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1 **Nutrient limitation, bioenergetics, and stoichiometry: a new model to predict elemental**
2 **fluxes mediated by fishes**

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28 **Author contributions**

29 NMDS conceived the idea and NMDS, VP, DRB and SV designed methodology; NMDS,
30 JMC, SJB, AM, FM, VP, KSM, JEA and DEB collected the data; NMDS analysed the data
31 and led the writing of the manuscript. All authors contributed significantly to the drafts and
32 approved the final version for publication.

1 Nutrient limitation, bioenergetics, and stoichiometry predict elemental fluxes mediated 2 by fishes

3 Abstract

4 1. Energy flow and nutrient cycling dictate the functional role of organisms in ecosystems.

5 Fishes are key vectors of carbon (C), nitrogen (N), and phosphorus (P) in aquatic systems, and
6 the quantification of elemental fluxes is often achieved by coupling bioenergetics and stoi-
7 chiometry. While nutrient limitation has been accounted for in several stoichiometric models,
8 there is no current implementation that permits its incorporation into a bioenergetics approach
9 to predict consumption rates. This may lead to biased estimates of elemental fluxes.

10 2. Here, we introduce a theoretical framework that combines stoichiometry and bioenergetics
11 with explicit consideration of limitation. We examine varying elemental limitations across
12 different trophic groups and life stages through a case study of three trophically-distinct reef
13 fishes. Further, we empirically validate our model using an independent database of measured
14 excretion rates.

15 3. Our model adequately predicts elemental fluxes in the examined species and reveals
16 species- and size-specific limitations of C, N, and P. In line with theoretical predictions, we
17 demonstrate that the herbivore *Zebrasoma scopas* is limited by N and P, and all three fish
18 species are limited by P in early life stages. Further, we show that failing to account for
19 nutrient limitation can result in a greater than two-fold underestimation of ingestion rates,
20 which leads to drastic underestimations of excretion rates.

21 4. Our model improved predictions of ingestion, excretion, and egestion rates across all life
22 stages, especially for fishes with diets low in N and/or P. Due to its broad applicability, its
23 reliance on many parameters that are well defined and widely accessible, and its straightfor-
24 ward implementation via the accompanying R-package `fishflux`, our model provides a user-
25 friendly path toward a better understanding of ecosystem-wide nutrient cycling in the aquatic
26 biome.

27 **Introduction**

28 Internal biological processes of consumer species, such as growth, respiration, and excretion
29 are important drivers of ecosystem-scale biogeochemical cycles (Welti et al., 2017). To sur-
30 vive, individuals need to gather resources from the environment and, in doing so, transfer en-
31 ergy and nutrients within and across ecosystems (Brown, Gillooly, Allen, Savage, & West,
32 2004; Mackenzie, Ver, Sabine, Lane, & Lerman, 1993). Therefore, the quantification of en-
33 ergy and nutrient fluxes in ecosystems hinges on our ability to understand how energy and
34 materials are utilized and transformed at the individual level (Allgeier, Yeager, & Layman,
35 2013; Kitchell et al., 1974; Sterner & Elser, 2002).

36 In aquatic ecosystems, fishes account for most of the heterotrophic biomass (Odum & Odum,
37 1955; Vanni, 2002) and contribute substantially to the storage and flux of carbon (C), nitro-
38 gen (N), and phosphorus P (Allgeier, Layman, Mumby, & Rosemond, 2014; Barneche et al.,
39 2014; Burkepile et al., 2013; McIntyre et al., 2008; Vanni, 2002). Storage is primarily dic-
40 tated by food that is assimilated and allocated to growth, which ultimately underpins criti-
41 cal ecosystem services (e.g. finfish fisheries). Fluxes are derived from assimilated (respired
42 carbon and excreted nutrients) and non-assimilated food (egested organic waste) (Schreck &
43 Moyle, 1990), and they can have important effects on ecosystem processes, such as primary
44 production (Allgeier et al., 2013; Capps & Flecker, 2013; McIntyre et al., 2008). Disentan-
45 gling how fishes partition ingested elements into biomass and waste products is therefore key
46 to link individual-level physiology to ecosystem-level processes, which are of inherent human
47 interest (Anderson, Hessen, Elser, & Urabe, 2005; Barneche & Allen, 2018; Hessen, Ågren,
48 Anderson, Elser, & De Ruiter, 2004; Hou et al., 2008).

49 Ecological stoichiometry provides a theoretical framework to understand how consumers par-
50 tition C, N, and P (Sterner & Elser 2002). On the basis of the conservation of mass, the mate-
51 rial ingested by consumers equals the sum of biomass accumulation and waste products such
52 as respired carbon, excreted nutrients, and egested organic material. Furthermore, stoichio-
53 metric theory predicts that the ratio of recycled elements depends on the elemental composi-
54 tion of the consumer body, diet, and the gross growth efficiency of the limiting element (Frost

55 et al., 2006; Sterner, 1990). Thus, given known consumption rates, stoichiometric mass bal-
56 ance models allow for the prediction of fish excretion rates (Kraft, 1992; Schindler & Eby,
57 1997). Consumption rates can be approximated using empirical relationships with body mass
58 and temperature (e.g. El-Sabaawi, Warbanski, Rudman, Hovel, & Matthews, 2016), but these
59 estimates are highly species-specific, require extensive lab experiments, and may not reflect
60 fish consumption rates in the wild.

61 Alternatively, consumption rates can be estimated using bioenergetic models. In fact, there is
62 a rich history of bioenergetic modelling approaches to estimate energy allocation in fishes un-
63 der the assumption that they are limited by energy (C) (e.g. the “Wisconsin model”, Kitchell
64 et al. (1974); Hanson, Johnson, Schindler, & Kitchell (1997) and the “Dynamic Energy Bud-
65 get model”, Kooijman (2010)). Combined with elemental stoichiometry, bioenergetic models
66 therefore provide a conceptual basis to predict how fishes partition energy and elements into
67 growth, metabolism, and waste (Deslauriers, Chipps, Breck, Rice, & Madenjian, 2017; Kraft,
68 1992; Schindler & Eby, 1997; Schreck & Moyle, 1990). This approach has been widely used
69 to estimate consumption rates, given known growth rates in wild fish populations (especially
70 via the Fish Bioenergetics software Deslauriers et al., 2017). Nutrient cycling predictions are
71 then made by combining modeled ingestion rates based on energetic needs, assimilation ef-
72 ficiencies, and nutrient stoichiometry of both a fish’s body and diet (Anderson et al., 2005;
73 Kraft, 1992; Schindler & Eby, 1997).

74 Although useful and successfully implemented (Deslauriers et al., 2017), this approach is
75 limited in its application to fishes that are limited by C. This can be the case, especially for
76 trophic groups that feed on nutrient-rich prey (e.g. Schindler & Eby, 1997); yet, many fish
77 species in low trophic levels may be limited by N or P because their diets contain lower nu-
78 trient levels than their body tissues (McIntyre et al., 2008; Schindler & Eby, 1997). Thus, ap-
79 plying the traditional approach of combining stoichiometry and bioenergetics (Kraft, 1992)
80 to fish species that are limited by N or P normally results in biologically impossible predic-
81 tions of negative excretion rates. Indeed, there is mounting evidence that fishes can be limited
82 by nutrients, rather than energy (Benstead et al., 2014; El-Sabaawi et al., 2016; Hood2005;
83 Moody, Lujan, Roach, & Winemiller, 2019). While, negative predicted excretion rates can

84 provide evidence for nutrient limitation (e.g. Hood, Vanni, & Flecker, 2005), they do not aid
85 our understanding and prediction of realistic elemental fluxes in communities where nutrient-
86 limited species are prevalent. Thus, although many stoichiometric models take into account
87 nutrient limitation (e.g. Sterner, 1990; El-Sabaawi et al., 2016; Guariento, Luttbeg, Carneiro,
88 & Caliman, 2018; Moody et al., 2018, 2019), there is presently no solution for integrating nu-
89 trient limitation into bioenergetic models that quantify consumption rates. As fishes in low
90 trophic levels often account for a significant proportion of biomass (e.g. Graham et al., 2017)
91 and represent important vectors of nutrients, a new approach is needed to accurately predict
92 elemental fluxes in the absence of known consumption rates.

93 Here, we present a theoretical framework (and a companion R package for its implementa-
94 tion: `fishflux`) to predict elemental fluxes in fishes that combines bioenergetics and eco-
95 logical stoichiometry while directly accounting for N and P limitation, alongside C limita-
96 tion. The proposed model framework predicts ingestion rates based on the needs of a fish at
97 a certain size for all three elements and a known growth rate. We test our framework via a
98 case study of three trophically-distinct coral reef fish species: the herbivore *Zebrasoma scopas*
99 (family Acanthuridae), the omnivore *Balistapus undulatus* (family Balistidae), and the carni-
100 vore *Epinephelus merra* (family Serranidae). We also validate our model against independent
101 empirical excretion estimates for our three fish species. Furthermore, we test whether fishes
102 in different trophic levels and life stages are limited by different elements and hypothesize
103 that fishes at low trophic levels are limited by N or P rather than C. Finally, we posit that, by
104 building on existing approaches, our framework considerably improves the prediction of key
105 processes such as ingestion and excretion in the case of strong nutrient limitation, as compared
106 to models that only consider C-limitation.

107 **Materials and Methods**

108 **1. Theoretical framework**

109 Carbon, nitrogen, and phosphorus (CNP, expressed in grams) are the three chemical elements
110 considered in our model. The approach applies a mass-balance framework based on ecolog-
111 ical stoichiometry and the metabolic theory of ecology (Brown et al., 2004; Sterner & Elser,
112 2002). Further, the approach relies on the growth trajectory of natural fish populations. The
113 proposed model has four main steps (Fig. 1): (1) The minimal required ingestion or minimal
114 supply rate of CNP is defined as the sum of CNP needed for a given growth increment and
115 minimal inorganic flux (i.e. the minimal requirements of CNP needed for metabolism and the
116 maintenance of the body stoichiometry). In this step, we also consider assimilation efficiency,
117 which is defined as the capacity of an organism to assimilate C, N or P (input parameters of
118 the model). (2) Ingestion is estimated based on the limiting element that is defined by the im-
119 balance between the CNP composition of the minimal supply rate and that of the diet. (3) The
120 egestion rate is then quantified according to the ingestion rate and the assimilation efficien-
121 cies of each element. (4) The residual CNP are allocated toward the total inorganic flux of
122 CNP (i.e. the waste inorganic CNP that is produced from physiological transformation). For
123 the sake of comparison with existing literature, we note that the inorganic flux of C is gener-
124 ally called total metabolic rate, whereas the inorganic fluxes of N and P are called excretion
125 rates. Materials that are not assimilated are egested as organic waste. An overview of all main
126 variables predicted by the model and input parameters that need to be specified by the user is
127 given in Table 1, while other parameters mentioned in the text are fixed in the model. In the
128 following sections, we detail each component of the model.

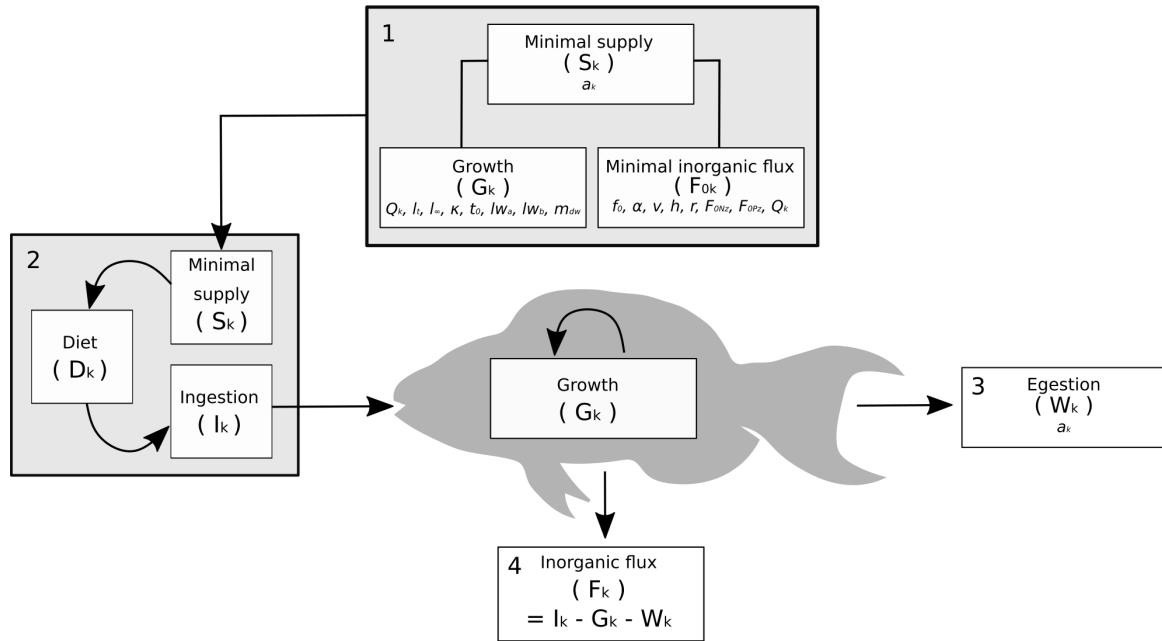


Figure 1. Conceptual diagram, explaining different model components. Required ingestion of C, N and P is calculated through the sum of elements needed for growth and minimal inorganic flux, taking into account the element-specific assimilation efficiencies, a_k (1). Based on the limiting element (due to the imbalance of food and the required CNP), the ingestion rate can be estimated (2). The ingested material is partitioned into egestion (3) and assimilation (body mass growth and flux (4)). The symbol of each component is indicated in between brackets. The input parameters needed to calculate the different variables are italicised. See Table 1 for a description of each parameter.

Table 1. Overview of model parameters and variables, including input parameters, to be specified by the user of the model, which are indicated with *. Main output variables, predicted by the model are indicated with ▲. VBGC = von Bertalanffy growth curve.

Symbol	Description	Unit
k	Index for element C, N or P	–
S_k ▲	Element-specific minimal supply rate	g d^{-1}
G_k ▲	Element-specific growth	g d^{-1}
F_{0k} ▲	Element-specific minimal inorganic flux	g d^{-1}
a_k *	Element-specific assimilation efficiency	–
l_t *	Total length of individual at time t	cm
t	Age	yr
l_∞ *	Asymptotic adult length (VBGC)	cm
κ *	Growth rate parameter (VBGC)	yr^{-1}
t_0 *	Age at settlement (VBGC)	yr
lw_a *	Parameter length-weight relationship	g cm^{-1}
lw_b *	Parameter length-weight relationship	–
Q_k *	Element-specific body content percentage of dry mass	%
m_w	Wet body mass	g
F_{0Cr}	Resting metabolic rate	g d^{-1}
F_{0Cz}	Mass-specific turnover rate of C	$\text{g C g}^{-1} \text{d}^{-1}$
F_{0Cs}	Rate of C spent in body mass growth	g d^{-1}
f_0 *	Metabolic normalisation constant independent of body mass	$\text{g C g}^{-\alpha} \text{d}^{-1}$
α *	Mass-scaling exponent	–
$m_{w\infty}$	Asymptotic wet mass of an adult individual	g
ϕ	Cost of growth	g C g^{-1}
θ *	Activity scope	–
v *	Environmental temperature	$^{\circ}\text{C}$
h *	trophic level	–
r *	Aspect ratio of caudal fin	–
F_{0Nz} *	Mass-specific turnover rate of N	$\text{g Ng}^{-1} \text{d}^{-1}$
F_{0Pz} *	Mass-specific turnover rate of P	$\text{g Pg}^{-1} \text{d}^{-1}$
m_{dw}	Ratio of dry mass and wet mass of fish	–
m_d	Dry body mass	g
D_k *	Element-specific diet content percentage of dry mass	%
I_k ▲	Element-specific ingestion rate	g d^{-1}
W_k ▲	Element-specific egestion rate	g d^{-1}
F_{rk} ▲	Element-specific residual inorganic flux	g d^{-1}
F_k ▲	Element-specific total inorganic flux	g d^{-1}

129 1.1. Minimal supply rate

130 The first step of the model is an estimate of the minimal supply rate of elements (C, N and P)
131 required per day for a given growth increment in an individual of a given size. The required
132 CNP is the sum of the elements needed for body mass growth and overhead metabolic and
133 maintenance costs (i.e. minimal inorganic flux). The minimal supply rate S_k (g d^{-1}) of the ele-
134 ment $k = \{C, N, P\}$ can therefore be estimated as

$$S_k = \frac{(G_k + F_{0k})}{a_k}, \quad (1)$$

135 where G_k , F_{0k} and a_k are element-specific growth rate (g d^{-1}), minimal inorganic flux (g d^{-1}),
136 and assimilation efficiency (%), respectively.

137 1.1.1. Growth

138 The aim of our model is to predict elemental fluxes of fishes in their natural environment.
139 Therefore, we use growth rates that can be calculated from otolith analysis. In our model, we
140 thus assume that there is enough food available to fulfill the observed growth pattern. We fur-
141 ther use the von Bertalanffy growth curve (VBGC) to describe the growth trajectory (Berta-
142 lanffy, 1957). Empirically, the VBGC is favorable because its parameters are statistically sim-
143 ple to obtain, easy to interpret, and are available for a large number of species (Morais & Bell-
144 wood, 2018). Body length, l_t (cm in total length, i.e. T.L.), at age t (yr) is

$$l_t = l_\infty \left(1 - e^{-\kappa(t-t_0)}\right), \quad (2)$$

145 where t_0 is age at settlement, l_∞ is the asymptotic adult length (i.e. length when growth rate
146 is 0), and κ is a growth rate parameter (yr^{-1}) (Bertalanffy, 1957). With this equation, we can
147 quantify the age of a fish of a certain size. Then, by adding one day to that age, we can also
148 approximate the amount a fish will grow in one day. Using length-weight relationships and
149 wet-to-dry mass conversion constants from the literature and FishBase (Froese & Pauly,
150 2018), we can finally calculate total growth rate (i.e. G) expressed in dry mass (g d^{-1}). Using

151 element-specific body content percentages, Q_k , we calculate element-specific growth as:

$$G_k = \frac{Q_k}{100} G. \quad (3)$$

152 1.1.2 Minimal inorganic flux

153 Traditionally, the field metabolic rate, F_{0C} , has been studied more intensively than minimal
154 excretion rates for N and P, F_{0N} , and F_{0P} . As a consequence, we currently have a better under-
155 standing of how assimilated carbon is partitioned into body mass growth (G_C) and metabolic
156 overhead costs (F_{0C}). For instance, we know that F_{0C} predictably scales with individual wet
157 body mass, m_w (g) (Hou et al., 2008):

$$\begin{aligned} F_{0C} &= \theta F_{0Cr} = \\ &\theta (F_{0Cz} m_w + F_{0Cs}) = \\ &\theta (f_0 m_{w\infty}^{\alpha-1} m_w + \phi G), \end{aligned} \quad (4)$$

158 where F_{0Cr} is the resting metabolic rate (g C d⁻¹), F_{0Cz} is the mass-specific turnover rate (g C
159 g⁻¹ d⁻¹), F_{0Cs} is the rate of carbon spent in body mass growth, and f_0 is a metabolic normal-
160 ization constant that is independent of body mass (g C g^{- α} d⁻¹) and varies among fish taxa,
161 environmental temperature, and trophic level (Barneche & Allen, 2018). α is a dimensionless
162 mass-scaling exponent (generally between 0.5 and 1), $m_{w\infty}$ is the asymptotic mass of an in-
163 dividual, and ϕ is the energy expended to produce one unit of body mass (g C g⁻¹; hereafter
164 the “cost of growth”). In equation 4, F_{0C} is defined as the sum of the resting metabolic rate,
165 F_{0Cr} , and the active rate that sustains locomotion, feeding, and other activities. We assume
166 that $F_{0C} = \theta F_{0Cr}$ in the expression above, where θ is a dimensionless parameter referred to as
167 ‘activity scope’, which is constrained to be greater than 1 and less than the ratio between max-
168 imum metabolic rate and resting metabolic rate (Barneche & Allen, 2018; Hou et al., 2008).
169 The cost of growth, ϕ , varies substantially among fishes, and it may increase with environ-

170 mental temperature, v , trophic level, h , and aspect ratio of caudal fin, r (a proxy for activity
 171 level) (Froese & Pauly, 2018). Following Barneche & Allen (2018), the cost of growth can be
 172 calculated as

$$\ln\phi = \beta_0 + \beta_v v + \beta_h \ln h + \beta_r \ln(r + 1), \quad (5)$$

173 where β_0 is a constant, β_v , β_h , and β_r are respectively the model slopes for v , h , and r . We
 174 note that h and r are two ecological variables that can be retrieved from FishBase (Froese &
 175 Pauly, 2018). For the purposes of our bioenergetic model, we use average, across-species esti-
 176 mates for β_0 , β_v , β_h , and β_r published in Barneche & Allen (2018).

177 Aside from inorganic fluxes of C, N and P will also be released at a minimal rate, even when
 178 they are limiting (Anderson et al., 2005; Sterner & Elser, 2002). The minimal inorganic flux
 179 of N and P can be experimentally measured as minimal excretion rates during starvation
 180 (Mayor et al., 2011). We can thus explicitly incorporate N and P turnover rates to estimate
 181 minimal inorganic flux of N and P (Anderson et al., 2005).

$$F_{0N} = F_{0Nz} \frac{Q_N}{100} m_d, \text{ and} \quad (6)$$

182

$$F_{0P} = F_{0Pz} \frac{Q_P}{100} m_d, \quad (7)$$

183 where F_{0Nz} and F_{0Pz} are nutrient-specific dry mass-specific turnover rates for N ($\text{g N g}^{-1} \text{d}^{-1}$)
 184 and P ($\text{g P g}^{-1} \text{d}^{-1}$), respectively, and m_d is the dry mass of the fish (g). Equations 6 and 7 as-
 185 sume that F_{0Nz} and F_{0Pz} remain constant during ontogeny.

186 1.2. Ingestion

187 In our model, the quantification of ingestion rate is a two-step process. First, we define the
 188 minimal required ingestion of CNP by summing element-specific minimal supply rates S_k .
 189 Second, we approximate the actual ingestion rates by using ecological stoichiometric theory
 190 (Sterner & Elser, 2002). With known elemental stoichiometry of the diet (D_C , D_N , D_P) we can

191 determine the limiting element as follows:

$$\text{limiting element} = \left\{ \begin{array}{l} C, \quad \text{if } \frac{S_C}{S_N} > \frac{D_C}{D_N} \text{ and } \frac{S_C}{S_P} > \frac{D_C}{D_P} \\ N, \quad \text{if } \frac{S_N}{S_P} > \frac{D_N}{D_P} \text{ and } \frac{S_C}{S_N} < \frac{D_C}{D_N} \\ P, \quad \text{otherwise} \end{array} \right\} \quad (8)$$

192 The actual ingestion rate is then approximated according to the limiting element, following
193 Liebig's minimum law. To do so, we assume fishes have enough food available to meet their
194 minimal needs (S_k). For example, if P is limiting, element-specific ingestion rates, I_k , (g d^{-1})
195 are

$$I_P = S_P, \quad (9)$$

196

$$I_N = I_P \frac{D_N}{D_P}, \quad (10)$$

197

$$I_C = I_P \frac{D_C}{D_P}, \quad (11)$$

198 where D_k represents element-specific body content percentage of dietary items. Once inges-
199 tion rate is estimated, the partitioning of the ingested matter into various pathways (i.e. eges-
200 tion, excretion and respiration) can be defined.

201 1.3. Egestion or organic waste production

202 The rate of organic waste production or egestion rate, W_k (g d^{-1}) can be computed using the in-
203 gestion rate of each element and element-specific assimilation efficiencies (Schreck & Moyle,
204 1990):

$$W_k = (1 - a_k)I_k. \quad (12)$$

205 1.4. Total inorganic flux

206 The rate of total inorganic waste production or flux (i.e. total respiration and excretion) equals
207 the ingestion rate minus body mass growth rate and egestion rate for each element (Schreck
208 & Moyle, 1990; Sterner & Elser, 2002). If an element is limiting, the individual is likely to
209 consume other elements in excess in order to meet the target for that limiting element. In
210 such cases, it is often assumed that the exceeding “residual” element will be subject to post-
211 absorptive release via inorganic waste production (i.e. residual flux F_{rk}) to maintain body
212 homeostasis (Anderson et al., 2005). When N or P are limiting, for example, a certain residual
213 amount of C, F_{rC} remains unutilised. However, if C is limiting instead of N or P, excretion
214 rates F_N and F_P will increase by an overhead residual flux F_{rk} . In the example of C limitation,
215 the residual flux F_{rC} would equal zero. We can thus quantify the total inorganic flux as fol-
216 lows:

$$F_k = F_{0k} + F_{rk}, \quad (13)$$

217 where

$$F_{rk} = I_k - G_k - F_{0k} - W_k. \quad (14)$$

218 2. Application

219 We validate our modelling approach using data from three reef fish species: the herbivore
220 *Zebrasoma scopas* (family Acanthuridae), the omnivore *Balistapus undulatus* (family Balis-
221 tidae), and the carnivore *Epinephelus merra* (family Serranidae). All parameters were quan-
222 tified using empirical data augmented with information from the literature when needed (see
223 supplementary methods, Appendix S1). An overview of all parameter estimates is provided in
224 Appendix S2, Table 1.

225 We ran the model using R (R Core Team, 2019) and Stan (Stan Development Team, 2018).
226 For an easy application of the presented framework, we developed the R package `fishflux`,
227 which provides a set of user-friendly functions to simulate the model, extract the output vari-

228 ables, and visualize the results (see Appendix S1). Parameter means and standard deviations
 229 are provided, and a Monte Carlo method is applied to randomly draw each parameter assum-
 230 ing normal distributions in each iteration. To account for co-variances among parameters, we
 231 used the Stan function `multi_normal_rng()`, which samples each parameter under consider-
 232 ation of the co-variance matrix. We included co-variances for body stoichiometry (Q_k), diet
 233 stoichiometry (D_k), length-weight parameters (ϵ and b), and metabolic parameters (α and
 234 f_0). These parameters were sampled from their log-transformed multinormal distribution then
 235 back-transformed to natural scale. All other parameters were sampled from truncated normal
 236 distributions, where the lower and upper bounds are the possible ranges of each respective
 237 parameter. For our case study, we used 5,000 iterations. If the standard deviation of a given
 238 parameter is unknown (e.g. r , reported on FishBase), the function automatically fills in the
 239 standard deviation with a very low value of 10^{-9} in order to keep the respective parameter ap-
 240 proximately constant at each iteration of the simulation.

241 To compare the predictions of ingestion and excretion rates of our model framework with the
 242 case where only C-limitation is considered, we simulated ingestion and excretion rates, based
 243 only on the minimal supply rate of C, thus where I_c equals S_c . Excretion rates or total inor-
 244 ganic flux rates of N and P are then defined as follows:

$$F_N = S_C \frac{D_N}{D_C} - G_N - W_N, \quad (15)$$

245

$$F_P = S_C \frac{D_P}{D_C} - G_P - W_P. \quad (16)$$

246 We compared the predicted excretion rates for N and P with our own independent database
 247 of experimental excretion rates. We collected individual fish using barrier nets, dip nets, cast
 248 nets, traps, clove oil, and hook and line across different reef habitats around Moorea, French
 249 Polynesia during austral winter of 2016 and 2017 ($n = 128$). We aimed to collect individuals
 250 across the size spectrum present in each species. We immediately transported individuals back
 251 to shore in an aerated cooler for excretion experiments (see Appendix S1). Excretion rates
 252 were measured within a maximum of 3 hours after capture. The capture and handling of fishes

253 for this project were approved in a protocol from the University of California Santa Barbara's
254 Institutional Animal Care and Use Committee (IACUC #915 2016-2019).

255 Finally, to illustrate the effect of diet stoichiometry, we simulated the model with varying
256 % of N and P. For this simulation, we used the parameters of *Z. scopas* and ran the simula-
257 tion for an individual of 10cm. We kept D_C constant at 6%. The values of D_N and D_P var-
258 ied around the elemental ratio of S_k . Color palettes were used from the R package fishualize
259 (Schiettekatte, Brandl, & Casey, 2019).

260 **Results**

261 The application of the developed modeling framework reveals distinct elemental limitations
262 across the three species at different lengths (Fig. 2). *Z. scopas* is limited by either N or P over
263 its full size range, with P being the limiting element early in its ontogeny and N becoming the
264 limiting element after reaching approximately 7 cm TL. While *B. undulatus* and *E. merra* are
265 also limited by P at an early life stage, they are predominantly limited by C upon maturation.

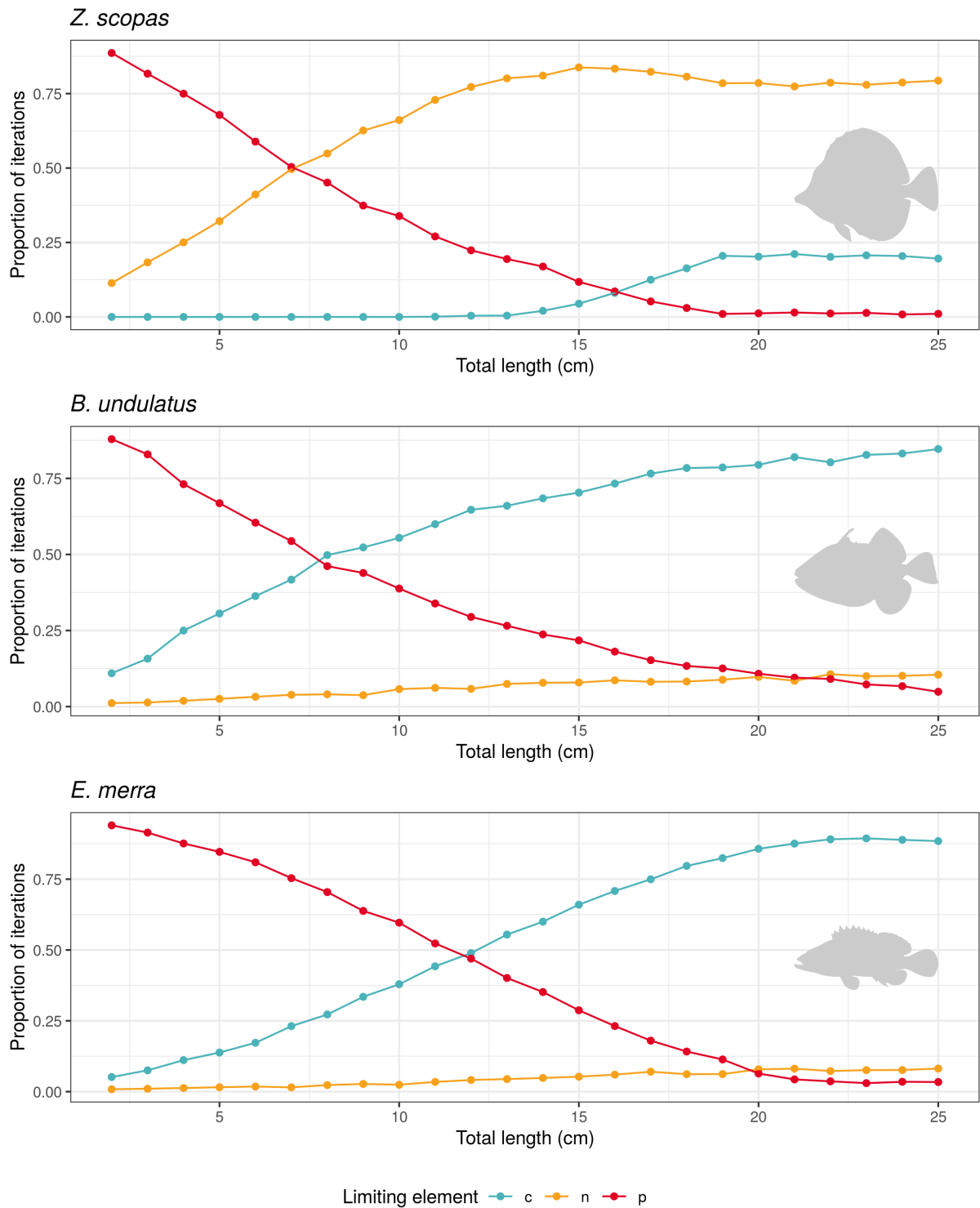


Figure 2. Proportion of the simulation iterations that determine C, N and P as the limiting element for *Zebrasoma scopas*, *Balistapus undulatus*, and *Epinephelus merra*.

266 Our approach demonstrates that defining the limiting element can be critical to predict a
267 species' ingestion rate, which affects all downstream calculations in the model (e.g. excretion
268 rates of N and P) compared to models only considering C limitation (Fig. 3). Specifically,
269 assuming C limitation in *Z. scopas* results in a severe underestimation of ingestion and
270 excretion rates (Fig. 3, A, B and C). In the omnivore *B. undulatus* and the carnivore *E.*
271 *merra*, the limiting element has less bearing on ingestion rates. Still, without incorporation
272 of P limitation, model predictions may result in negative excretion rates of P for growing
273 individuals of *B. undulatus* and *E. merra*. In the case of *E. merra*, C-only models predict
274 negative P excretion rates for more than half of the simulations under a total length of 10 cm
275 (Fig.3, I). Thus, our framework reveals that nutrient limitations and their consequences for
276 ingestion rate estimations are highly specific to the three study species and their ontogenetic
277 stage.

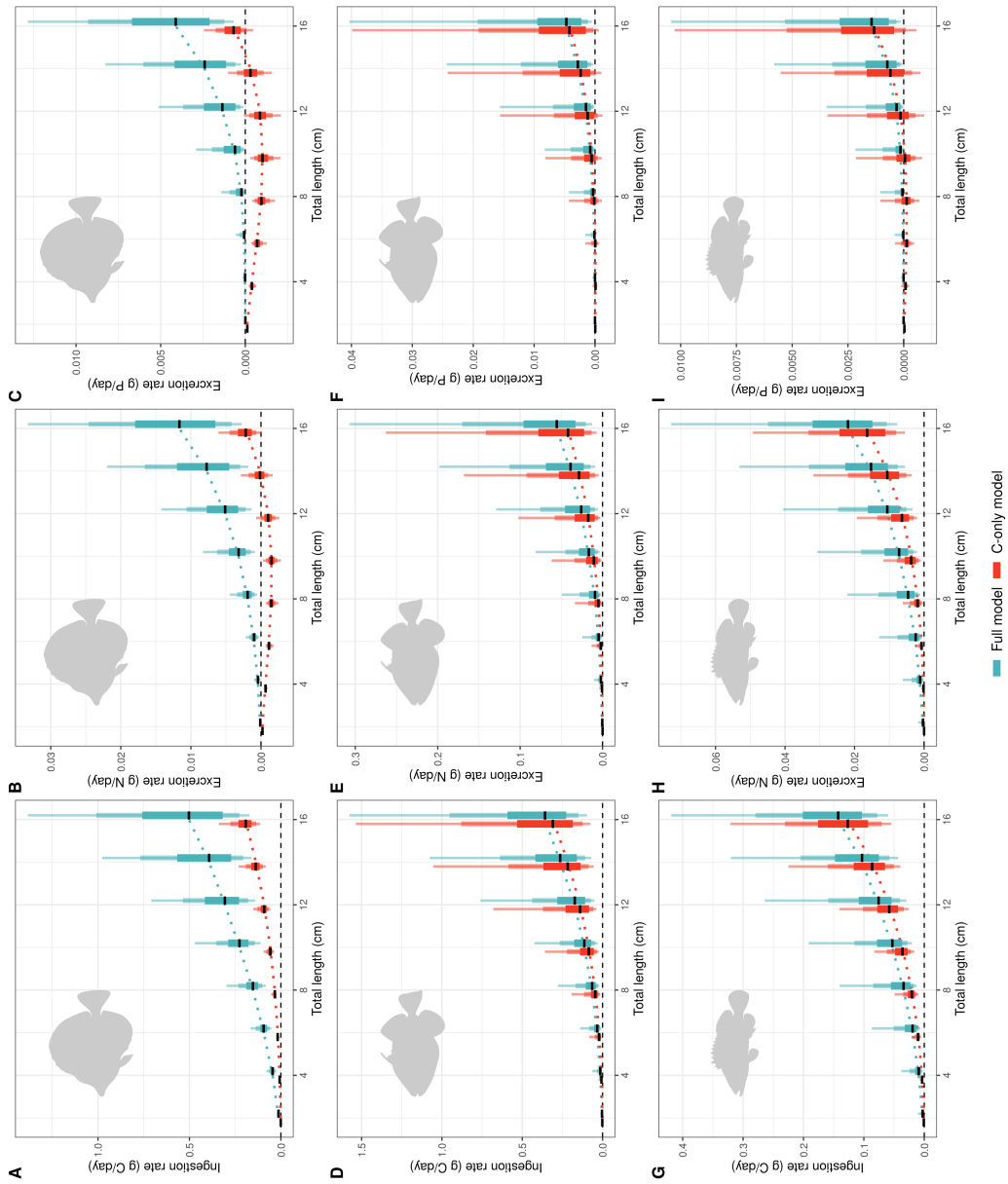


Figure 3. Predicted daily ingestion of carbon and excretion rates for the full model, considering nutrient limitation and for a model, only taking into account C-limitation. Horizontal lines show the median values and 95%, 80%, and 50% confidence intervals are illustrated respectively in vertical lines. A. C ingestion rates of *Z. scopas*, B. N excretion rates of *Z. scopas*, A. P excretion rates of *Z. scopas*, A. C ingestion rates of *B. undulatus*, A. N excretion rates of *B. undulatus*, A. P excretion rates of *B. undulatus*, A. C ingestion rates of *E. merra*, A. N excretion rates of *E. merra*, A. P excretion rates of *E. merra*.

278 Our model predicts ingestion rates for *Z. scopas*, *B. undulatus* and *E. merra* at 15 cm TL to be
279 28.2 (11.7 – 68.4), 12.9 (3.7 – 56.7), 14.1 (5.5 – 40.1), respectively (in mg dry weight per g
280 wet weight of fish per day, median and 95% confidence interval (C.I.)) (see Appendix S2, Ta-
281 ble 2). Comparing our predicted excretion rates with empirical data on excretion rates shows
282 that our model adequately predicts excretion rates with almost all experimental data falling
283 inside the predicted 95% confidence interval (Fig. 4). For N excretion, 100%, 97% and 94%
284 of the experimental excretion rates are captured by our predictions for *Z. scopas*, *B. undulatus*
285 and *E. merra*, respectively. For P excretion, we adequately predict 93%, 94%, and 90% of the
286 experimental excretion rates for the three species, respectively. Predictions for *E. merra* are
287 slightly overestimated compared to experimental excretion rates. Groupers feed infrequently,
288 and their stomachs were often found empty, which may have impacted the measured excretion
289 rates.

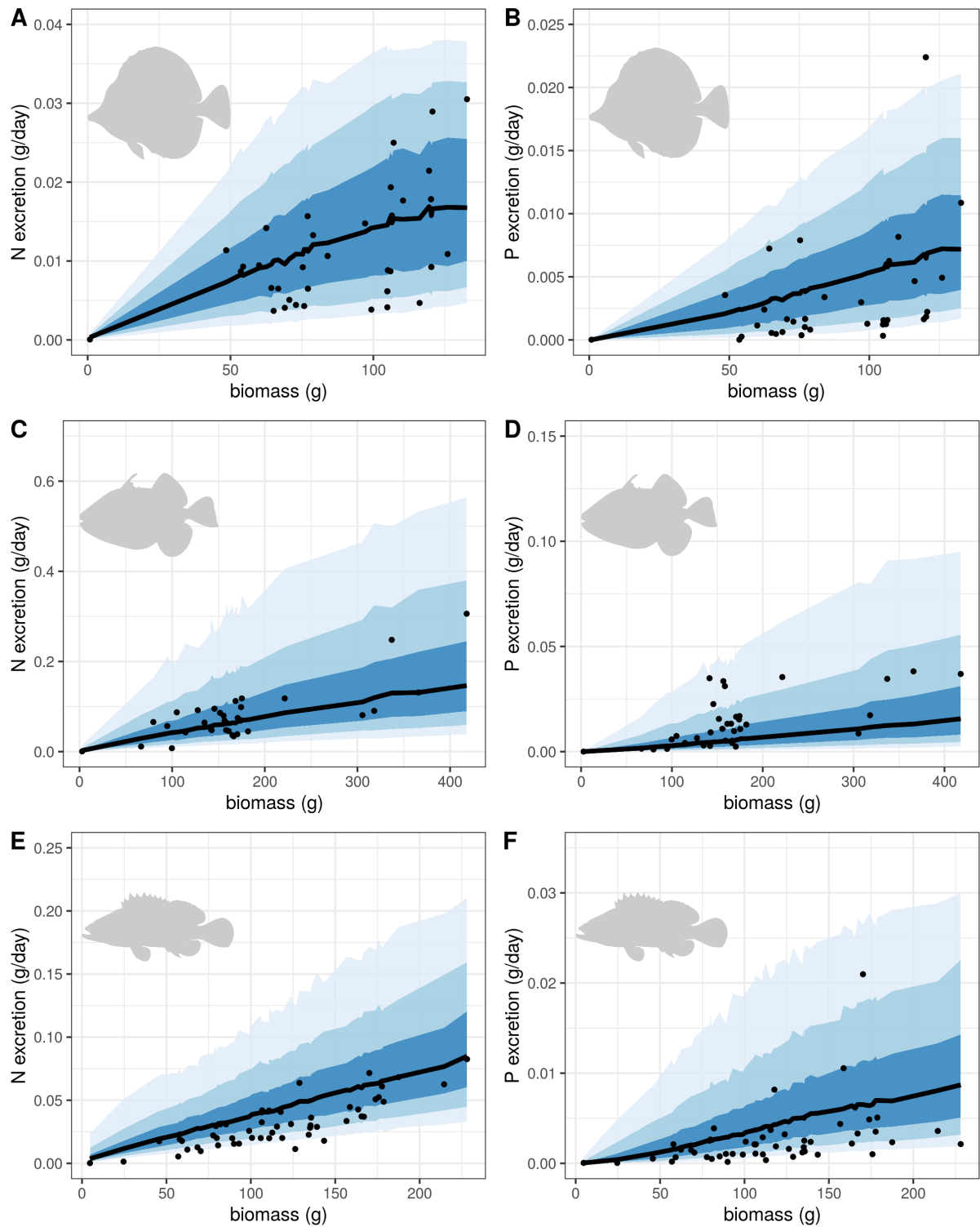


Figure 4. Predicted excretion rates for each species of both N and P. The 50%, 80% and 95% confidence intervals are presented around the median. Points show the experimental excretion rates, obtained from an independent database. A. N excretion rates of *Z. scopas*, B. P excretion rates of *Z. scopas*, C. N excretion rates of *B. undulatus*, D. P excretion rates of *B. undulatus*, E. N excretion rates of *E. merra*, F. P excretion rates of *E. merra*.

290 Predictions are substantially affected by variability in the stoichiometry of dietary sources. To
291 illustrate how the diet stoichiometry affects limitations by different elements and ingestion
292 and excretion rates, we simulated different scenarios by varying the diet percentages of N and
293 P around the stoichiometry of the minimal supply rate of an individual of *Z. scopas* of 10 cm
294 (Fig. 5). When diet stoichiometry differs from this ideal stoichiometry of the minimal supply
295 rate, either C, N or P is the limiting element, which in turn affects all downstream biologi-
296 cal processes. For example, when the percent of P in the diet is low, P is the limiting element
297 (Fig. 5, A). This leads to an increased ingestion rate (Fig. 5, B), a minimal excretion rate of P
298 (Fig. 5, C), and a high excretion rate of N (Fig. 5, D).

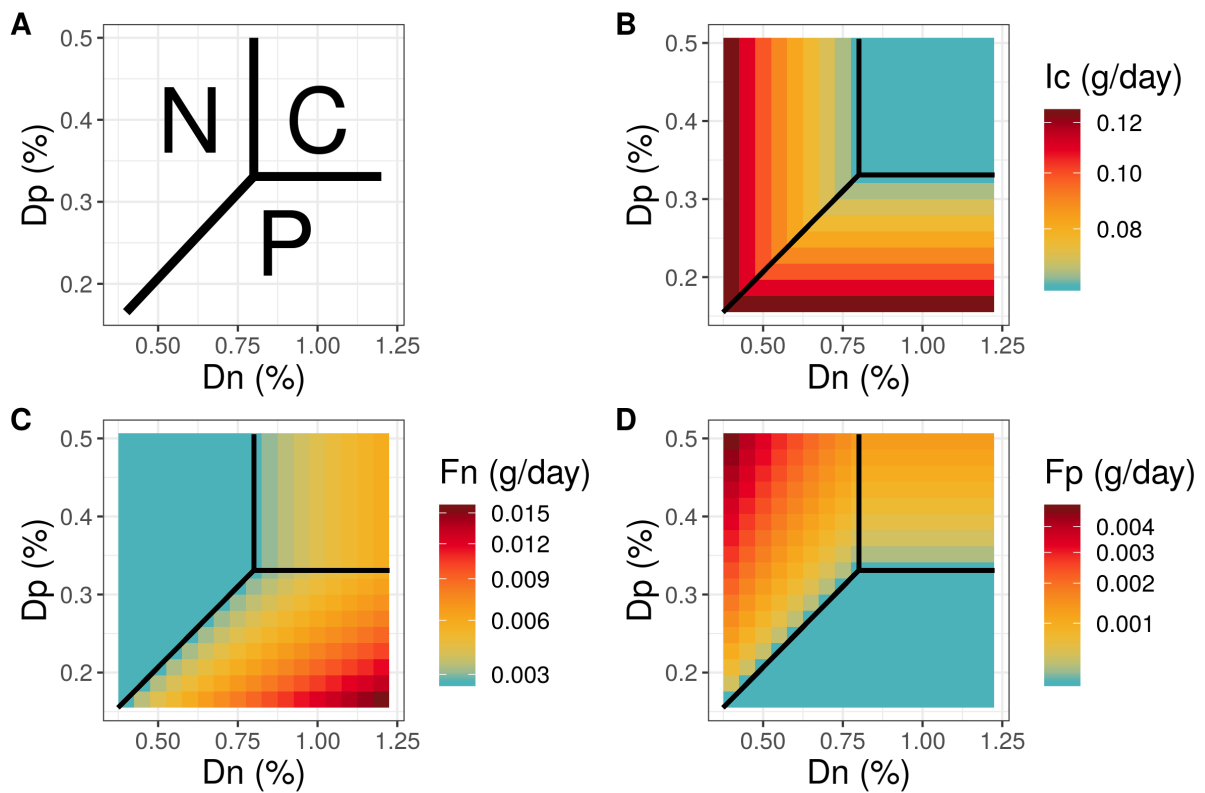


Figure 5. Model simulations with varying levels of D_N and D_P . D_C is kept constant. Diet stoichiometry affects the limitation and the rates of multiple processes, such as the ingestion rate and excretion rates. A. The limiting element is indicated for varying levels of diet stoichiometry (D_N and D_P). Lines indicate where one limiting element switches to another. This is equivalent to the threshold elemental ratios, B. I_C or Ingestion rates of C (g/day), C. F_N or Total inorganic flux of N (g/day), D. F_P or Total inorganic flux of P (g/day).

299 Discussion

300 Combining stoichiometry and bioenergetic modeling provides a framework to predict elemen-
301 tal fluxes in consumers and their contribution to key biogeochemical cycles. Here, we intro-
302 duce a model that incorporates the nutrient requirements of fishes alongside their energetic
303 needs to provide accurate predictions of their ingestion, respiration, excretion, and egestion
304 rates. With our framework, we confirm the existence of nutrient limitation in fishes, specific
305 to the trophic group and life stage, and its effect on multiple processes. We demonstrate the
306 accuracy and applicability of the model to predict ingestion and excretion rates for three tropi-
307 cal reef fish species, while also reflecting the natural variability of these variables. Our frame-
308 work provides an accurate tool to predict CNP fluxes in fishes across diverse trophic groups
309 and gauge the role of fish consumers in ecosystems worldwide.

310 There is a growing consensus that many fishes are limited by nutrients (Benstead et al., 2014;
311 El-Sabaawi et al., 2016; Hood2005; Moody et al., 2019). Yet, fish growth and maintenance
312 are often assumed to be limited by energy (C) when applying coupled bioenergetic and stoi-
313 chiometric models (Allgeier et al., 2013; Burkepile et al., 2013; Kraft, 1992; Schindler & Eby,
314 1997). Our case study confirms that ingestion rates can indeed be determined by N or P lim-
315 itation rather than C limitation, especially in species with nutrient-poor diets. This finding is
316 expected given the elemental imbalance between the consumer's body and dietary CNP con-
317 tent; however, failing to account for nutrient limitation substantially skews predictions of in-
318 gestion rates. For example, assuming only energy limitation for a herbivorous adult *Z. scopas*
319 would result in a greater than two-fold underestimation of its ingestion rate and consequently
320 drastic underestimations of excretion and egestion rates. Given the high densities of species
321 with nutrient-poor diets across a variety of ecosystems (e.g. herbivorous and detritivorous
322 species; Williams & Hatcher (1983); Takeuchi, Ochi, Kohda, Sinyinza, & Hori (2010); Hood
323 et al. (2005)), such underestimates may result in strong misconceptions about ecosystem-scale
324 nutrients and energy fluxes. Our model framework provides a way to facilitate the direct in-
325 corporation of varying elemental limitation across species.

326 The developed model predicts ingestion through the integration of metabolic theory and ele-

327 mental limitation, thus circumventing the difficult task of measuring ingestion rates in natural
328 populations. Therefore, the first step of our framework focuses on quantifying the minimal
329 supply rate for each element (S_k) and determining the limiting element. This includes both
330 maintenance rates and element-specific growth rates based on the growth trajectory of nat-
331 ural populations. Then, by comparing the stoichiometry of these minimal supply rates with
332 diet stoichiometry, we can determine the limiting element. This approach is inspired by the
333 threshold elemental ratio (TER) theory, which predicts the ratio at which growth limitation
334 switches from one element to another (Sterner & Elser, 2002; Urabe & Watanabe, 1992). In
335 fishes, it is widely accepted to integrate metabolic rate into the calculation of TER's (Frost et
336 al., 2006). We built on this work to account not only for maintenance requirements of C, but
337 also of N and P. Similar to the energy (C) that is needed to sustain the metabolic rate of fishes
338 in the wild, minimal N and P is needed to replace decaying cells and maintain body compo-
339 sition. The specific turnover rate of P (F_{0Pz}) is lower than the turnover rate of N (F_{0Nz}) be-
340 cause bone cells, which contain the majority of P, degrade slowly compared to other cell types
341 (Manolagas, 2000; Sterner & Elser, 2002). Thus, including minimal requirements for all three
342 elements lowers the TER of C and nutrients of fishes and increases the probability of detecting
343 nutrient limitation.

344 The inclusion of nutrient limitation ensures that predicted excretion rates (F_P , F_N) are always
345 higher than zero. This is crucial since N and P will always be released at a minimal rate, even
346 when they are limiting (Anderson et al., 2005; Mayor et al., 2011; Sterner & Elser, 2002). Our
347 approach reveals that all three study species are limited by P in their early life. By explicitly
348 including minimal supply rates in our model, we move beyond simply detecting evidence for
349 nutrient limitation (i.e. negative excretion rates; Hood et al, 2005) towards quantifying its ef-
350 fect on vital processes across species and ontogeny. Bone growth, for example, requires sub-
351 stantial amounts of P and is most rapid during early life-stages (Vanni, 2002), and evidence
352 from freshwater ecosystems shows that P can limit fish growth (Benstead et al., 2014; Hood
353 et al., 2005). The ontogenetic variation in elemental limitation presented herein confirms the
354 importance of considering P-limitation for growth when predicting elemental fluxes in fishes.
355 Beyond the incorporation of nutrient limitation, our model framework provides a way to esti-

356 mate uncertainty of predictions. Empirically-measured excretion rates can considerably vary
357 for similarly sized individuals of the same species (Allgeier, Wenger, Rosemond, Schindler,
358 & Layman, 2015; Francis & Côté, 2018; Whiles, Huryn, Taylor, & Reeve, 2011). Yet, exist-
359 ing models that combine stoichiometry and bioenergetics do not account for this natural vari-
360 ability (e.g. Deslauriers et al., 2017), which hampers our ability to gauge the uncertainty of
361 resulting estimates. With the use of MCMC iterations, the R package `fishflux` incorporates
362 the distribution of parameters with their means and standard deviations, resulting in realistic
363 credibility intervals of ingestion and excretion rates, although variability in model output does
364 not necessarily reflect natural variability. The utility of this approach is clear when compar-
365 ing our predictions to reported ingestion rates. For example, *Z. scopas* reportedly ingests 49
366 mg of dry mass per gram of wet fish weight (Polunin, Harmelin-Vivien, & Galzin, 1995), a
367 value centered within the predicted range of our model (11.7 – 68.4 at 15 cm TL). Similarly,
368 the ingestion rate of juvenile coral trout, *Plectropomus leopardus*, a predatory species in the
369 same family as *E. merra* (family Serranidae), ranges between 9 to 14 mg of dry mass per gram
370 of wet weight (Sun et al., 2014), which lies within the 95% prediction for *E. merra* from our
371 model (5.5 – 40.1). Tracing the sensitivity of predictions to uncertainty in specific parameters
372 enables the determination of the main sources of variability that may shift estimates among
373 studies or species.

374 As all models, our approach relies on several simplifying assumptions. First, our model
375 assumes that fishes maintain homeostasis (Sterner, 1990). Since fishes can have flexible body
376 stoichiometry depending on dietary nutrient content (Benstead et al., 2014; Dalton et al.,
377 2017), this assumption may impose biases when simulating effects of varying diet stoichiom-
378 etry on elemental fluxes. Yet, empirically measures relationships between nutrient content
379 of body and diet can easily be incorporated into our model simulations, thus ameliorating the
380 effects of this simplification. Second, similar to most stoichiometric mass balance models,
381 our framework is based on Liebig’s minimal rule, which states that growth is strictly limited
382 by the element in shortest supply relative to demand. However, there is emerging evidence
383 that consumers may simultaneously be limited by more than one element (Sperfeld, Martin-
384 Creuzburg, & Wacker, 2012). For example, P plays an essential role in fish energy uptake

385 (Xie et al., 2011), and the incorporation of interactive co-limitation into stoichiometric models
386 may further improve predictions of elemental fluxes. Finally, we assume that fishes follow a
387 growth trajectory defined by the VBGC curve, and that there is enough food available in the
388 natural environment to meet the growth requirements for each element. The VBGC is fitted
389 on size-at-age data that are mostly acquired via annual otolith readings. In our model, we use
390 this fitted growth function to estimate daily growth rates for each element through integration
391 with length-weight relationships and body stoichiometry. This does not capture, for instance,
392 seasonal variation of food availability. Other stoichiometric models mostly use gross growth
393 efficiencies, or GGE's (i.e. growth/ingestion of the limiting element) (e.g. El-Sabaawi et al.,
394 2016; Frost et al., 2006; Guariento et al., 2018; McManamay, Webster, Valett, & Dolloff,
395 2011; Moody et al., 2019). However, consumer GGE's vary widely, and specific values are
396 poorly understood (McManamay et al., 2011). Furthermore, even if element-specific GGE's
397 are quantified, they may not reflect growth observed in natural populations. Therefore, we
398 suggest that the use of otolith-based growth quantification provides a reasonable alternative to
399 model elemental fluxes of natural fish populations.

400 Beyond model assumptions, the accuracy of our model naturally relies on the accuracy of each
401 parameter estimate. Yet, parameters are often difficult to obtain. We sought to balance the ac-
402 curacy of predictions and ease of application. Parameters involving growth, length-weight
403 relationships, metabolism, and stoichiometry are increasingly accessible for many species
404 due to predictive modeling and open-access databases (e.g. Froese, Thorson, & Reyes, 2014;
405 Barneche et al., 2014; Froese & Pauly, 2018; Killen et al., 2016; Morais & Bellwood, 2018;
406 Vanni et al., 2017). Yet, there are a number of parameters that are still sparsely quantified
407 and may limit the applicability of our framework. In particular, data on diet stoichiometry
408 and assimilation efficiencies are rare. In our case study, we used assimilation efficiency con-
409 stants for C, N and P, that are predominantly based on predatory fishes. In reality, assimila-
410 tion efficiencies can vary substantially, and, in particular, assimilation efficiency of phospho-
411 rus is likely correlated with diet quality (Czamanski et al., 2011). Further, N- and P-specific
412 turnover rates are newly introduced parameters and therefore poorly known. As these parame-
413 ters depend on the cell turnover rates of N- and P-rich tissues (e.g. bone for P), we suggest that

414 these parameters may be applicable across species. Nevertheless, further research is needed
415 to gain further insight. While variation in these parameters can impact the model output via
416 the limiting element and ingestion rate, ongoing compilations of databases of poorly known
417 parameters will improve the application of the proposed modeling framework.

418 In addition, we quantified the activity scope (i.e. field metabolic rate) as the average of
419 maximum metabolic rates (MMR) and standard metabolic rates (SMR) divided by the SMR,
420 assuming that a fish reaches values close to MMR when undertaking activities in the wild
421 (Murchie, Cooke, Danylchuk, & Suski, 2011). In reality, activity scope may vary depending
422 on life history traits and behavior (Killen, Norin, & Halsey, 2017), and field metabolic rates
423 can be elevated with the presence of predators, which in turn can affect nutrient cycling
424 (Dalton, Tracy, Hairston, & Flecker, 2018; Guariento et al., 2018). Recent advances, such
425 as bio-telemetry (Norin & Clark, 2016) or otolith chemistry (Chung, Trueman, Godiksen,
426 Holmstrup, & Grønkjær, 2019) may improve estimates of field metabolic rates. Similarly,
427 specific dynamic action (SDA), which is the metabolic rate needed to assimilate food (Hou et
428 al., 2008) depends on the quality and quantity of food (McCue, 2006) and may thus influence
429 ingestion rates, but it is poorly known across most species. Finally, reproduction is not yet
430 incorporated into the model because data on both gonad stoichiometry and reproductive
431 growth is rare. This may underestimate energy and nutrient investment of fishes, thus skewing
432 model predictions. Nonetheless, as new data on reproductive growth, activity scope, or SDA
433 become available, these elements can be incorporated in the future.

434 Despite these limitations, our framework provides new avenues for addressing pressing ques-
435 tions in ecology. Data on the daily actions of fishes are difficult to obtain due to the chal-
436 lenges of conducting research in aquatic environments. Novel techniques such as fish gut
437 content DNA metabarcoding (Casey et al., 2019) or compound-specific stable isotope anal-
438 yses (Hopkins & Ferguson, 2012) permit improved insights into species-specific ingestion
439 of prey resources. However, no current empirical technique can estimate rates of food inges-
440 tion via these linkages across a broad range of species. Combining our model with emerging
441 techniques to quantify species-specific resource use can help us to address long standing ques-
442 tions. How much prey do top predators consume daily? How do rates of algal consumption

443 differ among herbivorous species? How much production by lower trophic levels is needed
444 to fuel the growth of predatory fisheries species? By providing a tool to answer these ques-
445 tions, our model empowers fundamental and applied researchers to tackle some of the most
446 outstanding questions in fish ecology.

447 Beyond single species and their pairwise interactions, our model provides means to examine
448 community- and ecosystem-scale dynamics. Specifically, based on simple census data of fish
449 communities, our model can help decompose system-wide fluxes (cf. Burkepile et al., 2013;
450 Allgeier et al., 2014; Francis & Côté, 2018). This is particularly important for open ecosys-
451 tems in which the dominant sources of energy and nutrients are unclear or variable. For exam-
452 ple, on coral reefs, debates persist on the importance of external (i.e. pelagic) subsidies versus
453 internal nutrient cycling (e.g. Brandl, Tornabene, et al., 2019; Morais & Bellwood, 2019). Our
454 model can help estimate how much pelagic or benthic prey is consumed by reef fishes and
455 how these resources are propagated through food webs, which enables researchers to quantify
456 reef functioning (Brandl, Rasher, et al., 2019). Thus, merging what is eaten (i.e. food web as-
457 sembly) with how much is eaten (i.e. realistic consumption rates as provided by our model)
458 can significantly augment our understanding of ecosystem functioning, especially in systems
459 where fishes are the dominant consumers.

460 Finally, given the heavy exploitation of fish communities for global human consumption, our
461 model offers a tool for understanding and predicting the effect of human-driven changes on
462 ecosystem functioning. Yearly, more than 100 million tons of fishes are caught in marine
463 systems worldwide (Cashion et al., 2018), imposing an unparalleled top-down stressor on
464 global fish communities, which erodes biomass and alters the size and trophic structure of
465 fish communities (Essington, Beaudreau, & Wiedenmann, 2006; Pauly, Christensen, Dals-
466 gaard, Froese, & Torres, 1998). As exemplified here, elemental fluxes are influenced by diet
467 and life stage. Thus, our model provides a tool to estimate the impact of size and trophic struc-
468 ture shifts on elemental cycling. In addition, increasing temperatures resulting from climate
469 change can affect primary production in the world's oceans, thus imposing a bottom-up effect
470 on fish communities (Lotze et al., 2019), which are likewise affected by rising temperatures
471 (Pinsky, Eikeset, McCauley, Payne, & Sunday, 2019). Temperature is known to affect mul-

472 tiple parameters in this model, such as metabolic rate and growth rate (Morais2018; Killen et
473 al., 2016), which enables assessment of the impact of temperature on elemental fluxes. Given
474 human-driven alterations in both primary production through climate change and fish com-
475 munity structure through extensive fishing, it is urgent to understand how these changes may
476 impact biogeochemical fluxes. Our model and its implementation provide a path toward rising
477 to this challenge.

478 **Data accessibility**

479 All data and code to reproduce figures will be available online on GitHub <https://github.com/nschiett/>.

480 The full model code is available on GitHub through the R package `fishflux`: <https://github.com/nschiett/fishflux>.

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