to predict biomass and production for all mapped reef cells (~6.25 km2) in the Western Indian Ocean (WIO).[42] These cells contain a number of ecosystems, including hard bottom reefs, sandy bottom seagrass and mangroves, and pelagic systems. The spatial scale of the model is also contained within the area from which fish are captured in this region (i.e., ~20 km²). This area is variable but has been measured as ~9 km between fishing landing sites along shorelines.[60] Therefore, for the purpose of utilizing a realistic space and ecosystem access of artisanal fishers, we estimated

access and production for the 15–20 km^2 areas next to a landing site location. We therefore extracted the mean biomass and production values from the nearest three cells offshore from each landing site. Environment, management, and biomass parameters used in the model drew from successfully predicted fishable biomass at 591 reef sites with an 85% fit to training data, with estimates based on environmental data collected between 1985 and the time of the biomass field sample.[42] For the 10 jurisdictions included in this study, the model included 11,678 cells covering a total reef area of >70,000 km^2. Here, we only include yields lost due to overfishing. While production could also be increased by expanding fishing into underexploited and protected areas, this was not considered as a viable or recommended option.

We converted the model's estimates of biomass and lost yields into lost nutrient yields using our reconstructed nutrient catch densities for each jurisdiction. Nutrient yields are presented as a factor of nutrient density for all six nutrients (0–600%) and yield (kg) per square kilometer per day $\left(\frac{\%DRI \times Lost\ Yield}{km^2 \times Day}\right)$. Selenium was capped at 100%, so that 100 g of lost yield would be reported as 100% (0.17) of a combined serving km^{-2} day^{-1} plus the losses due to other nutrients. Lost nutrient yields were mapped by reef cell and aggregated for analysis by jurisdiction. In order to provide a sense of the scale of nutrient demand, we also extracted population estimates for each jurisdiction from the *UN World Population Prospects Data Portal*.[72] These population estimates are of the total population aged 1–3 years as of July, 2023 based on projections revised and published in 2022.[72] Although we used national population estimates, it should be noted that artisanal fisheries in the WIO primarily support coastal populations.[36] For jurisdictions with large inland populations, such as Kenya, Tanzania, Mozambique, and Madagascar, nutrient production from marine fisheries will not benefit inland communities without additional governance interventions.

QUANTIFICATION AND STATISTICAL ANALYSIS

Modeling drivers of nutrient density

We compiled data for environmental, catch, and management parameters that could influence the nutrient composition of artisanal fishery catches at 41 landing sites in Kenya, Mozambique, and Madagascar. Thirty-seven variables were compiled for each site that could be classified as environment (20 variables), management (7 variables), and catch characteristics (10 variables) (Table S1). The catch and management characteristics were derived directly from observations at each landing site and based on long-term or published monitoring studies that recorded catch, length, and effort data for nearshore artisanal fisheries (Table S1).[63–68] Data collection for these studies took place between 2001 and 2021 and observed a total of 5,188 fishing trips, defined as a unique combination of fisher/crew identity and date. Biomass and management variables were extracted from the biomass model used to estimate lost nutrient yields due to overfishing.[42] All other variables were derived from publicly available databases and previous studies (Table S1).[73–77]

We also compiled estimates of life history parameters for each species in our study and cross-referenced those parameters with observed lengths at capture to provide indicators of fishery status relative to management reference points. The life history parameters we used were length at first maturity (L_{mat}) and optimum fishing length (L_{opt}). If the ratio of length at capture to length at maturity (L/L_{mat}) was less than one, recruitment overfishing was likely taking place.[90] Growth overfishing was considered likely when the ratio of length at capture to optimum length (L/L_{opt}) was less than one.[90] Although these single-species, length-based indicators are most frequently used in yield per recruit models, we apply them here in the context of community surplus production.[17,50,91] L_{mat} for each species was obtained directly from the *Fish-Life* R package, which uses data found in FishBase and the RAM Legacy Stock Assessment Database to inform a Bayesian model that predicts life history parameters for all finfish species.[61,80,92] We derived L_{opt} from the life history parameters estimated by FishLife using the equation

$$L_{opt} = L_{inf} \times \left(\frac{3}{3+\frac{M}{K}}\right)$$

where L_{inf} is the asymptotic length, M represents natural mortality, and K is the von Bertalanffy growth coefficient.[93]

We used a machine learning Random Forest Model (RFM) to identify environment, catch, and management parameters influencing the nutrient density of artisanal catches at our 41 landing sites. To select variables for modeling, we added a vector of random numbers in an initial series of RFM runs and eliminated all variables that were consistently less important than random numbers.[94,95] This eliminated most variables, leaving only habitat, trophic level, growth coefficient (K), maturity (L/L_{mat}), and length at capture (cm). We then tested the remaining variables for autocorrelation using Spearman's correlation coefficient. We retained all variables after this test as no variable pair had a correlation coefficient greater than 0.75.[96] Uninformative variables do not hurt RFM performance, but removing them can streamline interpretation and computational efficiency.[94,95]

We split the retained data into a testing and training sample to construct and evaluate the RFM.[97] The training dataset was a bootstrapped sample the same size as the original, sampled with replacement (n = 5,188 fishing trips). The testing dataset was the out-of-bag sample after bootstrapping (n = 1,922 fishing trips). We tuned the RFM based on its performance in predicting the training and testing data, which peaked when three of the five variables were randomly selected at each tree.[94] After running the model, we plotted two measures of variable importance: the percent increase in mean squared error when a variable was eliminated, and the increase in node purity when a variable was included.[94] Increase in node purity is a measure of the increase in predictive accuracy of a node in a decision tree when a particular variable is included.[94]

We extracted RFM predictions for the partial dependence of nutrient densities on each of the five selected variables and used a feature-based measure to evaluate variable significance.[98] The only feature producing a mean squared error standard deviation of less than 0.01, catch per unit effort (CPUE), was deemed not significant and pruned from the model; its exclusion did not affect model skill.[98] We then plotted

the partial dependence of model predictions over the most important predictor variables and included a locally weighted smoothing function to aid interpretation. Finally, we used the same model structure to predict the relationships between each variable and all six studied dietary nutrients.

It is important to note that our 41 landing sites may not be representative of the whole WIO region. Our landing sites were in three of the most heavily fished nations of the WIO. Approximately 76% of the reef cells adjacent to these sites were overfished, while this is only true of 37% of reefs in the wider region. As a result, the reefs adjacent to our landing sites are likely to be less species rich and functionally diverse than other WIO coral reefs.[19,99] This may drive differences in the nutrient densities of artisanal catches and will not be captured by our data.