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
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Drivers of nutrient intakes from fisheries in French Polynesia


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20 **Abstract**

21 Small-scale fisheries provide nutrients to hundreds of millions of people worldwide, with yields
22 dependent on the condition of marine habitats such as coral reefs. Small-scale fisheries are a
23 particularly important food source in societies with nutrient deficiencies and where unhealthy food
24 alternatives are widely available. Using data from coral reef surveys around two islands in French
25 Polynesia (Moorea and Raiatea), we show how the availability of nutrients to fisheries changed in
26 relation to the condition of coral habitat. Fish biomass and nutrient availability were highest when
27 coral cover was low around both islands, driven predominantly by abundant herbivorous reef fish. We
28 also investigated the importance of fish in people's diets, to determine if fish consumption was
29 aligned with available fisheries resources on local reefs and if nutrient intakes from fish could be
30 explained by people's socioeconomic background. People ate a higher diversity of reef fish in
31 Raiatea, however nutrient intakes from fish were higher in Moorea. Most people ate more fish than
32 meat on both islands, however fish consumption declined over generations. People from fishing
33 households had higher nutrient intakes from reef and pelagic fish, and people from farming
34 households had higher intakes from reef fish. Preference for eating reef fish over pelagic fish in diets
35 was also associated with higher total nutrient intakes. Promoting traditional diets rich in fish could be
36 key to meeting people's nutritional needs in French Polynesia while reducing diet-related health
37 issues linked to the overconsumption of fat.

38 **Key words:** small-scale fisheries; coral reefs; marine resources; nutrition; Moorea; Raiatea

39 **Introduction**

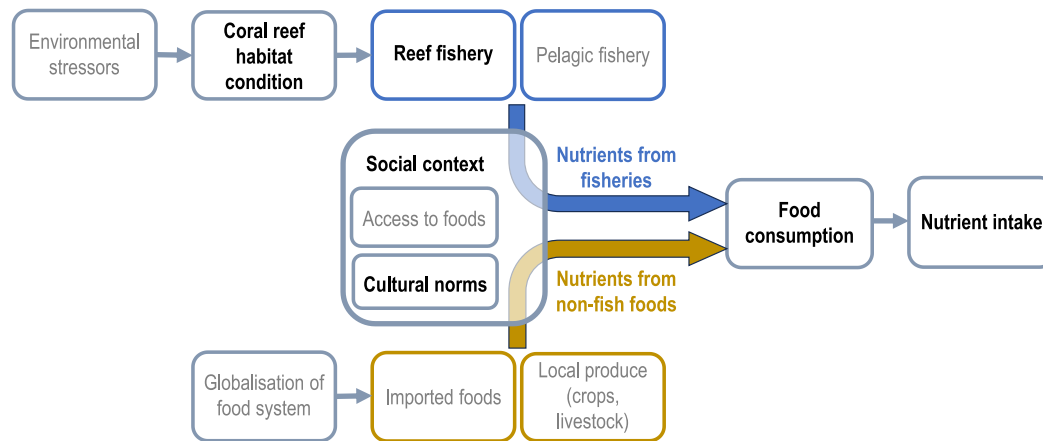
40 Small-scale fisheries support a wide diversity of fish accessible in many countries across the tropics
41 (Belton and Thilsted, 2014) and often provide an affordable animal-based source of protein and key
42 micronutrients that are lacking in people's diets (Kawarazuka and Béné, 2011; Hicks et al, 2019).
43 Tropical fisheries vary in their vulnerability to environmental stressors, such as climate change, as
44 well as in the nutrient density of yields (Maire et al, 2021). Therefore, tropical fisheries have the
45 potential to remain an important source of human nutrition as environmental conditions alter (Hicks et
46 al, 2021; Robinson et al, 2022a), although changes in the availability of fisheries resources may lead
47 to changes in people's fish consumption patterns.

48 Marine fisheries are sensitive to the condition of key habitats of targeted fish populations (Brown et
49 al, 2019), for example the condition of coral habitat influences the productivity, availability and long-
50 term sustainability of reef fisheries (Cruz-Trinidad et al, 2014; Morais et al, 2020a). Currently, there is
51 little understanding of how reef habitat condition impacts the provisioning of nutritious seafood
52 through fisheries (Hicks et al, 2021). Existing literature show variable responses of fishery catches to
53 changes in coral reef condition. For example, an increased abundance of herbivorous fish following
54 coral mortality maintained small-scale fisheries yields on some degraded reefs in Seychelles
55 (Robinson et al, 2019), while reef fisheries in the Pacific are expected to become less productive as
56 coral cover is progressively lost (Bell et al, 2013). The impacts of reef habitat condition on the
57 composition and size of fisheries catches may therefore influence the food provisioning services
58 provided by coral reefs (Woodhead et al, 2019). Decreases in fish catches would be expected to
59 reduce fish consumption, increasing risks of nutrient deficiencies in tropical coastal communities
60 (Golden et al, 2016). Reef-associated fish have relatively high concentrations of zinc and vitamin A,
61 while small pelagic (open-ocean) species have high calcium and omega-3 fatty acid concentrations
62 (Robinson et al, 2022b), therefore changes in seafood composition, for example through projected
63 catch increases of pelagic fisheries (Bell et al, 2013), would alter people's nutrient intakes from fish.

64 People's dietary choices are influenced by many factors beyond availability, including culture, price,
65 demographics, and convenience (Tilman and Clark, 2014). For example, increasing availability of
66 imported "Western" foods across the coastal tropics, driven by the globalisation of food trade systems
67 (Thow et al, 2011), has facilitated dietary transitions away from traditional diets of nutritious local
68 fish and plants, towards energy-dense and high-fat foods (Hughes and Marks, 2009). The nutritional
69 implications of moving away from traditional diets are a public health concern, as diets may become
70 deficient in essential nutrients, leading to micronutrient deficiencies, or contain excess nutrients
71 contributing to health conditions such as obesity and diabetes (Hughes and Marks, 2009; Sahal Estimé
72 et al, 2014; Stevens et al, 2022). For example, in the Peruvian Amazon, replacing wild caught
73 freshwater fish with chicken and farmed fish reduced intakes of essential fatty acids and iron,
74 nutrients that were already deficient in people's diets (Heilpern et al, 2021). If there is a shift away

75 from traditional fish-based diets towards modern diets with high fat content, it is important that people
76 balance local produce and imported foods in a way that minimises diet-related ill-health (Parry et al,
77 2010). Nutrition and diet-related health issues are unequally distributed within societies (Friel and
78 Baker, 2009), therefore it is imperative to determine which groups of people may be most at risk from
79 eating fewer traditional foods.

80 Here we focus on French Polynesia as a case study to examine linkages between ecological conditions
81 (coral reef habitat and fisheries resources), socioeconomic factors, and people's diets (Fig. 1).
82 Specifically, our research objectives are to 1) assess the availability of nutrients from reef fish in
83 relation to changes in coral reef habitat condition, and 2) investigate the importance of reef and
84 pelagic fish for people's nutrient intakes in relation to their socioeconomic background.



85

86 **Figure 1:** Conceptual diagram of links between coral reefs, fisheries, food supply, and dietary nutrition.
87 Environmental stressors (e.g. climate change, crown-of-thorns sea star outbreaks) affect coral reef habitat
88 condition, which in turn affects reef fisheries catches. People's nutrient intakes are determined by their
89 consumption of foods from reef and pelagic fisheries (blue) and other sources (orange). Food consumption is
90 influenced by social context, including culture and access to foods. Variables in grey text were not measured in
91 the current study (e.g. availability of reef fishery resources was estimated, but pelagic resources were not).

92 **Materials and methods**

93 *Study area*

94 This study focuses on two islands, Moorea and Raiatea, within the Society Archipelago, French
95 Polynesia (Fig. S1). Moorea is the second most inhabited island in French Polynesia after Tahiti, with
96 a population of 17, 463, while Raiatea has a population of 12, 291 (Institute of Statistics of French
97 Polynesia, 2017). Obesity is an urgent health concern in French Polynesia, with 68% of men and 67%
98 of women estimated to be overweight or obese in 2008 (Daigre et al, 2012). French Polynesia has

99 become dependent on Western imports of high-calorie foods since the 1980s, such as chicken which
100 has a particularly high fat content when fried (World Health Organisation (WHO), 2003). Food
101 imported into French Polynesia is mainly sourced from Europe, and the volume of unhealthy imported
102 foods has increased over time (Andrew et al, 2022).

103 Small-scale fisheries in French Polynesia use traps, hook and line, gillnets and spearguns to catch
104 reef-associated and pelagic fish, of which a large proportion is consumed locally (Chauvet and Galzin,
105 1996; Leenhardt et al, 2016). Reef and pelagic fish are sold at the roadside in Moorea, which provides
106 an income for fishing families and a local supply of fish for islanders (Nassiri et al, 2021). A large
107 proportion of fish caught around Raiatea is sold at a large market (Uturoa) at the north of the island
108 (Chauvet and Galzin, 1996). It is also common for islanders to order fish directly from fishers
109 (Leenhardt et al, 2016).

110 *Ecological data*

111 Live coral cover on reefs around Moorea and Raiatea was reduced to almost zero by 2010 after
112 crown-of-thorns sea star (*Acanthaster planci*; “taramea” in Tahitian) outbreaks, before being further
113 impacted by a cyclone and coral bleaching (Pérez-Rosales et al, 2021). We used underwater visual
114 census (UVC) surveys to collect data on live coral cover (photo-quadrats) and abundances and sizes
115 of reef fishes (belt transects) (details of transect methodology are in supplementary material). Surveys
116 were conducted every second year, in even years (2010-2020) at one site in Raiatea and two sites in
117 Moorea, and in odd years (2011-2019) at another site in Moorea (Fig S1).

118 We classified fish species into three trophic groups: “herbivore” (including detritivores and
119 microvores), “mobile invertivore” (including microinvertivores and macroinvertivores) and
120 “piscivore” (Parravicini et al, 2020) (Table S1). Fish weights were summed per trophic group to
121 estimate the total biomass per transect in kilograms per hectare. We calculated mean biomass and
122 standard error across transects per site in each year.

123 *Socioeconomic and dietary surveys*

124 We developed a semi-structured survey to gather socioeconomic (Table S2) and dietary data in
125 Moorea and Raiatea. The semi-structured interview was piloted in both islands, alongside informal
126 discussions, to create a final version that incorporated island-specific context while still allowing
127 comparisons to be made between islands. In total, 183 household interviews were conducted in
128 Raiatea, between June and September 2019 and 96 in Moorea in September 2019. We followed a
129 purposive snowball sampling approach (Ayhan, 2011) stratified across administrative districts,
130 targeting fishing and non-fishing households (Table S2). Initially, a few influential people in a district
131 were identified for interview, and subsequent interviews were then based on their recommendations
132 and introductions. Sample sizes satisfied our chosen 95% confidence level given the population of

133 each island (with 10% margin of error as we only sampled one person per household, even though
134 households often contained multiple people). Approximately two thirds of respondents on each island
135 were women as they were most commonly at home during the day to answer questions (pers. obs.).
136 Interviews were conducted in either French or Tahitian with a translator (English version of the
137 questionnaire available in online supplementary material).

138 We collected dietary data on the frequency of consumption of various food groups (based on the
139 Global Individual Food consumption data Tool, GIFT; Food and Agriculture Organisation (FAO),
140 2022; Table S3) and the types of fish people ate. Options for the frequency of consumption were:
141 “never”, “1-2 times per month”, “3-4 times per month”, “1-2 times per week”, “3-5 times per week”
142 and “6 or more times per week”. All responses were standardised by converting to number of times
143 per week. Some food categories were grouped together prior to analyses using a similar approach to
144 Kennedy et al (2011), for example “nuts/seeds” and “legumes” were separate questionnaire responses
145 but were combined to give a total consumption frequency (Table S3).

146 The types of fish eaten were identified to species level where possible, otherwise to taxonomic family
147 level. Fish names given in Tahitian were matched to scientific taxa based on local knowledge and
148 FishBase (Table S1). Frequency of consumption was not collected for each type of fish, only for fish
149 in general. Respondents were also asked about their fish consumption in comparison to their meat
150 consumption and their fish and meat consumption in comparison to previous generations
151 (parents/grandparents).

152 *Nutrient content of fish*

153 Fish nutrient estimates were obtained from the Nutrient Analysis Tool in FishBase
154 (www.fishbase.org, Froese and Pauly, 2022), developed by Hicks et al (2019). We used nutrient
155 prediction updates from August 2022. Nutrient concentrations in a 100 g portion of muscle tissue
156 were estimated for five nutrients (calcium, Ca; iron, Fe; zinc, Zn; vitamin A, Vit A; omega-3 fatty
157 acids (eicosapentaenoic acid (EPA) + docosahexaenoic acid (DHA)), O3) that are highly concentrated
158 and bioavailable in fish and lacking in diets across the tropics (Beal et al, 2017; Ferguson et al, 2019;
159 Golden et al, 2021). Nutrient content data were extracted for each species observed in reef surveys
160 and for species mentioned by respondents during interviews. When fish were not identified to species
161 level, or when nutrient estimates were not available for a particular species, genus or family level
162 estimates were used by taking medians across species belonging to the same taxonomic grouping also
163 found in French Polynesia (according to FishBase).

164 Nutrient concentrations (100 g⁻¹) per individual fish were scaled up to reef survey biomass estimates
165 to represent the total quantity of each nutrient per hectare (i.e. potential nutrient yield for fisheries).
166 Only fish ≥ 15 cm in total length were included to represent the nutrients within fish deemed large

167 enough to be captured by fisheries (i.e. the minimum fishable size; Rassweiler et al, 2020). Values
168 were then summed per functional group in each transect and then the mean calculated across transects
169 at each survey site.

170 We then estimated the mean nutrient concentration of a 100 g fish portion for each respondent, by
171 averaging nutrient concentrations across all fish species they provided during interviews. Nutrient
172 estimates per person were then expressed as the percentage contribution to each daily recommended
173 nutrient intake (RNI) or equivalent for adult women (Ca = 1000 mg, Fe = 19.6 mg, Zn = 4.9 mg, Vit
174 A = 270 µg; WHO/FAO, 2004) (O3 = 250 mg; European Food Safety Authority, 2010) (Table S4).

175 *Calculating nutrient density and intakes*

176 We assessed the nutritional quality of different food groups by calculating the nutrient density based
177 on our five nutrients (Drewnowski, 2009). Nutrient density was defined as the sum of percentage
178 contributions to RNIs for all five nutrients in a 100 g portion of food, with the maximum possible
179 value for each nutrient capped at 100%, or a maximum of 500% when all five nutrients are fully
180 meeting dietary needs. The nutrient contents of 100 g food portions were obtained from Pacific Island
181 food composition tables (FAO, 2004) by taking a median across all food items within a food group for
182 each nutrient. Specific food items were removed from the composition tables if they were not eaten in
183 the form given, for example raw flour or raw plant-based foods that were toxic unless cooked prior to
184 consumption (see online supplementary material for details). The total fat content of 100 g food
185 portions was also obtained from food composition tables and expressed as a percentage of the
186 maximum recommended daily fat allowance (65 g; Drewnowski, 2009).

187 We represented each respondent's average diet by calculating the total nutrient density across all food
188 groups, weighted by frequency of consumption for each food group, i , up to the total number of food
189 groups eaten by a respondent, n (Equation 1).

$$190 \quad ND_{weighted} = \frac{\sum(NutrientDensity \times ConsumptionFrequency)_{i...n}}{\sum ConsumptionFrequency_{i...n}}$$

191 [1]

192 These weighted nutrient density scores represented the nutritional value of each person's diet, based
193 on the content of our five nutrients. As frequency of fish consumption was across all species eaten per
194 respondent, we estimated separate weighted nutrient densities for reef and pelagic fish by equally
195 splitting consumption frequency.

196 In addition to nutrient density of diets, we then estimated people's nutrient intake using information
197 on typical portion sizes from the food composition tables (FAO, 2004), as these data were not
198 collected during interviews. We rescaled the nutrient content in 100 g of each food item to estimated

199 portion sizes. Medians across food items were then used to represent the nutrients in a typical portion
200 for each food group. Nutrient values were multiplied by the frequency each food group was consumed
201 in a week and divided by seven to give a daily estimate of nutrient intake per respondent. It should be
202 noted that foods eaten more than once per day were not captured in our questionnaire, for example the
203 most frequent response for consumption for any food was “every day”, without indicating whether a
204 particular food was eaten multiple times a day or not. As such, our nutrient intake estimates are not
205 intended to be a complete daily profile of people’s nutrition, but rather a representation of which
206 foods people tended to eat on a regular basis, allowing comparisons to be made between people eating
207 more or less of various foods.

208 *Statistical analyses*

209 All analyses were run in R (version 4.2.2; R Core Team, 2022). We investigated the association between
210 the nutrient density of fish consumed and socioeconomic backgrounds of respondents by conducting a
211 redundancy analysis (RDA) for each island using the “*easyCODA*” package (Greenacre, 2018).
212 Response variables were the percentage contributions to RNI for each of five nutrients and the total
213 nutrient density estimate of each respondent’s diet. Explanatory variables were gender (male or female),
214 age, education level (at least high school level or lower), wealth, ability to speak at least one Polynesian
215 language (yes or no), fisher or farmer households (both, fisher only, farmer only or neither), preference
216 for reef or pelagic fish (based on the number of fish families eaten), how often takeaway food was eaten,
217 and how often traditional Tahitian dishes (“Maa Tahiti”) were eaten.

218 Wealth was determined using a principal component analysis (PCA) that included details of each
219 respondent’s home ownership (own house, renting or lodger), financial difficulties (yes or no) and
220 vehicle ownership. Each respondent was given a vehicle score, calculated by multiplying each item by
221 a score that reflected its value (bicycles = 0.1, pirogues (small boats) = 0.2, motorcycles = 0.5, cars and
222 motorboats = 1) and summing scores for all vehicles owned. Some households may have had shared
223 access to certain items, for example pirogues (pers. obs.), however this was not accounted for in our
224 analysis. Values from PCA axis 1 explained 39% of variation in the data and were used as a wealth
225 indicator in analyses, with higher values indicating higher wealth (Fig. S2). All numerical explanatory
226 variables in the redundancy analyses (age, wealth, fish preference, takeaway food and Maa Tahiti
227 frequencies) were scaled, with mean = 0 and standard deviation = 1, to allow the effects of variables to
228 be examined relative to one another.

229 Variance explained by each variable, the global significance of the model, and the significance of axes
230 and terms in the model were examined for each redundancy analysis. Variance inflation factors for
231 model terms were assessed using the “*vegan*” package (Oksanen et al, 2022) to ensure that none had a
232 value >2.

233 Generalised linear models (GLM) were used to investigate the effects of various socioeconomic
234 variables on nutrient intakes. Separate models were used to analyse nutrient intakes from entire diets,
235 reef fish only and pelagic fish only (Equation 2, for i questionnaire respondents), all with Gaussian
236 distributions.

$$\begin{aligned} 237 \quad \text{Nutrient.Intake}_i &\sim \alpha + \text{gender}_i + \beta_1 \times \text{age}_i + \text{education}_i + \text{language}_i + \text{fishing.farming}_i \\ 238 \quad &+ \beta_2 \times \text{wealth}_i + \beta_3 \times \text{takeaway.food}_i + \beta_4 \times \text{Maa.Tahiti}_i \\ 239 \quad &+ \beta_5 \times \text{fish.preference}_i + \text{island}_i \end{aligned}$$

240 [2]

241 Model assumptions of each GLM were verified using the protocol described by Zuur and Ieno (2016),
242 by plotting residuals against fitted values and each covariate in the model. Residuals were assessed to
243 confirm there were no temporal or spatial dependencies.

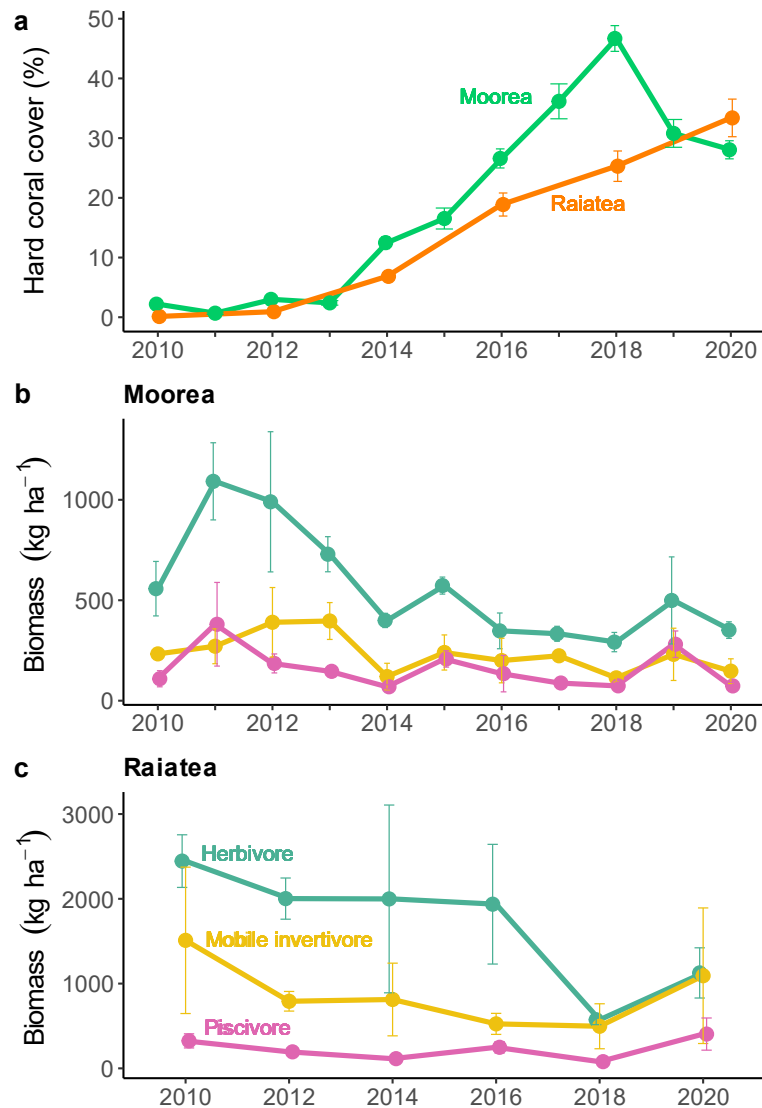
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245 **Results**

246 *Availability of reef fish biomass and nutrients to fisheries*

247 Coral cover increased from ~0-33% between 2010 and 2020 in Raiatea and, in Moorea, from 2-47%
248 between 2010 and 2018 before declining to 28% by 2020 (Fig. 2 a). Over this period of coral
249 recovery, reef fish biomass generally decreased (Fig. 2). In Moorea, biomass of all trophic groups
250 decreased from 2010 to 2020 (by 37% for both herbivores and invertivores, 33% for piscivores) (Fig 2
251 b). A 54% decrease in herbivore biomass occurred in Raiatea from 2010 to 2020 (2444.9 ± 310.4 to
252 1126.0 ± 296.2 kg ha⁻¹), while invertivore and piscivore biomass gradually declined from 2010 to 2018
253 before rising for all trophic groups from 2018 to 2020 (Fig. 2 c). Fish biomass was higher in Raiatea
254 than Moorea, particularly for herbivores and mobile invertivores.

255 Nutrient availability from reef fish was similar to biomass trends for most nutrients and was also
256 higher in Raiatea than Moorea (Fig. S3). Availability of all five nutrients from mobile invertivores
257 and piscivores were at similarly low levels in Moorea over the time series, however in Raiatea,
258 nutrient quantities from invertivores were higher than piscivores. Vitamin A availability from
259 invertivores in Raiatea was particularly high (and variable) in 2010 and 2020 compared to other
260 trophic groups (Fig. S3).



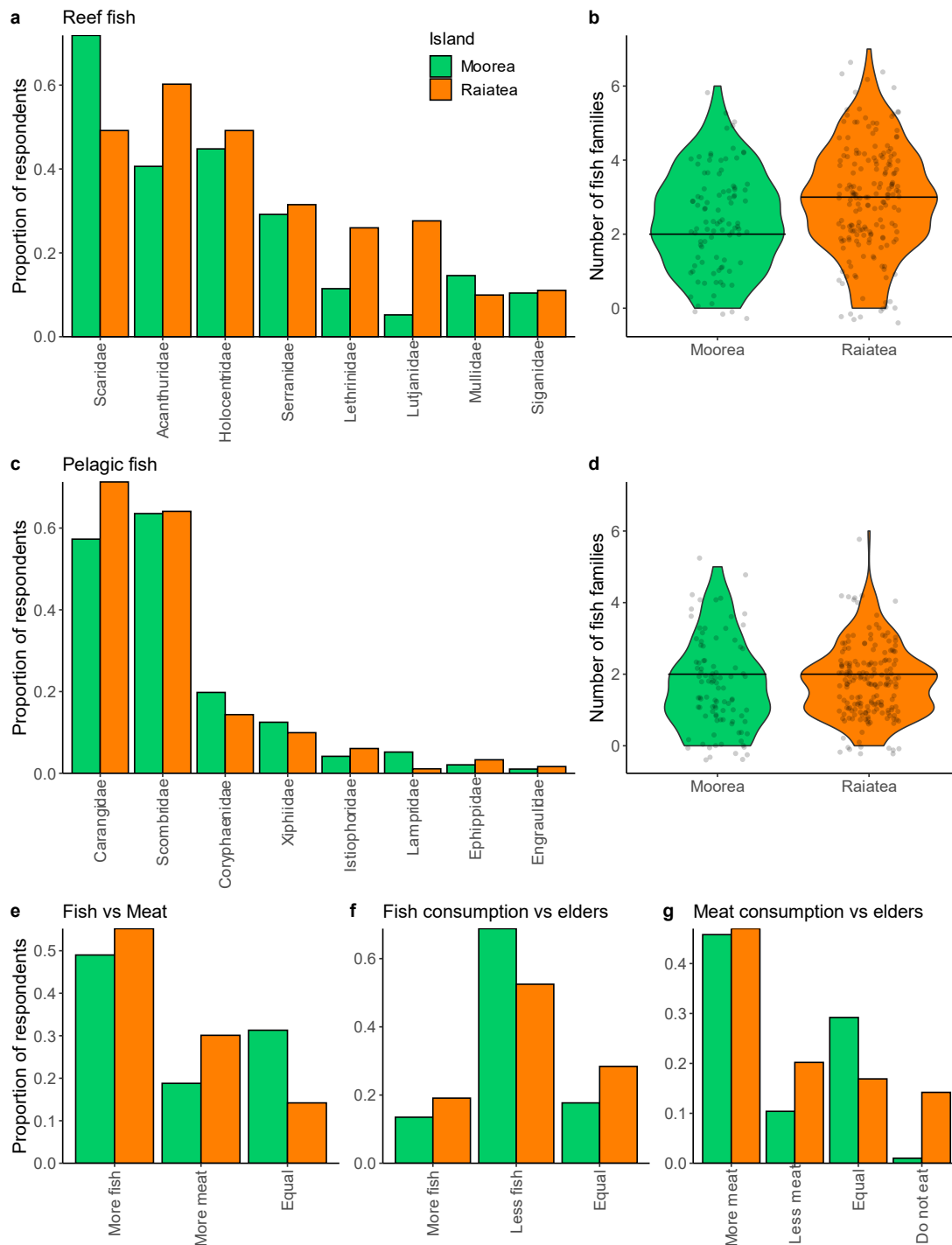
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262 **Figure 2:** Trends of hard coral cover (a) and fish biomass on reefs in Moorea (b) and Raiatea (c) from 2010 to
 263 2020. Biomass trends are for three trophic groups of reef fish (herbivore, mobile invertivore and piscivore).
 264 Only fish above the minimum fishable size (≥ 15 cm) with the potential to contribute to human nutrition were
 265 included. Errors bars are the standard error of the mean across transects. Note y-axis scales for biomass differ
 266 between islands (b and c).

267 *Fish consumption and nutrient intakes*

268 The reef fish families eaten by most respondents were herbivores on both islands; Scaridae in Moorea
 269 (72% of respondents) and Acanthuridae in Raiatea (60% of respondents) (Fig. 3 a). With the
 270 exceptions of Scaridae and Mullidae, all reef fish families were eaten by a higher proportion of
 271 respondents in Raiatea compared to Moorea. Three reef fish families were typically eaten in Raiatea,
 272 compared to two in Moorea (Fig. 3 b). The pelagic fish families eaten by most respondents were
 273 Scombridae in Moorea (64% of respondents) and Carangidae in Raiatea (71% of respondents) (Fig. 3
 274 c). The proportion of respondents eating each pelagic family was more similar between islands than

275 for reef fish, although a lower proportion of people ate carangids in Moorea (57%; Fig. 3 c). The
 276 median number of pelagic families consumed was two on both islands (Fig. 3 d).



277
 278 **Figure 3:** Proportion of respondents who ate the top eight reef (a) and pelagic (c) fish families, as stated during
 279 interviews in Moorea (green, $n = 96$) and Raiatea (orange, $n = 181$, two respondents who did not eat fish were
 280 not included). The total number of fish families consumed by each respondent is shown for reef (b) and pelagic
 281 (d) fish, with medians represented as solid horizontal lines. A comparison of fish to meat consumption per
 282 respondent (e), as well as perceptions of fish (f) and meat (g) consumption compared to their elders are also
 283 shown.

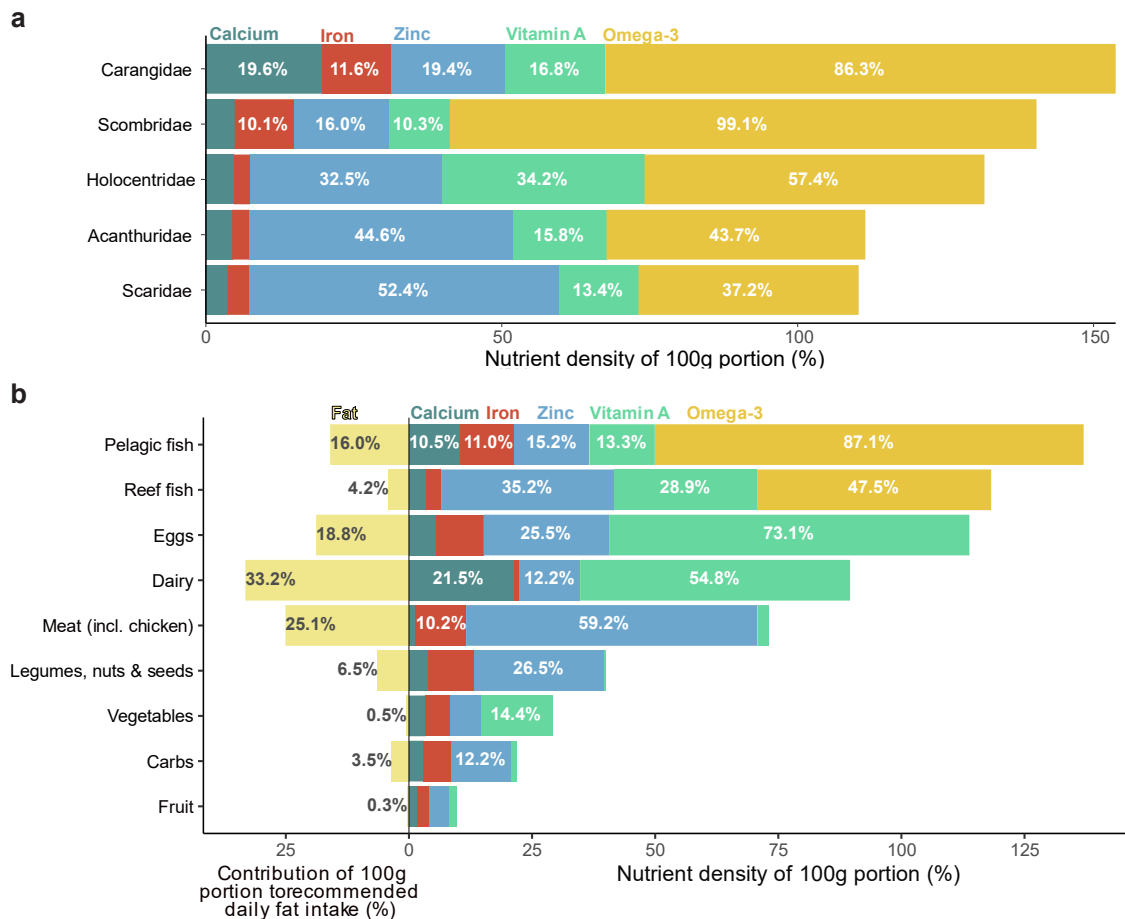
284 On both islands, around half of respondents said they ate more fish than meat (Moorea = 50%, Raiatea
285 = 55%) (Fig. 3 e). The second most popular response in Moorea was eating equal amounts of fish and
286 meat (31%), while in Raiatea it was eating more meat (30%). Although most people ate more fish
287 than meat, the majority of people on both islands said they ate less fish (Moorea = 69%, Raiatea =
288 53%) and more meat (Moorea = 46%, Raiatea = 47%) compared to previous generations (Fig. 3 f, g).
289 A higher proportion of people in Raiatea (28%) said their fish consumption was equal to their elders
290 (18% in Moorea), while a higher proportion in Moorea (29%) said their meat consumption was equal
291 to their elders (17% in Raiatea). 14% of respondents in Raiatea did not eat meat, as they were
292 pescatarian (compared to only 1% in Moorea) (Fig. 3 g).

293 Out of the top five fish families eaten (reef: Holocentridae, Scaridae and Acanthuridae; pelagic:
294 Carangidae and Scombridae), Carangidae was the most nutrient dense (153% in total across all five
295 nutrients; Fig. 4 a). Both pelagic fish families had the highest concentrations of omega-3 (Carangidae:
296 86% of RNI, Scombridae: 99%) and iron (Carangidae: 12%, Scombridae: 10%) compared to reef fish
297 families. Calcium concentrations were variable between pelagic families, with Carangidae having the
298 highest (20%), whereas Scombridae was more similar to reef families (<5%). Reef families had
299 higher zinc concentrations, particularly Scaridae (52%) and Acanthuridae (45%). Vitamin A
300 concentrations were variable among reef and pelagic families and highest in Holocentridae (34%)
301 (Fig. 4 a).

302 Pelagic fish was the most nutrient dense of all food groups for these five nutrients (137%) and reef
303 fish was second (118%) after eggs and dairy (Fig. 4 b). The five most nutrient dense food groups were
304 all animal-based, though there was considerable variation in the concentration of each nutrient
305 between food groups. Dairy foods had the highest calcium contribution (22% of RNI) but the lowest
306 iron contribution (1%), whereas iron-rich foods were pelagic fish (11%) and meat (including chicken
307 and tinned meat, 10%). Meat had the highest zinc contribution (59%) followed by reef fish (35%), and
308 foods with high vitamin A content were eggs (73%), dairy (55%) and reef fish (29%) (Fig. 4 b).

309 As with nutrient density, the food groups with the highest fat content were from animal sources, with
310 dairy being the highest (33% of the recommended daily total fat intake in 100 g) (Fig. 4 b). Pelagic
311 fish had more fat content (16%) than reef fish (4%) and compared to other animal-based food groups,
312 reef and pelagic fish were relatively nutrient-dense and low in fat (Fig. 4 b).

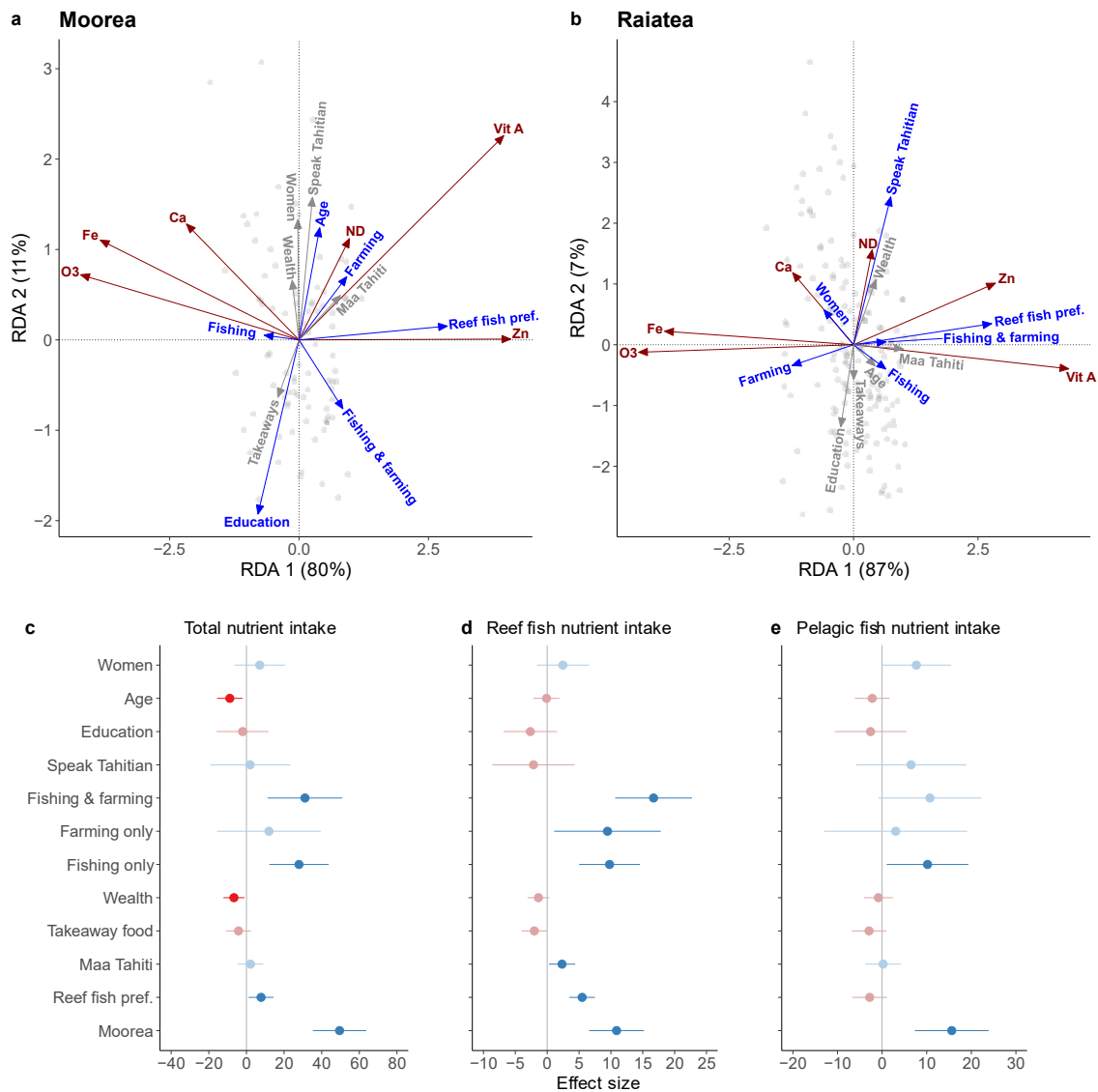
313 People on Moorea generally ate each food group more frequently compared to Raiatea (Fig. S4). Fish
314 was one of the food groups with the largest difference in frequency of consumption between Moorea
315 (median = 4.0) and Raiatea (median = 1.5). Most food groups were commonly eaten every day in
316 Moorea, however on Raiatea, few people stated they ate any food group every day (Fig. S4).



317

318 **Figure 4:** Nutrient densities of 100 g portions of the top five fish families eaten (a) and of food groups (b),
 319 calculated as the sum of contributions to daily recommended nutrient intakes (RNI) across five nutrients
 320 (calcium, iron, zinc, vitamin A, and omega-3 fatty acids). The contributions of 100 g portions to the maximum
 321 recommended daily fat intake (65 g, Drewnowski, 2009) are also shown for each food group (b, left). Values for
 322 fish families (a) are means of all fish species in each family mentioned by respondents during interviews.
 323 Nutrient estimates for reef and pelagic fish groups (b) are means of all fish species eaten by respondents.
 324 Omega-3 fatty acids (eicosapentaenoic acid (EPA) + docosahexaenoic acid (DHA)) were assumed to only be
 325 present in fish. Nutrient contents of food portions were obtained from Pacific Island food composition tables
 326 (FAO, 2004), except fish which were obtained from the Nutrient Analysis Tool in FishBase (Froese and Pauly,
 327 2022).

328 Redundancy analyses of the relationships between respondents' characteristics and nutrient density of
 329 their diets revealed what type of people tended to get more of certain nutrients from fish. Preference
 330 for reef fish had the strongest effect on the nutrients people received from fish on both islands
 331 (Moorea: $F = 31.9$, $p = 0.001$; Raiatea: $F = 28.7$, $p = 0.001$) (Fig. 5 a and b). People who preferred to
 332 eat reef fish had higher intakes of zinc and vitamin A and, conversely, those who ate more pelagic
 333 families had higher intakes of calcium, iron, and omega-3, consistent with the nutrient concentrations
 334 for those fish groups (Fig. 4 b).



335

336 **Figure 5:** Analyses of socioeconomic effects and dietary habits on the nutrients in people's diets. Redundancy

337 analyses for Moorea (a) and Raiatea (b) show associations between people's background (blue and grey arrows)

338 and the nutrient density (ND) of five nutrients received from fish, as well as the ND across all food groups in

339 their diet (red arrows). Explanatory variables with a significance level of $p < 0.1$ are shown in blue, others are

340 shown in grey. Axis percentages are the variance explained by the data (note different axis scales for RDA 2

341 between islands). Generalised linear model estimates for the effect of socioeconomic factors on nutrient intakes are

342 shown for total dietary intakes (c), and from reef (d) and pelagic (e) fish only, with confidence intervals ($1.96 \times$

343 standard error). Significant terms ($p \leq 0.05$) are shown in solid colour and non-significant terms are faded.

344 Nutrient estimates for fish species were obtained from the Nutrient Analysis Tool in FishBase (Froese and

345 Pauly, 2022).

346 On Moorea, older people and those from farming (but not fishing) households had diets that consisted

347 of more nutritious foods, although effects were small (age: $F = 2.4$, $p = 0.074$), while those with a

348 higher level of education had less nutritious diets ($F = 5.7$, $p = 0.005$) (Fig. 5 a). People from

349 households involved in fishing and farming got fewer nutrients associated with pelagic species

350 (calcium, iron, omega-3) and were more aligned with nutrients from reef fish (zinc and vitamin A)
351 (fishing and/or farming: $F = 3.5$, $p = 0.002$). On Raiatea, those who spoke Tahitian had more nutrient-
352 dense diets ($F = 5.1$, $p = 0.003$) and women to a lesser extent ($F = 2.2$, $p = 0.066$) (Fig. 5 b). People
353 from fishing households (including those who also farmed) got more nutrients associated with reef
354 fish, while people from farming only households got more nutrients from pelagic fish (fishing and/or
355 farming: $F = 4.3$, $p = 0.001$).

356 We fitted models to estimate the relative strength of the drivers identified in redundancy analysis on
357 people's nutrient intakes. People from fishing households and people in Moorea had higher total
358 nutrient intakes (fishing: effect size = 27.9 ± 8.0 standard error, $t = 3.5$, $p < 0.001$; Moorea: 49.5 ± 7.3 , t
359 = 6.8 , $p < 0.001$), as well as nutrient intakes from reef (fishing: 9.8 ± 2.4 , $t = 4.0$, $p < 0.001$; Moorea:
360 10.9 ± 2.2 , $t = 5.0$, $p < 0.001$) and pelagic fish (fishing: 10.2 ± 4.7 , $t = 2.2$, $p = 0.030$; Moorea: 15.6
361 ± 4.2 , $t = 3.7$, $p < 0.001$) (Fig. 5 c, d and e). However, for people from fishing households that were
362 also involved in farming, this was not significant for nutrient intakes from pelagic fish (total nutrient
363 intake: 31.1 ± 10.1 , $t = 3.1$, $p = 0.002$; reef fish: 16.7 ± 3.1 , $t = 5.4$, $p < 0.001$) (Fig. 5 e). People from
364 farming households with no involvement in fishing also had higher nutrient intakes from reef fish (9.5
365 ± 4.3 , $t = 2.2$, $p = 0.027$). People who preferred to eat reef fish had higher nutrient intakes from reef
366 fish, which could be expected, however they also had higher total nutrient intakes in their diets (7.8
367 ± 3.4 , $t = 2.3$, $p = 0.022$). Older people and wealthier people had slightly lower total nutrient intakes
368 (age: -8.8 ± 3.4 , $t = -2.6$, $p = 0.010$; wealth: -6.6 ± 2.9 , $t = -2.3$, $p = 0.021$) (Fig. 5 a). Eating Maa Tahiti
369 more often was associated with slightly higher nutrient intakes from reef fish (2.3 ± 1.0 , $t = 2.2$, $p =$
370 0.027). Women had higher nutrient intakes, while education and eating more takeaway food had
371 negative effects on nutrient intakes, however these effects were weak and non-significant (Fig. 5 c, d
372 and e).

373 Discussion

374 We investigated the resources available to coral reef fisheries and the importance of fish in islander
375 diets through a nutrition lens. Nutrient availability to reef fisheries was highest when live coral cover
376 was low, mainly due to the high biomass of herbivorous fishes, suggesting that nutrient provisioning
377 services can be maintained on these reefs despite periods of habitat degradation. We found that fish
378 was a key component of people's diets on both islands (despite differences in available reef fish
379 biomass), although there was evidence that the amount of fish people were eating had decreased over
380 time while meat consumption had increased. Socioeconomics were a major driver of fish
381 consumption, for example people from fishing and farming households had higher nutrient intakes
382 from fish. Collectively, our results suggest local food cultures and norms may be stronger drivers of
383 nutrition from fisheries, relative to ecological factors on coral reefs.

384 High herbivorous fish biomass when live coral cover was low underpinned large contributions of
385 nutrients from reefs. Herbivorous fishes important to fisheries, such as parrotfish, often increase in
386 biomass and productivity following reductions in live coral due to greater benthic algal and detrital
387 food sources (Rogers et al, 2018; Morais et al, 2020b; Rassweiler et al, 2020). In Moorea, the initial
388 increase in herbivore biomass following a prolonged crown-of-thorns sea star outbreak and a cyclone
389 facilitated the recovery of hard corals through the removal of competitive algae, leading to altered
390 compositions of reef fish assemblages as corals recovered (Lamy et al, 2016). Herbivore biomass (and
391 nutrients) also increased in Moorea in 2019 (Figs 2 and S3) after coral cover was reduced once more
392 following a coral bleaching event (Speare et al, 2022). We highlight the nutritional benefits that low
393 trophic-level fishes (e.g. herbivores) provide to small-scale fisheries on low-coral cover reefs, which
394 will likely continue to be important for food provisioning if reefs become degraded again in future.
395 Comparatively low reef fish biomass in Moorea could potentially be linked to higher fishing pressure
396 in response to high fish consumption and thus market demand for reef fish, particularly as larger fish
397 are preferentially targeted by spearfishers (Rassweiler et al, 2020). Fish biomass trends can help
398 inform if the fish consumption patterns on Moorea and Raiatea may be sustained and continue to
399 provide essential nutrients, given the level of reef resources available. Our results suggest careful
400 management may be necessary when fisheries become more dependent on low trophic-level fishes to
401 maintain a plentiful supply of nutrients from these species, particularly when coral cover is relatively
402 high.

403 As multiple reef and pelagic fishes were important components of diets, it is likely that many
404 islanders receive nutritional benefits from reef and pelagic fisheries. For example, people in fishing
405 households had high nutrient intakes from both fish groups (Fig. 5) and would have had high zinc and
406 vitamin A intakes from reef fish, and iron, calcium, and omega-3 intakes from pelagic fish. This could
407 explain why less wealthy people (for example from lower income households, such as fishers and
408 farmers) had slightly higher nutrient intakes, if their diets contained plenty of locally produced foods,
409 such as fish and vegetables they harvested themselves. For example, it is common for fishers to keep a
410 share of their catch to eat within their household (Kawarazuka and Béné, 2010). The popularity of
411 carangid and scombrid fishes on both islands (Fig. 3 c) suggests islanders received health benefits
412 associated with eating pelagic fish rich in omega-3, calcium and iron. Adequate omega-3 intakes can
413 help to prevent obesity-related health issues, which are particularly prevalent in French Polynesia
414 (Inamo et al, 2011), and so pelagic fish could be hugely beneficial to those who regularly eat them, for
415 example fishing households and Mooreans (Fig. 5). Fish is available at many roadside points around
416 Moorea, whereas in Raiatea, fish and other foods tend to be sold at a large market in the north of the
417 island (pers. obs.), which would have influenced people's access to fish and could explain the higher
418 frequency of fish consumption in Moorea.

419 Although fisheries in French Polynesia were important for supporting people's nutritional needs, we
420 also found evidence that fish consumption may have decreased from one generation to the next, along
421 with an increase in meat consumption. Meat is nutrient-dense and could provide people with higher
422 zinc intakes compared to reef fish, but with the added cost of having a higher fat content (Fig. 5 b).
423 Globalisation of French Polynesia's food system may have contributed to the loss of some traditional
424 food cultures (Hughes and Lawrence, 2005), with an increase in Western, industrialised food imports,
425 particularly processed meat high in saturated fat and foods with high amounts of added sugar (Brewer
426 et al, 2023). The increasing reliance on imported food in French Polynesia has corresponded to the
427 high proportion of overweight and obese adults (Hawley & McGarvey, 2015), therefore promoting
428 traditional Polynesian diets and reducing reliance on imported foods could help to address these diet-
429 related health issues (DiBello et al, 2009; Thow et al, 2011). As omega-3 can counteract the negative
430 health effects of saturated fat found in red meat and many other Western foods (Shahidi and
431 Ambigaipalan, 2018), locally caught fish (especially pelagics) may be a particularly important food
432 source alongside meat for those with a high reliance on imported foods.

433 The varying effects of people's socioeconomic attributes on their consumption habits indicates social
434 norms, habit, and identity can have a large influence on their nutrition (Baumhofer et al, 2020). We
435 found that aspects of Polynesian culture, such as regularly eating Maa Tahiti, and speaking Tahitian in
436 Raiatea, had positive effects on nutrition, suggesting traditional customs may be associated with
437 health benefits. Lower total nutrient intakes in the elderly could be of concern, however this has
438 previously been observed in French Polynesia as food intakes decrease with age (WHO, 2003).
439 Although there were no strong effects, our results indicate women may have had more nutritious diets
440 and had higher nutrient intakes compared to men, which is typical worldwide (Miller et al, 2022).
441 Therefore, efforts to promote nutritious diets in French Polynesian men could result in health benefits.
442 The causes of the large differences in nutrient intakes between people in Moorea and Raiatea are
443 presumably due to Mooreans generally consuming foods more frequently. It is unclear from our
444 results whether this is an indication of overconsumption in Moorea or of limited nutrient intakes in
445 Raiatea. This island effect on nutrition may stem from differences in food culture and may warrant
446 further investigation.

447 **Conclusion**

448 Our study highlights the importance of nutrient-dense reef and pelagic fish from local fisheries to
449 societies in French Polynesia. The nutrient provisioning services provided by coral reef ecosystems
450 can be maintained when the condition of coral habitat is reduced. Despite the globalisation and
451 industrialisation of the food system increasing reliance on imported food, it was apparent that
452 traditional diets rich in nutritious fish had persisted in French Polynesia. While more research is
453 needed into specific drivers of people's food acquisition and consumption habits, our study highlights

454 which demographics benefited most from fisheries-derived nutrition and reveals those where potential
455 improvements to nutrition could be made. Time series of social data alongside ecological data would
456 be immensely valuable for similar studies in the future to more closely connect reef ecosystems and
457 their influence on human nutrition, particularly as islander diets transition over time.

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471 **Declaration of interests**

472 On behalf of all authors, the corresponding author reports there are no competing interests to declare.

473 **Data availability**

474 Data and R code used in analyses and to produce figures can be found in the following repository on
475 GitHub: <https://github.com/Mark-H-22/FP-fish-diets/>

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