1 **Appendix S1: Supplementary methods**

2 Here, we provide more information on the quantification of the experimental excretion rates
3 used for model validation in the main text and the parameters needed to run the model. Table
4 1 shows the sample size for each part of data collection per species.

5 **Table 1**. Sample size for each component of data collection conducted within the framework
6 of this study.

Species	Excretion	Turnover	Metabolism	Growth	Body CNP	Diet CNP
Zebrasoma scopas	43	11	21	13	16	NA
Balistapus undulatus	34	8	11	8	26	15
Epinepehlus merra	51	8	15	17	43	10

7 **1. Fish excretion**

8 We measured excretion estimates in situ following the methodologies of Schaus et al. (1997),
9 as modified by Whiles, Huryn, Taylor, & Reeve (2011). We placed individual fish in an in-
10 cubation chamber (0.47 – 75 L Ziploc bag) containing a known volume (0.08 to 19.5 L) of
11 pre-filtered seawater (0.7 µm pore size Gelman GFF) for 30 minutes (Allgeier, Wenger, Rose-
12 mond, Schindler, & Layman, 2015; Whiles et al., 2011). We incubated a set of controls (typ-
13 ically n = 6) for the same time period at each sampling event. All incubated fishes and con-
14 trols were kept at a constant temperature during the excretion trial (25 – 27.5˚C). We extracted
15 seawater samples from each bag (filtered with 0.45 µm pore size Whatman nylon membrane
16 filters) and immediately placed them on ice. We analysed samples for ammonium and phos-
17 phorous.

18 Seawater samples extracted from each incubation container (filtered with 0.45 µm pore size
19 Whatman nylon membrane filters) and placed immediately on ice. Within 12 hours, samples
20 were analysed for ammonium using the methodologies of Taylor et al. (2007), or frozen for
21 transport to University of California Santa Barbara (UCSB) for soluble reactive phosphorus
22 analyses using the ascorbic acid method and colorimetric analyses (Eaton, Clesceri, Green-
23 berg, & Franson, 1995). Excretion rates were converted to g d^{-1} by multiplying hourly esti-
24 mates by 24.

25 **2. Turnover rates of N and P**

26 Following equations 6 and 7, we measured F_N and F_P as minimal excretion rates for N and P.
27 Fish (n = 27) were collected by divers in Moorea in 2018 and placed in a holding tank (1,000
28 L) with flow-through seawater for 72 hours with no food. Following the starvation period,
29 individuals were placed in incubation containers and nutrient samples were taken using the
30 same methodology as for excretion rates. Water samples were frozen immediately after filtra-
31 tion and analysed in Moorea at CRIOBE using standard methods following Aminot & Kérouel
32 (2007). Here we assume turnover to be equal to the measured excretion rates of starved fish.
33 As expected, $F_{0Pz} < F_{0Nz}$ because bone cells, which contain most P, generally degrade slowly
34 compared to other cell types ($F_P \approx 0.0003$ g P d^{-1}, 10% per year; Manolagas, 2000; Sterner &
35 Elser, 2002). There were no significant differences in minimal excretion rates among the three
36 species, so average across-species values were used.

37 **3. Metabolism**

38 We used flow-through respirometry to measure standard metabolic rate (SMR) and maximum
39 metabolic rate (MMR), which is defined as the maximum rate of oxygen consumption that a
40 fish can achieve at a given temperature (Norin & Clark, 2016) for a wide range of body sizes
41 (see 3.2). Here SMR is considered a synonym of F_{Cr}. The parameters α, f_0 and θ were ob-
42 tained by fitting a Bayesian regression model of SMR and MMR (g C d^{-1}) as a function of
43 body mass (g) using the R package `brms` (see 3.3, Bürkner, 2017). Estimates for the cost of
44 growth, ϕ, were obtained using the model of Barneche & Allen (2018) (equation 5, main text),
45 and values for trophic level and aspect ratio were extracted from FishBase using `fishflux`
46 functions `trophic_level()` and `aspect_ratio()`, respectively.

47 *3.1 Fish capture*

48 Fish were caught by divers using nets and clove oil in the lagoon at 1–8 m depth near Op-
49 unohu Bay in Moorea, French Polynesia during fall 2018. After capture, fish were transported
50 to the lab and were starved for 24 to 48 h at 27–28°C in large tanks.

51 *3.2 Respirometry*

52 Oxygen consumption was measured using intermittent-flow respirometry combined with py-
53 roscience optic fibre, following the methods described by Svendsen, Bushnell, & Steffensen
54 (2016). Intermittent-flow respirometry combines short measurement periods in a recirculating,
55 but closed, respirometer with clean water flush periods (Svendsen et al., 2016). One complete
56 measurement cycle consists of three timing periods: the flush period where the chamber is
57 open followed by two closed periods, wait and measure. The wait period is required before
58 measuring oxygen consumption to allow all the water in the chamber to mix and the oxygen
59 content to decline linearly (Svendsen et al., 2016). The respirometer volume should be cho-
60 sen depending on the fish's volume and behaviour while still being small enough to result in a
61 readable decline in oxygen concentration. A respirometer:organism volume ratio between 20
62 and 50 appears to be comfortable for most organisms but is small enough to result in a 10%
63 drop in oxygen concentration (Svendsen et al., 2016). Three different volumes of chambers
64 (0.36 L, 0.97270 L and 4.4 L) were used to have a chamber volume-to-fish volume ratio of
65 61:1–9:1 for *Epinephelus merra*, 358:1–10:1 for *Zebrasoma scopa*, and 241:1–10:1 for *Bal-*
66 *istapus undulatus*. When the ratio was too high or too low, the closing time (respirometry cy-
67 cle) of the chamber was adapted to obtain accurate MO_2 measurements. Respirometry cycles
68 were processed during a 20 h period (12 p.m. to 8 a.m. the following day) while leaving the
69 fish undisturbed in the chamber. For each measurement and each chamber size, a blank cham-
70 ber was used simultaneously, and a post blank measurement was processed for each chamber
71 at the end of the run to account for microbial respiration. Temperature was kept constant to
72 28.20 ± 0.35˚C, and a light cycle of 12 h was used (6 a.m. to 6 p.m.).

73 SMR was calculated using MO_2 measurement during the entire period. Noisy measurements
74 were removed by checking the R^2 of the drop in oxygen. Then, SMR was defined, using the
75 average of the lowest 10% of the MO_2 values, after removal of the outliers, following recom-
76 mendations by Chabot, Steffensen, & Farrell (2016).

77 At the start of a respirometry run, all fish where chased for 1 min and immediately placed in
78 the chamber to estimate maximum metabolic rates (MMR) by recording the first 30 s of the
79 first respirometry cycle. This seems to be the most efficient way to get the MMR for a wide

80 range of species (Norin & Clark, 2016).

81 *3.3 Metabolic parameters*

82 To obtain parameters $f0$ and α, we fit linear regression models for each species with the log-
83 transformed SMR (g/day) as the response variable and the log-transformed biomass (g) as the
84 explanatory variable. Models were fit in a Bayesian framework using the R package RStan
85 (Stan Development Team, 2018). The body mass-independent metabolic normalisation con-
86 stant (g C $g^{-\alpha}$ d^{-1}), $f0$ (see eqn 4 in the main text), was obtained by exponentiating the in-
87 tercept of this log-log regression. The slope of the regression equals α, the a dimensionless
88 mass-scaling exponent in eqn 4. We used weakly informative priors. We assumed the ac-
89 tivity scope, θ to equal $(SMR + MMR)/2SMR$. A second linear model was applied, similar
90 to the above mentioned model, but with the log-transformed MMR as the response variable.
91 The slope of each species of this regression did not differ from the slope of the SMR regres-
92 sions, as their respective 95% credible intervals overlapped substantially. Thus, our data sug-
93 gests that the intra-specific ratio of mass scaling exponents (SMR and MMR) is 1 on aver-
94 age. Therefore, for each species, we averaged values of θ across all individuals to calculate an
95 overall θ.

96 **4. Growth**

97 We used otoliths to fit growth curves for each species. Individuals were collected in Moorea,
98 French Polynesia with the use of spearguns, and otoliths were extracted, processed and read
99 for annual growth increments (see 4.1, 4.2). `fishflux` provides the function `oto_growth()`
100 to estimate VBGC parameters from otolith readings, using a Bayesian hierarchical regression
101 model (see 4.3). If original otolith readings are unavailable, VBGC parameters l_∞, k and t_0 can
102 be retrieved from FishBase for many species. The `fishflux` function `growth_params()` re-
103 turns estimates that are available on FishBase. We note that parameter estimates from otolith
104 analysis are considered better than other methods, and parameters can vary with location due
105 to temperature differences, thus introducing potential biases (Barneche & Allen, 2018; Morais
106 & Bellwood, 2018). We suggest using the standardised estimates and standard deviations fol-
107 lowing the fish growth model of Morais & Bellwood (2018) when location-specific otolith

108 data is unavailable.

109 We convert mass from total length using the length-weight equation $m = \varepsilon l^b$, where ε (g cm^{-b})
110 is constant, and b is a dimensionless exponent. Their respective standard deviations were
111 retrieved from FishBase and estimated using a Bayesian model (Froese, Thorson, & Reyes,
112 2014). `fishflux` provides the function `find_lw()` to obtain means and standard deviations
113 of these parameters. Wet-to-dry mass conversion constants were measured from the same
114 specimens that were used for the nutrient content analysis (see 5. Elemental stoichiometry).

115 *4.1 Sample collection*

116 A total of 288 specimens belonging to 20 species were collected in March 2016 and Novem-
117 ber 2018 in Moorea, French Polynesia using spear guns. Total (TL) and standard length (SL)
118 were measured to the nearest millimetre. For each individual, pairs of sagittae were extracted,
119 cleaned with distilled water, dried and transported to Perpignan, France.

120 *4.2 Otolith processing and back-calculation*

121 For each species, one or both of the otoliths was cut transversely, using a diamond disc saw
122 (Presi Mecatome T210) to obtain a section of 500 µm. Sections were then fixed on a glass
123 slide with thermoplastic glue, sanded with abrasive discs of decreasing grain size (2 400 and
124 1 200 grains per 2 cm) to get closer to the nucleus and polished using a 0.25 µm diameter dia-
125 mond suspension. All sections were photographed under Leica DM750 light microscope with
126 a Leica ICC50 HD microscope camera and LAS software (Leica Microsystems). For each
127 species, a reading transect was chosen and distances across annual growth increments were
128 measured using ImageJ (version 1.51j8). This procedure was repeated twice by two readers
129 in order to limit observer bias on age estimates. The measurements realised by the different
130 readers were averaged for each section. To estimate the fish lengths for previous ages, the
131 back-calculation procedure, proposed by Vigliola & Meekan (2009) was used.

132 *4.3 Growth parameters*

133 The von Bertalanffy growth curve (VBGC) was selected to describe the fish growth (eqn 2 in
134 the main text; Bertalanffy, 1957). The VBGC was fitted on length-at-age data with a hierar-

135 chical non-linear regression in a Bayesian framework using stan (Carpenter et al., 2017) and
136 (RCore Team, 2018). In the model, l_∞ varies among individuals, unlike $t0$. It has been shown
137 that VBGC parameters l_∞ and κ are correlated in a consistent way, where the slope of the log-
138 transformed regression theoretically has an average of -2.31 (Morais & Bellwood, 2018). This
139 correlation is explicitly included in the regression model where $\kappa = exp(sl * log(l_\infty) + gp)$,
140 where sl is the slope and gp is the intercept, which is the growth performance index (Morais
141 & Bellwood, 2018). Informative priors for sl and gp were specified, using published informa-
142 tion (Morais & Bellwood, 2018) and a weakly-informative prior was set for l_∞:

$$\begin{aligned} sl &\sim normal(-2.3, 0.22), \\ gp &\sim normal(3, 2), \\ l_\infty &\sim normal(15, 5). \end{aligned} \tag{1}$$

143 Estimates for l_∞ can vary substantially among populations or even individuals (Morais &
144 Bellwood, 2018). We standardised κ to the maximum measured total length in Moorea (un-
145 published data), to avoid individuals reaching the asymptotic length prematurely and growth
146 equalling zero in the application of the bioenergetic model for the case study.

147 **5. Elemental stoichiometry of fish and diet**

148 Sixteen individuals were collected in 2016 in Moorea, their gut contents were removed, and
149 the whole body was freeze-dried and ground to powder with a Precellys homogeniser. Q_k (%)
150 were then measured in the lab using standard methods. Ground samples were analysed for
151 %C and %N content using a CHN Carlo-Erba elemental analyzer (NA1500) for %P using dry
152 oxidation-acid hydrolysis extraction followed by a colorimetric analysis (Allen, Grimshaw,
153 Parkinson, & Quarmby, 1974). Elemental content was calculated based on dry mass. Means
154 and standard deviations for C, N and P were obtained through a hierarchical multivariate
155 model with fixed effects per family, genus and species. C, N and P content of diet items were
156 analysed using the same methods as described above.

157 Values for D_k (%) were approximated from published estimates. *Zebrasoma scopas* is known

158 to feed on red algae (Choat, Clements, & Robbins, 2002). We adopted Q_N (0.68 %; Lin &
159 Fong, 2008) and Q_C (20.9%; Pillans, Franklin, & Tibbetts, 2004) from *Acanthophora spi-*
160 *cifera*, and Q_P (0.33%; Suzumura et al., 2002) from another red algae species, *Galaxaura*
161 sp. D_k values for *B. undulatus* and *E. merra* were estimated based on a collection of poten-
162 tial diet items of similar families (Allgeier et al., 2015). *B. undulatus* feeds on a wide range
163 of plant and animal matter, but the majority of their prey items are in the phylum Arthropoda,
164 followed by Chordata and Mollusca (Casey et al., 2019). Therefore, we averaged D_k values
165 of molluscs, crustaceans and small fishes (n = 15). Finally, *E. merra* feeds primarily on crabs
166 (Randall & Brock, 1960). Thus, we averaged D_k values measured from small crabs (n = 5).
167 Stoichiometry of diet items were analysed using similar methods as described above.

168 **6. Assimilation efficiencies**

169 Element-specific assimilation efficiencies, a_k, are needed to estimate the available proportion
170 of matter after ingestion. These parameters were treated as fixed, with values of 0.8, 0.8 and
171 0.7 for C, N and P respectively (Deslauriers, Chipps, Breck, Rice, & Madenjian, 2017).

172 **7. R package `fishflux`**

173 `fishflux` makes the application of our theoretical framework user-friendly with the use of
174 the main function `cnp_model_mcmc()`. We devised our model to rely on parameters that are
175 widely available, while accounting for uncertainties. Several parameters for `fishflux` are
176 publicly accessible, and the package provides user-friendly functions to retrieve them. For
177 example, growth parameters for the VBGC are available on FishBase or can be extrapolated
178 with basic traits such as temperature and body size (Morais & Bellwood, 2018). Moreover,
179 length-weight parameters have been predicted for all species on FishBase (Froese et al., 2014),
180 and metabolic parameters F_0 and α can be extracted from flow-through respirometry exper-
181 iments. To calculate the energetic cost of growth, we use traits that are likewise available on
182 FishBase (i.e. aspect ratio and trophic level, Barneche & Allen, 2018). Equipped with these
183 parameters, the most critical input data is body size, which is frequently collected at the indi-
184 vidual level in underwater visual censuses or fisheries catch data (Samoilys & Carlos, 2000).
185 As such, our model offers a unique opportunity to infer biogeochemical dynamics from stan-

186 dardized and widely used survey techniques in fish ecology. Furthermore, `fishflux` provides
187 functions to extract specific results (`extract()`), plot output (`cnp_plot()`), extract the limit-
188 ing element (`limitation()`), and investigate the sensitivity of the predictions due to the un-
189 certainty of input parameters (`sensitivity()`). For details, see the help pages and vignettes
190 of `fishflux`.

191 **Bibliography**

192 Allen, S. E., Grimshaw, H. M., Parkinson, J. A., & Quarmby, C. (1974). *Chemical analysis of*
193 *ecological materials,* (p. 565). Blackwell Scientific Publications.

194 Allgeier, J. E., Wenger, S. J., Rosemond, A. D., Schindler, D. E., & Layman, C. A. (2015).
195 Metabolic theory and taxonomic identity predict nutrient recycling in a diverse food
196 web. *Proceedings of the National Academy of Sciences*, *112*(20), E2640–E2647. doi:
197 10.1073/pnas.1420819112

198 Aminot, A., & Kérouel, R. (2007). *Dosage automatique des nutriments dans les eaux marines*
199 *: méthodes en flux continu.* (p. 188). doi: 10.2307/302397

200 Barneche, D. R., & Allen, A. P. (2018). The energetics of fish growth and how it constrains
201 food-web trophic structure. *Ecology Letters*, *21*(6), 836–844. doi: 10.1111/ele.12947

202 Bertalanffy, L. von. (1957). Quantitative laws in metabolism and growth. *The Quarterly Re-*
203 *view of Biology*, *32*, 217–231. doi: 10.1086/401873

204 Bürkner, P.-C. (2017). brms : An R Package for Bayesian Multilevel Models using Stan.
205 *Journal of Statistical Software*, *80*(1), 1–28. doi: 10.18637/jss.v080.i01

206 Carpenter, B., Gelman, A., Hoffman, M. D., Lee, D., Goodrich, B., Betancourt, M., … Rid-
207 dell, A. (2017). Stan : A Probabilistic Programming Language. *Journal of Statistical Soft-*
208 *ware*, *76*(1), 1–31. doi: 10.18637/jss.v076.i01

209 Casey, J. M., Meyer, C. P., Morat, F., Brandl, S. J., Planes, S., & Parravicini, V. (2019).
210 Reconstructing hyperdiverse food webs: gut content metabarcoding as a tool to disentan-
211 gle trophic interactions on coral reefs. *Methods in Ecology and Evolution*, *00*, 1–14. doi:
212 10.1111/2041-210X.13206

213 Chabot, D., Steffensen, J. F., & Farrell, A. P. (2016). The determination of standard metabolic
214 rate in fishes. *Journal of Fish Biology*, *88*(1), 81–121. doi: 10.1111/jfb.12845

215 Choat, J. H., Clements, K. D., & Robbins, W. D. (2002). The trophic status of herbiv-
216 orous fishes on coral reefs 1: Dietary analyses. *Marine Biology*, *140*(3), 613–623. doi:
217 10.1007/s00227-001-0715-3

218 Deslauriers, D., Chipps, S. R., Breck, J. E., Rice, J. A., & Madenjian, C. P. (2017). Fish
219 Bioenergetics 4.0: An R-Based Modeling Application. *Fisheries*, *42*(11), 586–596. doi:
220 10.1080/03632415.2017.1377558

221 Eaton, A. D., Clesceri, L. S., Greenberg, A. E., & Franson, M. A. H. (1995). *Standard Meth-*
222 *ods for the Examination of Water and Wastewater*. American Public Health Association.

223 Froese, R., Thorson, J. T., & Reyes, R. B. (2014). A Bayesian approach for estimating
224 length-weight relationships in fishes. *Journal of Applied Ichthyology*, *30*(1), 78–85. doi:
225 10.1111/jai.12299

226 Lin, D. T., & Fong, P. (2008). Macroalgal bioindicators (growth, tissue N, δ15N) detect nutri-
227 ent enrichment from shrimp farm effluent entering Opunohu Bay, Moorea, French Polynesia.
228 *Marine Pollution Bulletin*, *56*(2), 245–249. doi: 10.1016/j.marpolbul.2007.09.031

229 Manolagas, S. C. (2000). Birth and Death of Bone Cells: Basic Regulatory Mechanisms and
230 Implications for the Pathogenesis and Treatment of Osteoporosis 1. *Endocrine Reviews*, *21*(2),
231 115–137. doi: 10.1210/edrv.21.2.0395

232 Morais, R. A., & Bellwood, D. R. (2018). Global drivers of reef fish growth. *Fish and Fish-*
233 *eries*, *19*(5), 874–889. doi: 10.1111/faf.12297

234 Norin, T., & Clark, T. D. (2016). Measurement and relevance of maximum metabolic rate in
235 fishes. *Journal of Fish Biology*, *88*(1), 122–151. doi: 10.1111/jfb.12796

236 Pillans, R. D., Franklin, C. E., & Tibbetts, I. R. (2004). Food choice in Siganus fuscescens:
237 Influence of macrophyte nutrient content and availability. *Journal of Fish Biology*, *64*(2),
238 297–309. doi: 10.1111/j.0022-1112.2004.00261.x

239 Randall, J. E., & Brock, V. E. (1960). Observations on the Ecology of Epinepheline and Lut-

240 janid Fishes of the Society Islands, with Emphasis on Food Habits. *Transactions of the American Fisheries Society*, *89*(1), 9–16. doi: 10.1577/1548-8659(1960)89[9:OOTEOE]2.0.CO;2

242 RCore Team. (2018). R: A Language and Environment for Statistical Computing. *R Foundation for Statistical Computing, Vienna.*

244 Samoilys, M. A., & Carlos, G. (2000). Determining methods of underwater visual census for estimating the abundance of coral reef fishes. *Environmental Biology of Fishes*, *57*(3), 289–304. doi: 10.1023/A:1007679109359

247 Schaus, M. H., Vanni, M. J., Wissing, T. E., Bremigan, M. T., Garvey, J. E., & Stein, R. A. (1997). Nitrogen and phosphorus excretion by detritivorous gizzard shad in a reservoir ecosystem. *Limnology and Oceanography*, *42*(6), 1386–1397. doi: 10.4319/lo.1997.42.6.1386

250 Stan Development Team. (2018). *RStan: the R interface to Stan. R package version 2.17.3.* doi: 10.3168/jds.S0022-0302(63)89186-9

252 Sterner, R., & Elser, J. (2002). *Ecological Stoichiometry: The Biology of Elements from Molecules to the Biosphere* (pp. 1–439). Retrieved from `https://press.princeton.edu/titles/7434.html`

255 Suzumura, M., Miyajima, T., Hata, H., Umezawa, Y., Kayanne, H., & Koike, I. (2002). Cycling of phosphorus maintains the production of microphytobenthic communities in carbonate sediments of a coral reef. *Limnology and Oceanography*, *47*(3), 771–781. doi: 10.4319/lo.2002.47.3.0771

259 Svendsen, M. B., Bushnell, P. G., & Steffensen, J. F. (2016). Design and setup of intermittent-flow respirometry system for aquatic organisms. *Journal of Fish Biology*, *88*(1), 26–50. doi: 10.1111/jfb.12797

262 Taylor, B. W., Keep, C. F., Hall, R. O., Koch, B. J., Tronstad, L. M., Flecker, A. S., … J. (2007). Improving the fluorometric ammonium method: matrix effects, background fluorescence, and standard additions. *Journal of the North American Benthological Society*, *26*(2), 167–177. doi: 10.1899/0887-3593(2007)26[167:ITFAMM]2.0.CO;2

266 Vigliola, L., & Meekan, M. G. (2009). The Back-Calculation of Fish Growth From Otoliths.

267 In *Tropical fish otoliths: Information for assessment, management and ecology* (pp. 174–
268 211). doi: 10.1007/978-1-4020-5775-5_6

269 Whiles, M. R., Huryn, A. D., Taylor, B. W., & Reeve, J. D. (2011). Influence of handling
270 stress and fasting on estimates of ammonium excretion by tadpoles and fish: recommenda-
271 tions for designing excretion experiments. *Limnology and Oceanography: Methods*, *7*(1),
272 1–7. doi: 10.4319/lom.2009.7.1