**Supplementary methods of “Biological trade-offs underlie coral reef ecosystem functioning”**

We used individual-based bioenergetic models to estimate key fish-mediated functions in global coral reefs. We first assembled a global species list based on an openly accessible database of reef fish abundances and sizes collected during belt transects by divers1.We used a subset of available data (see methods) and included 1110 species that belong to 25 families: Acanthuridae, Balistidae, Bothidae, Chaetodontidae, Cirrhitidae, Fistulariidae, Haemulidae, Holocentridae, Kyphosidae, Labridae, Lethrinidae, Lutjanidae, Monacanthidae, Mugilidae, Mullidae, Ostraciidae, Pempheridae, Pomacanthidae, Pomacentridae, Sciaenidae, Scorpaenidae, Serranidae, Siganidae, Tetraodontidae, Zanclidae. To apply bioenergetic models and estimate fluxes of carbon (C), nitrogen (N), and phosphorus (P) for all species in the underwater visual census database across their entire temperature range, a number of parameters are required (Table 1)2. Here, we describe how these parameters were quantified for all 1110 species through a combination of literature, empirical measures, and Bayesian models. All protocols related to the capture and handling of fish complied to the ethical standards of CRIOBE and EPHE, and the University of California Santa Barbara’s Institutional Animal Care and Use Committee (IACUC #915 2016-2019). Extraction and transport of samples were approved by the government of French Polynesia. All analyzes were carried out in R v.3.6.3 and Bayesian modes were run using Stan3 and the R package brms4.

Table 1. Overview of model input parameters, adopted from Schiettekatte et al. (2020)2. VBGC = von Bertalanffy growth curve.

|  |  |  |
| --- | --- | --- |
| Symbol | Description | Unit |
| , , | Element-specific assimilation efficiency | \_ |
|  | Total length of individual at time t | cm |
|  | Asymptotic adult length (VBGC) | cm |
|  | Growth rate parameter (VBGC) |  |
|  | Age at settlement (VBGC) |  |
|  | Parameter length-weight relationship |  |
|  | Parameter length-weight relationship | \_ |
| , , | Element-specific body content percentage of dry mass | % |
|  | Wet body mass | g |
|  | Metabolic normalisation constant independent of body mass |  |
|  | Mass-scaling exponent | \_ |
|  | Activity scope | \_ |
|  | Environmental temperature | °C |
|  | Trophic level | \_ |
|  | Aspect ratio of caudal fin | \_ |
|  | Mass-specific turnover rate of N |  |
|  | Mass-specific turnover rate of P |  |
|  | Ratio of dry mass and wet mass of fish | \_ |
| , , | Element-specific diet content percentage of dry mass | % |

1. **Growth parameters**

The bioenergetic model uses the Von Bertalanffy growth function to estimate daily growth.2 This growth function relies on three parameters: (i.e. the population asymptotic body length of a fish), (i.e. the rate at which fish in a population, on average, approaches its population asymptotic body size), and (i.e. the theoretical age at which length is zero). For , we used a standardized coefficient that describes the potential growth trajectory of an individual if were to be equal to its maximum length (i.e., )5 For simplicity, we kept constant at 0 for all species.

*1.1 Data compilation*

We first compiled maximum lengths for all species using Fishbase6 and used these lengths for the . Then, we extracted the available data for from Morais & Bellwood (2018), which are estimated using growth curve parameters from Fishbase, standardized to the maximum length5. We selected the species of our species list and only included the estimates coming from otolith studies. In total, this selection process resulted in 439 observations of for varying species and temperatures.

Further, we used an openly accessible otolith dataset, including measurements of fishes from five French Polynesian islands7. This dataset includes total length measurements to the nearest millimeter and fish weights to the nearest 0.1 grams. Further, it includes distances between annual growth increments, measured by two independent researchers to prevent biases induced by a single observer. These data can be used to estimate growth rate parameters using a two-step approach: back-calculation to achieve individual-level size-at-age data and hierarchical regression to fit the Von Bertalanffy growth curve7. Specifically, we used the Modified Fry back-calculation model8 to estimate fish lengths at previous ages. We adapted the traditional model to also estimate the uncertainty around the obtained length estimates and allow for the inclusion of missing values using a Bayesian approach (see R package fishgrowbot). Then, we fitted the Von Bertalanffy growth model to all species at each location for which there were at least three individuals, using Bayesian hierarchical regression models. Both steps of this procedure were carried out using the developed R package ‘fishgrowbot’. The package also automatically estimates the parameter . After combining the two data sources, we obtained 496 estimates of for 181 species across varying temperatures.

*1.2 Data analysis and extrapolation*

Aside from phylogeny, is mostly determined by body size and temperature5. We therefore aimed to predict based on body size, temperature, and phylogeny by using a phylogenetic regression model.

We extracted the phylogenetic position of all species included through the Fish Tree of Life9. We retrieved 100 synthetic stochastically resolved phylogenies where missing taxa were placed according to the highest level of taxonomy using the function fishtree\_complete\_phylogeny() in the R package fishtree10. For each tree, we then calculated the correlation matrix and averaged each element across the 100 matrices to get one correlation matrix that could be used in the regression model.

We then fitted the Bayesian phylogenetic regression to predict the growth rate parameter of fishes depending on body size, temperature, and phylogeny using the R package brms4 :

where represents the natural log-transformed value, is the predicted average, and is the standard deviation, is the fixed-effect intercept, is the random-effect coefficient that accounts for the residual intercept variation, based on the relatedness as described by the phylogeny, is the slope for the natural transformed maximum body size, is the slope for the average SST. We used uninformative priors and ran the model for 2000 iterations with a warm-up of 1000 iteration for 4 chains.

The model fit confirmed a negative relationship of with maximum body size ( = -0.76, 95%CI: -0.96,-0.57 ), and a positive relationship with sea surface temperature ( = 0.02, 95%CI: 0.00,0.05 ). We verified model convergence and fit by checking the posterior predictive plot, inspecting parameter trace plots, and checking the R statistic. The Bayesian R2 of the model was 0.738 (95%CI: 0.702,0.769).

The phylogenetic heritability (equivalent to Pagel’) was estimated as the proportion of total variance, conditioned on the effects attributable to the phylogeny:

.  
This calculation resulted in a phylogenetic signal of 0.74 (95% CI: 0.70 - 0.77). This means that most of the variation, independent of the effect of body size and SST, is explained by phylogeny.

We extrapolated for all species across the full SST range in which those species occur in the database, with SST rounded to the °C, which results in 4712 unique SST and species combinations. There is currently no streamlined method to make predictions for new species from a phylogenetic regression model. We circumvented the issue by extracting draws of the phylogenetic effect, for each species included in the model. We subsequently predicted these phylogenetic effects for missing species with the help of the function phyEstimate in the picante package for R11. This function uses phylogenetic ancestral state estimation to infer trait values for new species on a phylogenetic tree by rerooting the tree to the parent edge for the node to be predicted12. We repeated this for all 100 trees and 1000 draws. Per draw, we averaged the extrapolated values per species for the hundred trees. Then, by combining the predicted phylogenetic effects with the global intercept and slopes for body size and temperatures for each draw, we predicted for each species. We only use one chain in order to keep computational time reasonable. Finally, we summarized all predictions per SST per species by taking the mean and standard deviation across the 1000 draws.

Finally, we tested our phylogenetic extrapolation approach by performing a leave-one-out cross validation. Specifically, we conducted the above-described approach 496 times, each time removing one species from the analysis and extrapolating to that species. We then compared the extrapolated values for to the predicted values based on the full model. These values were positively correlated with a correlation coefficient of 0.88.

**2 Body stoichiometry**

*2.1 Data collection*

individuals of 108 species and 25 families were collected between 2015 and 2017 in Mo’orea13 , the Caribbean13,14 ,and Palmyra (Table 2). Their gut contents were removed and the whole body was freeze-dried and ground to powder with a Precellys homogenizer. Whole body elemental proportions () were then measured in the lab using standard methods. Specifically, ground samples were analyzed for %C and %N content using a CHN Carlo-Erba elemental analyzer (NA1500), and for %P using dry oxidation-acid hydrolysis extraction followed by a colorimetric analysis15. Elemental content was calculated based on dry mass.

Table 2. Overview number of species and individuals per fish family, used for body stoichiometry analysis. Per species, there was a minimal replication of 4.

|  |  |  |
| --- | --- | --- |
| Family | # Species | # Individuals |
| Acanthuridae | 10 | 188 |
| Balistidae | 5 | 104 |
| Bothidae | 1 | 6 |
| Chaetodontidae | 11 | 129 |
| Cirrhitidae | 1 | 26 |
| Fistulariidae | 1 | 6 |
| Haemulidae | 4 | 54 |
| Holocentridae | 9 | 123 |
| Kyphosidae | 1 | 4 |
| Labridae | 19 | 308 |
| Lethrinidae | 2 | 31 |
| Lutjanidae | 6 | 146 |
| Monacanthidae | 1 | 5 |
| Mugilidae | 1 | 8 |
| Mullidae | 4 | 50 |
| Ostraciidae | 1 | 5 |
| Pempheridae | 1 | 10 |
| Pomacanthidae | 3 | 20 |
| Pomacentridae | 15 | 201 |
| Sciaenidae | 1 | 5 |
| Scorpaenidae | 1 | 12 |
| Serranidae | 4 | 132 |
| Siganidae | 2 | 14 |
| Tetraodontidae | 3 | 41 |
| Zanclidae | 1 | 5 |

*2.2 Data analysis and extrapolation*

The CNP% content of organisms is known to be highly conserved within taxa13,14. We therefore use phylogeny to extrapolate these values. We fitted C, N and P contents (%) through a hierarchical phylogenetic multivariate normal model with phylogenetic effects and random effects per species.

where , and are the % content of , , and respectively, represents the average % content of element (, , and ) per species, is the covariance matrix of the residual errors of , , and , is the fixed-effect intercept for each element , is the random-effect coefficient that account for the intercept variation, based on the relatedness as described by the phylogeny per element , is the random-effect coefficient that account for the residual species-level intercept variation per element k.

We used uninformative priors and ran the model for 2000 iterations with a warm-up of 1000 iteration for 4 chains. The Bayesian R2 of the model was 0.39 (95%CI: 0.36-0.42), 0.50 (95%CI: 0.48-0.53), and 0.43 (95%CI: 0.40-0.46) for C, N and P respectively. The phylogenetic heritability was 0.41 (95%CI: 0.28-0.55), 0.58 (95%CI: 0.4-0.66), and 0.57 (95%CI: 0.46-0.69) for C, N, and P respectively.

We used 1000 fitted draws for each species, and 100 phylogenetic trees to extrapolate to all species with unknown body stoichiometry, similar to the methods described above. Specifically, we used the phylopars function from the Rphylopars package16. This function uses ancestral state reconstruction and Brownian motion, and takes the correlation between C, N, and P into account.

Finally, we tested the phylogenetic extrapolation approach by performing a leave-one-out cross validation, similar to the methods described in 1.2. The extrapolated species-level estimates were correlated with the mean species-level estimates from the full model with correlations of 0.61, 0.67, and 0.67 for C, N, and P, respectively.

**3 Diet**

*3.1 Data collection*

We collected 571 adult individuals of 51 species between 2018 and 2019 in Mo’orea and Tetiaroa, and Mangareva, three Polynesian islands. We extracted the stomach content and stored it in a 2ml tube. After freezing the samples, we dry-froze all samples for at least 24 hours, and ground to powder. Then, samples were sent to the lab for CNP content analysis using similar methods as for the fish body stoichiometry described above.

*3.2 Data analysis and extrapolation*

Using trophic guilds defined by Parravicini et al. (2020)17, we fitted a multivariate Bayesian regression model to summarize CNP% content data per trophic guild with random effects at the species level. This model had a median Bayesian R2 of 0.62, 0.62, and 0.48 for C, N and P respectively. Next, we extracted 1000 draws of the predicted CNP% per trophic guild. Parravicini et al.(2020)17 provides the probability of reef fish species to be assigned to each of the eight defined trophic guilds (i.e. sessile invertivores; herbivores, microvores, and detrivores; corallivores; piscivores; microinvertivores; macroinvertivores; crustacivores; planktivores). By combining these probabilities with the predicted diet contents per trophic guild, we finally estimated the diet CNP content for each species in our database. Essentially, we performed a weighted average of CNP content across diet groups for each species, where the weights represent the probability of being in a certain trophic guild. We then took the average and standard deviation across all 1000 draws. While we recognize the bias of using diet CNP% estimates of a dataset in one region, we argue that variability between food categories e.g. animal material and primary producers is likely to be higher than regional differences within trophic categorizations. Further, since the used trophic guild classification includes probabilities to belong to each group, variation is included when the trophic categorization is not well known. For example, if a species has a 50% probability to be a herbivore and a 50% probability to be a sessile invertivore this uncertainty will be reflected the estimation of the diet CNP%.

**4 Metabolic parameters**

*4.1 Data collection and lab experiments*

To quantify standard metabolic rate (SMR) and maximum metabolic rate (MMR), we carried out intermittent-closed respirometry experiments18,19. In the period between 2018 and 2019, we collected 1393 individuals of 61 species and 18 families with a minimum of 3 replicates per species in Moorea, French Polynesia. Fishes were captured by scuba divers using hand nets and clove oil and immediately transported to the laboratory in coolers with ambient seawater and oxygen stones. After an acclimatization and fasting period of 48 h in aquaria, the fishes were individually transferred to a water-filled tub at 28°C (ambient sea water temperature) and manually chased by the experimenter until exhausted20,21. Then, they were placed in respirometry chambers submersed in an ambient and temperature-controlled tank, where they were left for ~23 h. The intermittent respirometry cycles started immediately after a fish was placed in its respirometry chamber. The cycles consisted of a measurement (sealed) period followed by a flush period during which the respirometry chambers were flushed with fully aerated water from the ambient tank. Because fishes were exhausted right before entering the respirometry chambers, it was possible to measure the approximate MMR. Depending on fish size, 8 respirometry chambers ranging in volume (including tubes and pumps) from 0.4 to 4.4 L were run in parallel, and measurement and flush periods lasted between 3 to 15 min and 3 to 5 min, respectively. SMR was calculated as the average of the 10% lowest values measured during the entire period, after the removal of outliers22. MMR was calculated from the slope of the first measurement period.

*4.2 Data analysis and extrapolation*

To retrieve the parameters (Metabolic normalisation constant independent of body mass; ), (mass-scaling exponent), and (factorial activity scope), we fitted a normal Bayesian mixed effect model predicting the log10-transformed metabolic rate using the log10-transformed biomass including random effects of family, species, and metabolic rate type (SMR or MMR) on both the intercept and slopes using brms4:

We ran the model for 4000 iterations, with a warm-up of 2000 iterations, and four chains. Further, we used an informative prior, for the slope (), based on previous work23. The model had a Bayesian R2 of 0.973 (95%CI: 0.972-0.974). We then predicted the family-level by summing the slope of the model with the effects of the family on the slope of the SMR. We did this for all iterations and then took the mean and standard deviation. In a similar way, we extracted the family-level intercept for SMR and MMR, and then quantified mean and standard deviation of after the back-transformation of all iterations of the intercept (i.e., the intercept for SMR).

Finally, we estimated as followed, based on the assumption that fishes rest 12h a day and they on average spend the remaining 12 hours at a metabolic rate that is the average of their SMR and MMR:

where all iterations of the back-transformed family-level intercepts were used for SMR and MMR. We then summarized these predictions by taking the mean and standard deviation. We used the family-level estimates for these parameters for all species in our database. We used the average across all families for families that were not represented in our respirometry dataset, (Bothidae, Chaetodontidae, Fistulariidae, Haemulidae, Kyphosidae, Lethrinidae, Lutjanidae, Mugilidae, Ostraciidae, Pempheridae, Sciaenidae, Siganidae).

The parameter was adjusted for each temperature in the varying locations of the underwater visual census database, following Barneche et al. (2014)23.

where is the Boltsmann’s constant (), is the activation energy (0.59 eV, extracted from)23, is the value of the metabolic normalization at a fixed reference temperature (301.15 K = 28 + 273.15K), is the temperature of interest (K).

5. **Additional parameters**

We retrieved the parameters , , , and from fishbase6. For the mass-specific turnover rates for N and P(; ), we used the estimates provided in Schiettekatte et al. (2020)2.

**References**

1. Barneche, D. R. *et al.* Body size, reef area and temperature predict global reef-fish species richness across spatial scales. *Global Ecology and Biogeography* **28**, 315–327 (2019).

2. Schiettekatte, N. M. D. *et al.* Nutrient limitation, bioenergetics and stoichiometry: A new model to predict elemental fluxes mediated by fishes. *Functional Ecology* **34**, 1857–1869 (2020).

3. Carpenter, B. *et al.* Stan : A Probabilistic Programming Language. *Journal of Statistical Software* **76**, 1–31 (2017).

4. Bürkner, P.-C. brms : An R Package for Bayesian Multilevel Models using Stan. *Journal of Statistical Software* **80**, 1–28 (2017).

5. Morais, R. A. & Bellwood, D. R. Global drivers of reef fish growth. *Fish and Fisheries* **19**, 874–889 (2018).

6. Froese, R. & Pauly, D. FishBase. *World Wide Web electronic publication.* (2018).

7. Morat, F. *et al.* Individual back-calculated size-at-age based on otoliths from Pacific coral reef fish species. *Scientific Data* **7**, (2020).

8. Vigliola, L., Harmelin-Vivien, M. & Meekan, M. G. Comparison of techniques of back-calculation of growth and settlement marks from the otoliths of three species of Diplodus from the Mediterranean Sea. *Canadian Journal of Fisheries and Aquatic Sciences* **57**, 1291–1299 (2000).

9. Rabosky, D. L. *et al.* An inverse latitudinal gradient in speciation rate for marine fishes. *Nature* **559**, 392–395 (2018).

10. Chang, J., Rabosky, D. L., Smith, S. A. & Alfaro, M. E. An R package and online resource for macroevolutionary studies using the ray-finned fish tree of life. *Methods in Ecology and Evolution* (2019) doi:[10.1111/2041-210X.13182](https://doi.org/10.1111/2041-210X.13182).X

11. Kembel, S. W. *et al.* Picante: R tools for integrating phylogenies and ecology. *Bioinformatics* **26**, 1463–4 (2010).

12. Kembel, S. W., Wu, M., Eisen, J. A. & Green, J. L. Incorporating 16S Gene Copy Number Information Improves Estimates of Microbial Diversity and Abundance. *PLoS Computational Biology* **8**, e1002743 (2012).

13. Allgeier, J. E. *et al.* Phylogenetic conservatism drives nutrient dynamics of coral reef fishes. *Nature Communications 2021 12:1* **12**, 1–9 (2021).

14. Allgeier, J. E., Wenger, S. & Layman, C. A. Taxonomic identity best explains variation in body nutrient stoichiometry in a diverse marine animal community. *Scientific reports* **10**, (2020).

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

16. Bruggeman, J., Heringa, J. & Brandt, B. W. PhyloPars: Estimation of missing parameter values using phylogeny. *Nucleic Acids Research* **37**, W179–W184 (2009).

17. Parravicini, V., Casey, J. M., Schiettekatte, N. M. D. & Brandl, S. J. Global gut content data synthesis and phylogeny delineate reef fish trophic guilds. *bioRxiv* 0–3 (2020) doi:[10.1101/2020.03.04.977116](https://doi.org/10.1101/2020.03.04.977116).X

18. Steffensen, J. F. Some errors in respirometry of aquatic breathers: How to avoid and correct for them. *Fish Physiology and Biochemistry* **6**, 49–59 (1989).

19. Clark, T. D., Sandblom, E. & Jutfelt, F. Aerobic scope measurements of fishes in an era of climate change: Respirometry, relevance and recommendations. vol. 216 2771–2782 (2013).

20. Norin, T. & Malte, H. Repeatability of standard metabolic rate, active metabolic rate and aerobic scope in young brown trout during a period of moderate food availability. *Journal of Experimental Biology* **214**, 1668–1675 (2011).

21. Clark, T. D. *et al.* Physiological benefits of being small in a changing world: Responses of coho salmon (Oncorhynchus kisutch) to an acute thermal challenge and a simulated capture event. *PLoS ONE* **7**, 1–8 (2012).

22. Chabot, D., Steffensen, J. F. & Farrell, A. P. The determination of standard metabolic rate in fishes. *Journal of Fish Biology* **88**, 81–121 (2016).

23. Barneche, D. R. *et al.* Scaling metabolism from individuals to reef-fish communities at broad spatial scales. *Ecology Letters* **17**, 1067–1076 (2014).