

1 **Nutrition contributions of coral reef fisheries not enhanced by**  
2 **capture of small fish**

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4 Bryan P. Galligan<sup>1,2,\*</sup> & Timothy R. McClanahan<sup>3</sup>

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6 <sup>1</sup> Jesuit Justice and Ecology Network Africa, Nairobi, Kenya

7 <sup>2</sup> Department of Biology, Loyola University Chicago, Chicago, I.L., U.S.A.

8 <sup>3</sup> Wildlife Conservation Society, Global Marine Programs, Bronx, N.Y., U.S.A.

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10 \* Corresponding author. Email: [bgalligan@jesuits.org](mailto:bgalligan@jesuits.org). Postal address: Jesuit Justice and  
11 Ecology Network Africa, P.O. Box 1540, Karen, Nairobi 00502, Kenya.

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20  
21 **Abstract**

22 Recent policy recommendations have highlighted the nutritional benefits of fisheries  
23 that capture small finfish species. Small fish, particularly those that feed in the pelagic zone,  
24 tend to be more nutrient dense than larger species, with increased concentrations of calcium,

25 zinc, and omega-3 fatty acids. However, capturing fish below some recommended size limit  
26 (i.e., length at first maturity =  $L_{mat}$ ) in coral reefs is frequently considered to be unsustainable  
27 and associated with reduced yields and losses of ecosystem functions. To evaluate the  
28 potential effects of fish body size, we analyzed nutrient concentrations of 424 demersal and  
29 pelagic finfish species reported from Western Indian Ocean artisanal fisheries. We found that  
30 length and food source are associated with only small differences in nutrient density in the  
31 artisanal catches of this region ( $\leq 7\%$  of a child's daily requirement in most cases). We also  
32 analyzed 20 years of catch monitoring data from Kenya, where many of the common species  
33 have  $L_{mat} \sim 20\text{--}25$  cm, to test the potential benefits and tradeoffs of capturing small fishes.  
34 Small capture sizes were associated with low yields and sexually immature catches with a  
35 mean length of 15 cm resulting in 38% lower catch per unit effort, 37% lower nutrient yield,  
36 and a 22% lower maturity index compared to a mean body length of 30 cm. Catches of  
37 undersized fish were not associated with substantial increases or decreases in nutrient content  
38 relative to human nutritional requirements. Thus, coral reef artisanal fisheries should target  
39 moderate to large fishes ( $> 20$  cm) to maximize overall yield, nutrient yield, and  
40 sustainability.

41

42 **Keywords:** fisheries, sustainability, nutrition, food security, coral reef

43

## 44 **1. Introduction**

45 Strategies for food production in the context of global environmental change should  
46 be oriented towards achieving sufficiency, nutritional quality, and sustainability (Mustafa et  
47 al., 2021). Fisheries are no exception, and recent policy guidance from academic and  
48 intergovernmental organizations has increasingly attempted to take these three goals into  
49 account (e.g. Andrachuk et al., 2022; FAO, 2021; HLPE, 2014; Kawarazuka et al., 2023).

50 However, the policy and science supporting it are relatively new, and significant  
51 disagreements remain about how best to maximize the quantity, quality, and sustainability of  
52 food produced by capture fisheries (Jones and Unsworth, 2020; Tilley et al., 2020; Zhou et  
53 al., 2019). Here, we show using catch data from the Western Indian Ocean (WIO) that an  
54 emerging policy recommendation to increase the consumption and capture of small fishes  
55 does not achieve food system goals in unselective coral reef artisanal fisheries and should not  
56 be considered a universal recommendation.

57         The nutritional benefits of small fish are celebrated in several recent policy  
58 publications (Ahern et al., 2021; Bavinck et al., 2023; FAO et al., 2023; HLPE, 2014;  
59 Kolding et al., 2019). Small fish are nutritionally valuable because (1) their muscle tissue  
60 tends to be more nutrient dense (Hicks et al., 2019; Mills et al., 2023); and (2) they are often  
61 consumed whole (Bavinck et al., 2023; HLPE, 2014; Kawarazuka and Béné, 2011). However,  
62 oversimplified summary statements and a variety in the definitions of ‘small fish’ might lead  
63 to a false impression that increasing the capture and consumption of small fish is a  
64 recommended policy in many or all contexts. For example, the Food and Agriculture  
65 Organization (FAO) of the United Nations observes that “the most nutrient-rich functional  
66 groups for both inland and marine fish catches are those that include small (< 25 cm total  
67 length), frequently pelagic species” (Mills et al., 2023, p. 151). This observation is then used  
68 to inform flexible policy recommendations that can be responsibly applied in different  
69 contexts (Mills et al., 2023, p. 148). Despite this nuance, however, the headline statement the  
70 FAO highlights in the executive summary of the same report is simply that “small fish are  
71 especially nutritious” (FAO et al., 2023, p. xxxv). Similarly, Kawarazuka and Béné review  
72 literature on fish consumption in poor households and conclude that “small fish species that  
73 are consumed whole with bones, heads, and viscera play a critical role in micronutrient  
74 intakes” (2011, p. 1931). They do not define ‘small fish,’ but they do recommend that “a

75 sustainable supply of these species should be prioritized” (Kawarazuka and Béné, 2011, p.  
76 1936). More recently, an FAO technical paper explicitly addressed the definitional challenge,  
77 but nonetheless recommended “substantially increasing fishing pressure on small fish,”  
78 including in multispecies fisheries (Bavinck et al., 2023, p. 152).

79         The wide diversity of approaches to, and definitions of, small fish risks a  
80 misalignment between science and policy. From the perspective of nutrition-sensitive harvest  
81 strategies, capturing small fishes raises two primary concerns. First, capturing juveniles of  
82 larger species could jeopardize production and sustainability in unselective multispecies  
83 fisheries (Ben-Hasan et al., 2021; Sun et al., 2023). Unselective fishing methods that capture  
84 small individuals can cause both recruitment and growth overfishing and potentially provoke  
85 fisheries collapse and losses of nutritious seafood and biodiversity (Hicks and McClanahan,  
86 2012; McClanahan, 2022; Myers and Mertz, 1998; Zamborain-Mason et al., 2023). Second,  
87 simple headline statements, such as “small fish are especially nutritious” (FAO et al., 2023, p.  
88 xxxv), risk obscuring the variability that is found across taxa, habitats, life histories, and  
89 management strategies (Hicks et al., 2019; Robinson et al., 2022d, 2023). There is a need to  
90 disarticulate these taxonomic, diet, and sustainability concerns to nuance and improve  
91 existing advice (Mustafa et al., 2021).

92         Coral reefs and associated ecosystems support complex multispecies fisheries that  
93 supply nutrition to many poor and subsistence stakeholders in the Global South. Therefore,  
94 we explore the potential benefits and trade-offs of capturing small fish from coral reefs based  
95 on (1) nutrient composition data of tropical finfish and (2) catch data from Western Indian  
96 Ocean (WIO) nearshore artisanal fisheries. In the unselective reef fisheries of the WIO, we  
97 define ‘small fish’ as < 20 cm, as this size class falls below the length at first maturity ( $L_{mat}$ )  
98 of the most frequently captured species and will thus include a mix of mature individuals of  
99 smaller species and juvenile individuals of larger species (Tuda et al., 2016). Artisanal

100 fisheries in the WIO target a diversity of species, including small pelagic and demersal fishes,  
101 and often reserve smaller fishes for home consumption (Cartmill et al., 2022; van der Elst et  
102 al., 2005; Wamukota and McClanahan, 2017). Specifically, we asked (1) how nutrient  
103 densities of WIO small pelagic fishes compared to human dietary requirements, (2) whether  
104 targeting small body sizes in these predominantly mixed species fisheries would increase the  
105 nutrient content of fish catches, and (3) how the mean length of fish catches affects yield and  
106 sustainability indicators, including nutrient yield. We do not address the nutritional benefits  
107 of whole fish consumption or targeted (selective) small pelagic fisheries, such as those that  
108 capture herring, sardines, and anchovy.

109

## 110 **2. Methods**

111 To address the above questions, we combined nutrition information from publicly  
112 available databases, landings reported in 10 Western Indian Ocean (WIO) fishing  
113 jurisdictions, and long-term continuous catch monitoring data collected in Kenya by the  
114 Wildlife Conservation Society (WCS) (Froese and Pauly, 2023; McClanahan and Azali, 2020;  
115 Thorson et al., 2023). From these data we explored the nutrient content, yield, and  
116 sustainability implications of targeting small fishes.

117

### 118 *2.1. WIO fish species nutrient concentrations*

119 We compiled a list of fish species captured by WIO artisanal fisheries from national  
120 catch statistics, published studies, and governments' and NGOs' monitoring data (Tables S1–  
121 2). This produced 480 species of which 34 had no nutrient estimates in FishBase and were  
122 therefore removed. We also removed an additional 22 species reported to reach maturity  
123 ( $L_{mat}$ ) at  $> 100$  cm in length. These species are outliers, rarely caught in these nearshore  
124 fisheries, and detract from the focus on small fish. We considered the 424 remaining species

125 representatives of the WIO artisanal catch as they accounted for 99.3% of all landings by  
126 weight observed in the 20-year Kenyan dataset. Using a species list rather than landings data  
127 allowed us to separate mature, small-bodied species from juvenile, large-bodied species and  
128 specifically test for species-level effects of body size and food source.

129         Densities of calcium, iron, omega-3, selenium, vitamin A, and zinc for each species  
130 (per 100 g) were obtained from FishBase using the *rfishbase* package (Boettiger et al., 2012;  
131 Froese and Pauly, 2023). FishBase values are estimates produced by a hierarchical Bayesian  
132 model that uses the functional traits of finfish species to estimate nutrient concentrations  
133 (Hicks et al., 2019). The predictive model includes tropical covariates such as temperature  
134 and latitude and is revised annually as nutrient data for new species are added (Froese and  
135 Pauly, 2023). One limitation of the FishBase nutrient values is that they assume no variability  
136 within species regardless of habitat or life stage (Froese and Pauly, 2023; Robinson et al.,  
137 2022b). Nevertheless, FishBase is the largest fish nutrient dataset available and is the most  
138 appropriate for large studies with many taxa (e.g., Cheung et al., 2023; Hicks et al., 2019;  
139 Maire et al., 2021; Robinson et al., 2022c, 2023).

140         All analyses were conducted in R (R Core Team, 2022). We tested the relationships  
141 between body lengths and food source (benthic or pelagic) on nutrient densities for all 424  
142 WIO species using linear mixed models. Length at maturity estimates ( $L_{mat}$ ) were obtained  
143 from the *FishLife* R package (Thorson et al., 2023). For each nutrient, we modeled  $L_{mat}$  and  
144 food source as interacting effects using the model structure  $\log Nutrient\ Density \sim L_{mat} \times$   
145  $Food\ Source$ . We first implemented mixed models for each nutrient in the *glmmTMB* R  
146 package and evaluated residuals and outliers using the *DHARMA* package (Brooks et al.,  
147 2017; Hartig, 2022). We evaluated quantile-quantile plots of residuals for over- and  
148 underdispersion and heteroscedasticity and used the *DHARMA* package's built-in outlier test  
149 to determine whether model predictions were overly influenced by extreme values (Hartig,

150 2022). For nutrients that failed one or more of these tests, we implemented a version of the  
151 same model using the *rlm* function from the *MASS* package in R, which generates model  
152 predictions that are robust to outliers and non-normal distributions using an M estimator  
153 (Venables et al., 2002). Vitamin A and zinc met the assumptions for linear regression, but all  
154 other nutrients required robust models as implemented in the *MASS* R package.

155

## 156 2.2. Kenya catch monitoring

157 Catch monitoring was conducted at 22 landing sites from 2001–2021. Observers  
158 recorded 1,163 fishing trips with a mean catch per unit effort (CPUE) of 1.78 kg fisher<sup>-1</sup> day<sup>-1</sup>  
159 ( $\pm 0.06$  SE). Fishers captured a total of 249 species ranging in size from a 1 cm marbled  
160 parrotfish (*Leptoscarus vaigiensis*) caught with a beach seine to a 121 cm pompano  
161 dolphinfish (*Coryphaena equiselis*) caught with a handline. Captured fish were identified to  
162 the species level and their total lengths were measured (total length, cm). The gear used and  
163 number of fishers per crew were also recorded. Individual fish weights were then calculated  
164 using the length-weight relationships in FishBase, which were accessed using the *rfishbase*  
165 package in R (Boettiger et al., 2012; Froese and Pauly, 2023). Finally, we combined catch  
166 monitoring data with estimates of nutrient densities and lengths at maturity ( $L_{mat}$ ) for each  
167 captured fish as described in section 2.1, with the added procedure of using genus-level mean  
168 nutrient values where no estimates were available for an observed species. We used the ratio  
169 of length at capture to length at maturity ( $L/L_{mat}$ ) as an indicator of stock sustainability  
170 (Froese, 2004). Using catch monitoring data allowed us to assemble a more accurate picture  
171 of the mix of mature and immature fishes captured by this unselective fishery when small  
172 lengths predominate in the catch (Tuda et al., 2016).

173

## 174 2.3. Analyses of Kenya catch data

175           Once catch monitoring data were supplemented with nutrition and sustainability  
176 indicators, the data were pooled by fishing trip, defined as the total landings per crew per day.  
177 This allowed the calculation of catch per unit effort (CPUE) and nutrient yields. Nutrient  
178 yields were calculated by developing a combined nutrient density score and multiplying this  
179 value by the number of 100 g portions caught per fisher per day (Maire et al., 2021). Other  
180 catch parameters included here (nutrient content, length, and  $L/L_{mat}$ ) are reported as the  
181 biomass-weighted mean value per trip. Using the biomass-weighted mean for  $L/L_{mat}$  is likely  
182 to overestimate the maturity of fish catches by assigning lower weights to small, immature  
183 fishes. However, this approach is also more conservative in the context of our hypothesis and  
184 more likely to favor a recommendation to capture small fish.

185           We tested the effect of fish length on nutrient densities in the Kenyan artisanal catch  
186 using linear models. We initially included site as a random effect to account for differences in  
187 species assemblages at different locations, but minimal amounts of variance were attributed  
188 to the random effect. We thus used a model structure of  
189  $\log \text{Nutrient Density} \sim \text{Length at Capture}$  for all nutrients except zinc, which did not  
190 need to be log transformed. As described in section 2.1, we implemented an outlier test and  
191 examined quantile-quantile plots of residuals to test for over- and under-dispersion and  
192 heteroscedasticity (Hartig, 2022). Outliers were dominated by a few extremely high nutrient  
193 densities that do not represent the more typical catches and were therefore removed.

194           The effects of length on overall yield, nutrient yield, and maturity ( $L/L_{mat}$ ) were also  
195 tested using linear models. For overall yield and nutrient yield, we used an initial model  
196 structure that included site and fishing gear as random effects. The initial model structure for  
197 maturity included only site as a random effect. Fishing gear was included for the yield  
198 indicators because gears are associated with different yields in this fishery (Hicks and  
199 McClanahan, 2012; McClanahan and Kosgei, 2018). However, similar to the nutrient



200 concentration models, neither random effect was informative, and removing them did not  
201 improve residual diagnostics. Examination of quantile-quantile plots found no signs of over-  
202 or underdispersion or heteroscedasticity, but outlier tests for all models were significant ( $p <$   
203  $0.05$ ). We thus implemented robust linear models as described in section 2.1 using the *MASS*  
204 package in R (Venables et al., 2002).

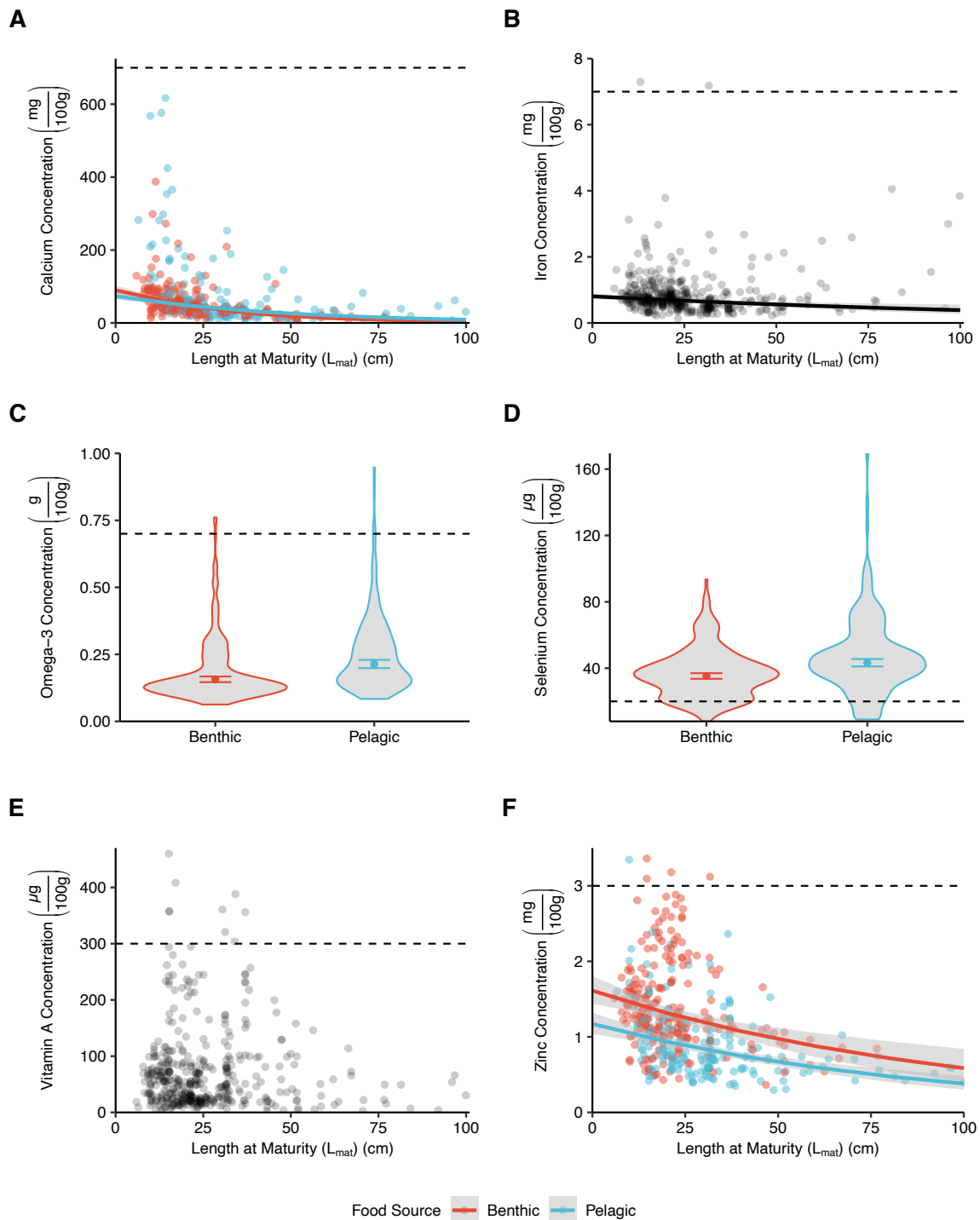
205

### 206 **3. Results**

#### 207 *3.1. Nutrient densities of Western Indian Ocean fishes*

208 Nutrient concentrations were negatively correlated with body lengths for calcium,  
209 iron, and zinc, but not for omega-3, selenium, or vitamin A. Significance was strong because  
210 of the large sample sizes, but effect sizes were small relative to human nutritional  
211 requirements (Table 1; Fig. 1). For example, a species of fish reaching maturity at 10 cm  
212 contains around 2.6 times the calcium concentration of a fish reaching maturity at 40 cm, but  
213 a 100 g portion of the comparatively nutritious smaller fish still contains only ~9% of the  
214 recommended daily allowance for a child 1–3 years old (Fig. 1A). Omega-3 and selenium  
215 densities had no relationship with length at maturity, but both were slightly higher in pelagic  
216 than in demersal species (Figs. 1C, D; Table 1). Again, however, differences were small, with  
217 a 100 g serving of a pelagic fish only providing an additional 8% of a child's adequate intake  
218 of omega-3, and both food sources providing 175–200% of a child's RDA for selenium (Fig.  
219 1C, D). Vitamin A densities did not respond to length or food source (Table 1).

220



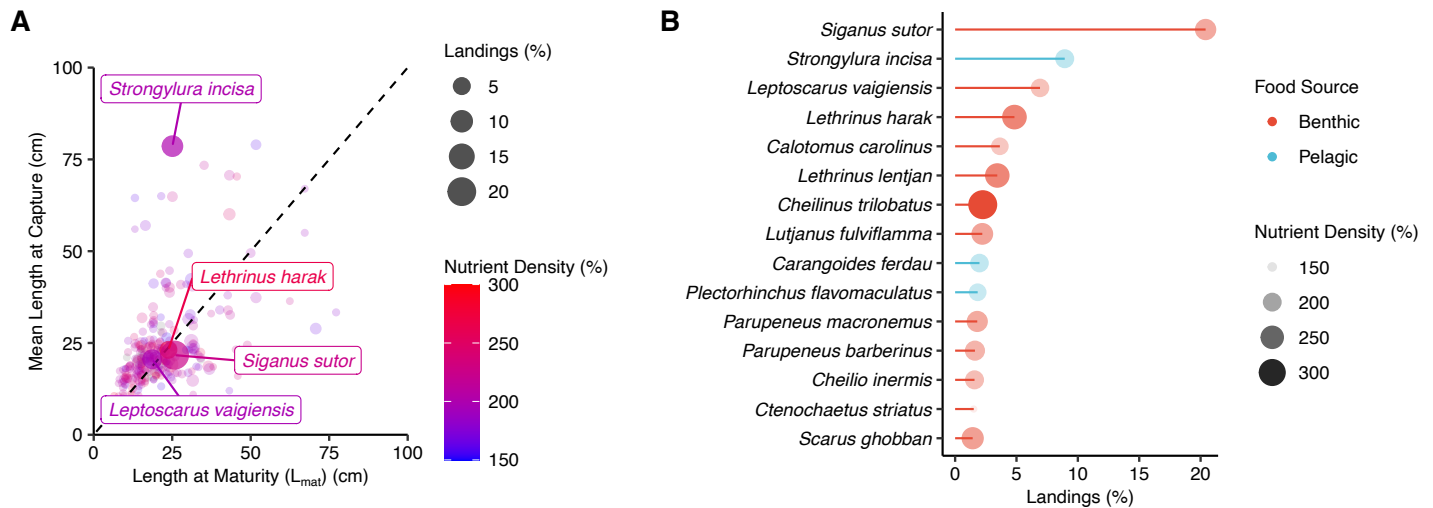
221

222 **Figure 1** Scatter plots and linear regressions for length at maturity ( $L_{mat}$ ) and nutrient  
 223 concentration of 424 species reported in nearshore artisanal fish catches of the Western Indian  
 224 Ocean. Model best-fit predictions for food source (benthic or pelagic) and length are only  
 225 displayed if they reached a significance threshold of  $p < 0.01$ . Dashed horizontal lines  
 226 indicate the dietary reference intake for each nutrient for a child 1–3 years old (Fig. 2C, F).

227

## 228 3.2. Nutrient densities in the Kenyan artisanal catch

229 Most species had combined nutrient densities slightly above 200% (out of 600%) of a  
230 child's recommended allowance of six nutrients in a 100 g daily portion (Fig. 1). Four  
231 species—*Siganus sutor*, *Strongylura incisa*, *Leptoscarus vaigiensis*, and *Lethrinus harak*—  
232 accounted for 41% of the catch by mass and ranged in nutrient density from 197–265% (Fig.  
233 1B). Over 71% of all landings and 12 of the top 15 species were benthic feeders (Fig. 1B).  
234 The mean length at first maturity ( $L_{mat}$ ) for all species was 23.5 cm ( $\pm 0.98$  SE) and the  
235 smallest of the top four species was *L. vaigiensis*, which accounted for 7% of the catch and  
236 had an estimated  $L_{mat}$  of 18.7 cm (Thorson et al., 2023). For all small fish captured ( $< 20$  cm),  
237 67% by mass were sexually mature and 11% of these were pelagic in this predominantly  
238 benthic fishery. The mean length at capture was 21.4 cm ( $\pm 0.08$  SE) and most fish were  
239 captured just above their length at first maturity, with a mean maturity index of  $1.05 L/L_{mat}$  ( $\pm$   
240  $3.5 \times 10^{-3}$  SE).



242 **Figure 2** Summary of catch data from Kenya's nearshore artisanal fisheries 2001–2021. (A)

243 Length at maturity ( $L_{mat}$ ) and mean length at capture for 249 species. Point size represents the

244 percent of landings by mass accounted for by each species, with the top four species labeled.

245 Point color represents the nutrient density of each species for the six nutrients included here,

246 with a possible range of 0–600%. (B) Landings accounted for (% by mass) by the 15 most

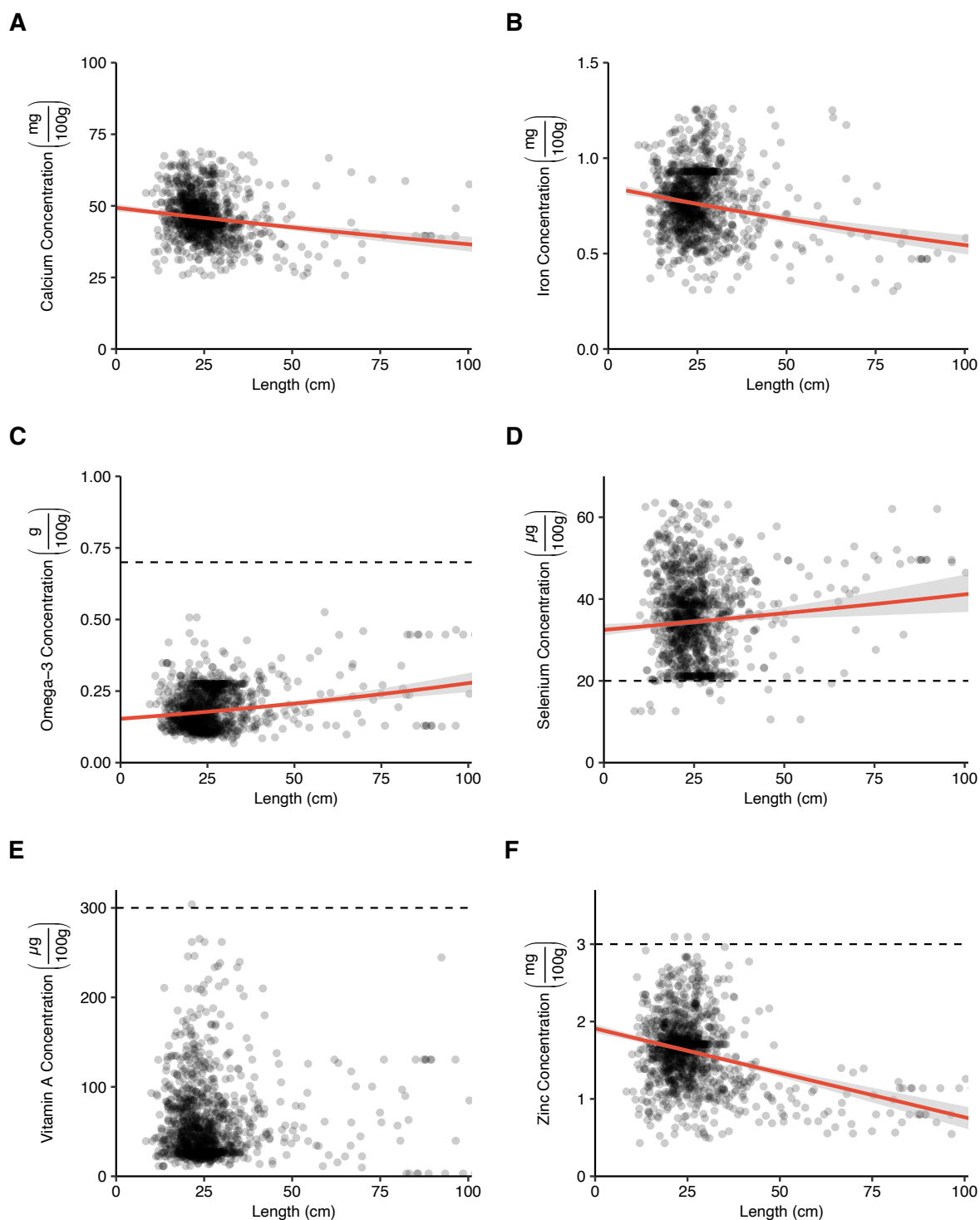
247 captured species. Point color represents food source (benthic or pelagic) while point size and

248 darkness indicate nutrient density with a possible range of 0–600%.

249           The biomass-weighted mean length at capture was significantly correlated with  
250 nutrient densities for all nutrients except vitamin A in the Kenyan artisanal catch. Again,  
251 however, the effect sizes were small relative to human nutritional requirements (0.3–5.7% of  
252 a child’s daily requirement between 15–30 cm), and the sign of the correlation varied among  
253 nutrients (Fig. 3; Table 2). Small capture sizes (15 cm) were associated with slightly higher  
254 densities of calcium, iron, and zinc, amounting to  $\leq 5\%$  of a child’s daily requirement in a  
255 100 g portion, and lower densities of omega-3 and selenium, amounting to  $\leq 6\%$  of a child’s  
256 daily requirement when compared with larger catch sizes (30 cm) (Fig. 3). For selenium, all  
257 nutrient predictions were well above the RDA of  $20 \mu\text{g day}^{-1}$  (Fig. 3D). The mean omega-3  
258 concentration was  $0.37 \text{ g } 100\text{g}^{-1} (\pm 8.7 \times 10^{-3} \text{ SE})$ , and the mean zinc concentration was  $1.6$   
259  $\text{mg } 100\text{g}^{-1} (\pm 3.1 \times 10^{-2} \text{ SE})$ , both of which fell just above half the daily requirement for a  
260 child 1–3 years old.

261

262



263

264 **Figure 3** Scatter plots and linear regressions for nutrient densities and biomass-weighted  
 265 mean length per trip based on 1,163 artisanal fishing trips recorded in Kenya from 2001–  
 266 2021. Model and best-fit predictions are only displayed if they reached a significance  
 267 threshold of  $p < 0.01$ . Dashed horizontal lines indicate the dietary reference intake of each

268 nutrient for a child 1–3 years old. Dietary reference intakes are not displayed for panels A and  
269 B because they are well above the range of observed data and model predictions. A child's  
270 recommended daily allowance (RDA) for calcium is 700 mg day<sup>-1</sup> and the RDA for iron is 7  
271 mg day<sup>-1</sup> (Institute of Medicine (IOM), 2011, 2006).

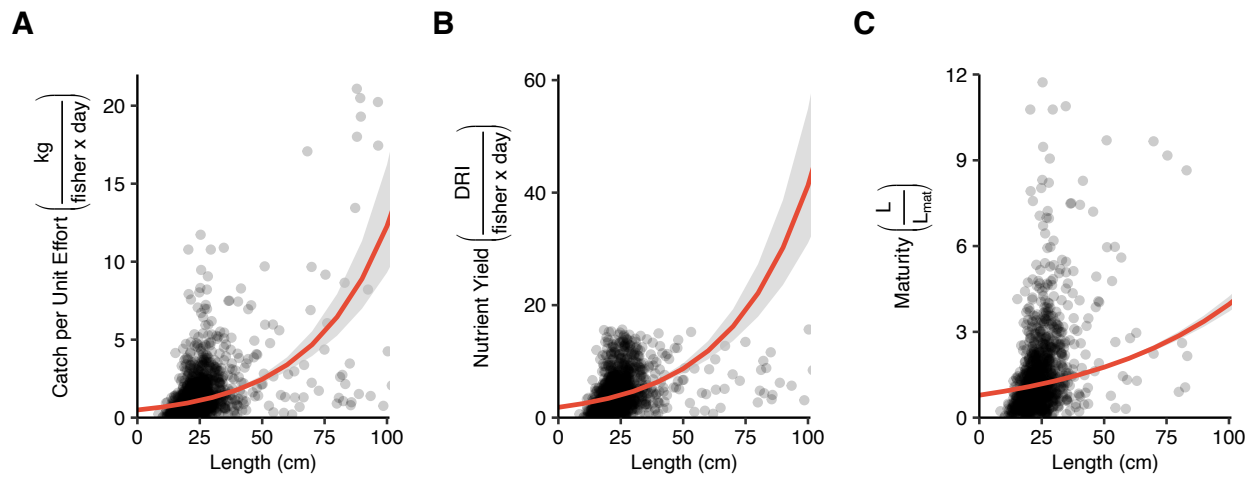
272

### 273 *3.3 Yield and sustainability indicators*

274 Biomass-weighted mean length was positively correlated with all three yield and  
275 sustainability indicators (Table 3; Fig. 4). Small capture sizes were associated with low yields  
276 and sexually immature catches, with a mean length of 15 cm generating 38% lower catch per  
277 unit effort, 37% lower nutrient yield, and a 22% lower maturity index compared to a mean  
278 length of 30 cm (Table 3; Fig. 4). Our linear model predicts that the maturity threshold of 1.0  
279 (biomass-weighted mean  $L/L_{mat}$  per trip) is achieved with a capture length averaging 15 cm  
280 (0.99, 1.02 95% CI) (Fig. 4C).

281

282



283

284 **Figure 4** Scatter plots and linear regressions for sustainability and yield indicators and  
285 biomass-weighted mean length per trip based on 1,163 artisanal fishing trips observed in  
286 Kenya from 2001–2021. All model best-fit predictions reached a significance threshold of  $p$   
287  $< 0.01$ . (A) Catch per unit effort is expressed in kilograms per fisher per day. (B) Nutrient  
288 yield is expressed as the number of complete servings of all six studied nutrients per fisher  
289 per day. (C) Maturity is the sexual maturity of the catch, evaluated as the biomass-weighted  
290 mean ratio of length at capture to length at maturity ( $L/L_{mat}$ ) per trip.

291

292



#### 293 4. Discussion

294 In the WIO and Kenyan nearshore catch, there was little or no apparent nutritional  
295 benefit associated with capturing small fish. Given the high numbers of species and the  
296 functional traits examined, these results are likely to apply to coral reefs more broadly. Coral  
297 reef fishes share a diversity of key functional traits that drive nutrient content (Hicks et al.,  
298 2019; McLean et al., 2021). This analysis also indicates that small pelagic fishes captured  
299 around reefs and associated nearshore ecosystems are not particularly nutrient dense, with the  
300 potential exception of specific targeted fisheries not studied here, such as the small pelagic  
301 fishery of the Pemba Channel in Tanzania (Sekadende et al., 2020). Small pelagic species are  
302 an important dietary resource in developing countries, and sometimes provide a win-win for  
303 nutrition and sustainability, but small fish cannot be said to provide a generally applicable  
304 and sustainable solution to malnutrition (Robinson et al., 2022a, 2022c; Wessels et al., 2023).  
305 Current recommendations seem to be based on differences in nutrient content among a few  
306 selected fish species (e.g., anchovies) and not on patterns seen across larger numbers of  
307 species or ecosystems. Coral reef fisheries are a particularly important case in point as they  
308 directly or indirectly support approximately 13% of the global population (Sing Wong et al.,  
309 2022).

310 Correlations between fish size, yield, and sustainability indicators (Fig. 3) confirm  
311 recommended best practices for coral reef fishery management (Hilborn et al., 2020;  
312 McClanahan, 2021). Moreover, that nutrient yield is critical for feeding people and is of  
313 greater importance than nutrient density in some contexts (Galligan et al., 2022; Robinson et  
314 al., 2022d). The conventional approach to reef fishery management recommended here  
315 includes a combination of spatial closures, gear restrictions, and effort reductions that would  
316 protect both juveniles and large spawners from overexploitation (MacNeil et al., 2015;  
317 McClanahan, 2021, 2018; Samoilyis et al., 2017). The theory behind this approach is based on

318 community surplus production curves, which have been used to predict biomass and yields in  
319 the WIO and globally (McClanahan and Azali, 2020; Zamborain-Mason et al., 2023). In coral  
320 reef artisanal fisheries, gear restrictions that limit the capture of small, sexually immature  
321 fishes are associated with increased yields and biomass (Hicks and McClanahan, 2012;  
322 McClanahan, 2021; Prince et al., 2015). Conversely, biomass depletion is correlated with  
323 truncated size and trophic structures, resulting in catches dominated by small body sizes  
324 (McClanahan, 2018; Zamborain-Mason et al., 2023).

325         One proposed alternative to conventional management is the concept of balanced  
326 harvest (BH), which recommends moderate fishing mortality distributed across species, sizes,  
327 and ecological functions in proportion to their productivity (Zhou et al., 2019). Advocates for  
328 BH argue that removing minimum size restrictions could provide coastal communities with  
329 increased access to highly nutritious small fish without compromising overall yields or  
330 depleting biomass (Bavinck et al., 2023; Garcia et al., 2012). Its critics argue that BH would  
331 lead to overfishing, that it relies on unrealistic ecosystem modeling, and that the empirical  
332 evidence supporting it is questionable (Froese et al., 2016; Zhou et al., 2019). While BH has  
333 not been explored in coral reef artisanal fisheries, some authors have observed that these  
334 fisheries tend to approximate BH naturally in the absence of regulations and market dynamics  
335 based on consumer preferences for large fish (Ranaivomanana et al., 2023; Ratusinski, 2023;  
336 Tuda et al., 2016). In light of the nutritional benefits of consuming small fish whole (Bavinck  
337 et al., 2023; Kawarazuka and Béné, 2011), facilitating increased access to small fish from  
338 coral reefs by relaxing minimum size restrictions according to BH might be a legitimate  
339 management strategy. However, doing so at current levels of effort would lead to reductions  
340 in species richness, maximum yield, nutrient yield, and fisher income (Galligan et al., 2022;  
341 Hicks and McClanahan, 2012; McClanahan, 2022; Zamborain-Mason et al., 2023).

342           We believe policy advice and headline statements should move beyond an  
343 oversimplified focus on the nutritional quality of fished species to consider optimizing long-  
344 term yields. Distinguishing nutrient density and nutrient yield as well as consistently  
345 incorporating recommended nutrient intakes are critical to improving recommendations. Most  
346 importantly, recommendations to increase the capture of small fish in unselective fisheries  
347 should be met with caution (Bavinck et al., 2023). The losses of income from these policies  
348 can be considerable, and they undermine the profitability and sustainability of fishing  
349 (McClanahan et al., 2023). Larger capture sizes were associated with increased nutrient yield  
350 even when size and nutrient concentration were unrelated (Figs. 2, 3B). While we found no  
351 conflict between yield and nutrient objectives here, stronger tradeoffs may exist in other  
352 systems (Galligan et al., 2022; Robinson et al., 2022d). As a result, maximizing the nutrient  
353 content of fish catches may seldom be a universally desirable goal. Rather, it is more likely to  
354 apply only to rare or local circumstances. While nutrient density is an important metric from  
355 a consumption perspective, it must be evaluated in the context of other goals such as total  
356 production, sustainability, and ecological resilience (Galligan et al., 2022; Maire et al., 2021;  
357 Mustafa et al., 2021; Robinson et al., 2022d).

358           Capturing larger, sexually mature fishes leads to increased yields and more  
359 sustainable catches and does not compromise nutrient capture in coral reef artisanal fisheries.  
360 Nonetheless, some fisheries may have the potential for increasing nutrient densities (Maire et  
361 al., 2021). However, increasing the capture of small fishes in coral reef fisheries is expected  
362 to undermine the production of an important source of dietary nutrients. Instead, the many  
363 people who rely on coral reefs for their nutrition should focus on sustaining high production  
364 of moderate sized fishes.

365

366

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375

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587

588 **Table 1** Results of mixed linear regression models for the effect of food source (benthic or pelagic) and length at maturity ( $L_{mat}$ ) on the nutrient  
589 densities of 424 finfish species captured in Western Indian Ocean artisanal fisheries. The first set of three columns contain slope estimates, the  
590 second set of columns contains the change in intercept estimates associated with pelagic feeders, and the final set of columns contains the change  
591 in slope estimates associated with pelagic feeders. Estimates are not back transformed. Values in italics reached a significance threshold of  $p <$   
592  $0.01$ .

	Length at Maturity			Food source (Pelagic)			Length x Food source (Pelagic)		
	Estimate	Std. Error	p-value	Estimate	Std. Error	p-value	Estimate	Std. Error	p-value
Calcium	$-3.2 \times 10^{-2}$	$3.1 \times 10^{-3}$	$5.4 \times 10^{-22}$	$-2.0 \times 10^{-1}$	$1.1 \times 10^{-1}$	$7.2 \times 10^{-2}$	$1.1 \times 10^{-2}$	$3.9 \times 10^{-3}$	$6.2 \times 10^{-3}$
Iron	$-7.3 \times 10^{-3}$	$2.7 \times 10^{-3}$	$6.2 \times 10^{-3}$	$3.0 \times 10^{-3}$	$9.5 \times 10^{-2}$	$9.8 \times 10^{-1}$	$3.0 \times 10^{-3}$	$3.3 \times 10^{-3}$	$3.7 \times 10^{-1}$
Omega-3	$3.1 \times 10^{-3}$	$2.7 \times 10^{-3}$	$2.5 \times 10^{-1}$	$3.0 \times 10^{-1}$	$9.7 \times 10^{-2}$	$2.0 \times 10^{-3}$	$3.5 \times 10^{-4}$	$3.4 \times 10^{-3}$	$9.2 \times 10^{-1}$
Selenium	$5.3 \times 10^{-3}$	$2.5 \times 10^{-3}$	$3.2 \times 10^{-2}$	$2.9 \times 10^{-1}$	$8.8 \times 10^{-2}$	$9.4 \times 10^{-4}$	$-3.5 \times 10^{-3}$	$3.1 \times 10^{-3}$	$2.6 \times 10^{-1}$
Vitamin A	$-6.8 \times 10^{-3}$	$5.3 \times 10^{-3}$	$2.0 \times 10^{-1}$	$3.5 \times 10^{-1}$	$1.9 \times 10^{-1}$	$7.0 \times 10^{-2}$	$-3.3 \times 10^{-3}$	$6.6 \times 10^{-3}$	$6.2 \times 10^{-1}$
Zinc	$-1.0 \times 10^{-2}$	$2.3 \times 10^{-3}$	$1.4 \times 10^{-5}$	$-3.2 \times 10^{-1}$	$8.4 \times 10^{-2}$	$1.4 \times 10^{-4}$	$1.1 \times 10^{-3}$	$2.9 \times 10^{-3}$	$7.0 \times 10^{-1}$

593

594

595 **Table 2** Results of linear regression models for the effect of biomass-weighted mean length  
 596 per trip on nutrient densities for 1,163 fishing trips observed in Kenya from 2001–2021.  
 597 Estimates and standard errors for regression coefficients of all nutrients except zinc are on a  
 598 logarithmic scale. All effect sizes are back transformed where necessary and presented in  
 599 both real terms and as a percent of a child’s (1–3 years old) dietary reference intake (DRI) for  
 600 each nutrient. Effect sizes are presented between 15–30 cm. Rows in italics are statistically  
 601 significant ( $p < 0.01$ ).

	Estimate	Std. Error	Effect <sub>15:30 cm</sub>	p-value
<i>Calcium</i>	$-3.0 \times 10^{-3}$	$4.8 \times 10^{-4}$	$-2.1 \text{ mg (0.3\%)}$	$6.4 \times 10^{-10}$
<i>Iron</i>	$-4.4 \times 10^{-3}$	$6.2 \times 10^{-4}$	$-0.05 \text{ mg (0.7\%)}$	$1.4 \times 10^{-12}$
<i>Omega-3</i>	$5.9 \times 10^{-3}$	$8.1 \times 10^{-4}$	$+0.01 \text{ g (1.4\%)}$	$5.0 \times 10^{-13}$
<i>Selenium</i>	$2.4 \times 10^{-3}$	$7.6 \times 10^{-4}$	$+1.2 \text{ } \mu\text{g (6\%)}$	$1.8 \times 10^{-3}$
Vitamin A	$1.1 \times 10^{-3}$	$1.5 \times 10^{-3}$	$+0.8 \text{ } \mu\text{g (0.3\%)}$	$4.5 \times 10^{-1}$
<i>Zinc</i>	$-1.1 \times 10^{-2}$	$9.7 \times 10^{-4}$	$-0.17 \text{ mg (5.7\%)}$	$1.9 \times 10^{-30}$

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604 **Table 3** Results of linear regression models for the effect of biomass-weighted mean length  
 605 per trip on yield and sustainability indicators for 1,163 fishing trips observed in Kenya from  
 606 2001–2021. Estimates and standard errors for regression coefficients are on a logarithmic  
 607 scale. Effect sizes are back transformed and presented between 15–30 cm. Catch per unit  
 608 effort and nutrient yield are expressed in terms of the daily catch per fisher. All relationships  
 609 displayed strong significance.

	Estimate	Std. Error	Effect <sub>15:30 cm</sub>	p-value
Catch per Unit Effort	$3.2 \times 10^{-2}$	$2.1 \times 10^{-3}$	+0.49 kg	$1.9 \times 10^{-50}$
Nutrient Yield	$3.1 \times 10^{-2}$	$2.1 \times 10^{-3}$	+1.7 servings	$1.1 \times 10^{-46}$
Maturity ( $L/L_{mat}$ )	$1.6 \times 10^{-2}$	$4.9 \times 10^{-4}$	+0.28	$2.0 \times 10^{-167}$

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