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The role of fish feces for nutrient cycling on coral reefs

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Abstract :

Consumers play an important role in biogeochemical cycles through the consumption and release of essential elements such as carbon (C), nitrogen (N), and phosphorus (P). Indeed, a large proportion of consumed elements are released into the environment in inorganic (i.e. excretion) or organic form (i.e. egestion). On coral reefs, fishes represent the bulk of consumer biomass and thus play a key role in the recycling of nutrients. In recent years, excretion rates have been studied intensively, but less is known about the rate and quality of coral reef fish egestion. In this study, we quantify the elemental contents of fish feces, estimate absorption efficiencies and compare egestion and excretion rates for 51 coral reef fish species. We show that elemental concentrations decrease remarkably little from food to feces. This is due to extremely low absorption efficiencies, resulting in the egestion of large amounts of energy and nutrients. Moreover, we show that while the quality of fish feces varies across trophic guilds, it remains highly variable within trophic guilds. Finally, we demonstrate that the release of N and P through egestion outweighs the amount of nutrients recycled through excretion. Our study highlights the need to incorporate animal egestion into assessments of ecosystem functioning and food web structure.

Keywords : consumer-mediated nutrient cycling, egestion, excretion, nitrogen, phosphorus, stoichiometry

Introduction

Aquatic consumers play an essential role in biogeochemical cycles through consumption, assimilation, and the release of major elements such as carbon (C), nitrogen (N), and phosphorus (P) (Sterner and Elser 2002). A large proportion of consumed elements is not assimilated, and is released back into the environment in either inorganic or organic forms (Kraft 1992, Sterner and Elser 2002). Inorganic nutrient release (i.e., excretion) strongly impacts primary producers, particularly in systems limited by nitrogen or phosphorus (Turner 2002, Doughty et al. 2016). Specifically, dense aggregations of consumers can create hotspots of N and P and boost primary productivity (e.g., McIntyre et al. 2008, Shantz et al. 2015). On the other hand, release of organic nutrients (i.e., egestion) can either serve as a food source for other consumers, which in turn release inorganic nutrients (Robertson 1982, Le Mézo and Galbraith 2021), or provide a substrate for heterotrophic bacterial communities (Turner 2002, Halvorson et al. 2017b, Parr et al. 2019).

Egestion represents a dominant and dynamic animal-mediated elemental flux (Halvorson and Atkinson 2019). While there is a general assumption that egestion is less important for elemental cycling because of its low bioavailability and nutrient-poor organic form (Atkinson et al. 2014, Halvorson and Atkinson 2019), N and P in the form of egestion exceed N and P excretion fluxes in many aquatic consumers (Liess 2014, Halvorson and Atkinson 2019). The quality of egesta, handling time, and the availability of other resources determines whether it may serve as a direct food source for other animals (Bailey and Robertson 1982, Rempel et al. 2022). In fact, coprophagy (i.e., the consumption of feces) is a common phenomenon across a variety of ecosystems and may play an important ecological role by immediately re-integrating valuable

elements into the food web (Frankenberg and Smith 1967, Robertson 1982, Sazima et al. 2003, Le Mézo and Galbraith 2021).

The rate and quality of egestion depend on the food, the nutritional needs of the consumer, and the element-specific absorption efficiencies (i.e., the proportion of the ingested material that is absorbed in the intestinal tract) of the consumer. Naturally, the quality of egestion (i.e., concentrations of C, N, and P) directly correlates with the quality of the food ingested (Sterner and George 2000), which also indirectly affects the rate of consumption and thus egestion (Schiettekatte et al. 2020). Consumers with low diet quality such as herbivores (i.e., animals feeding on primary producers) or detritivores (i.e., animals feeding on detritus), for instance, compensate for poor nutritional quality by increasing their consumption rates to reach their daily nutritional needs (Cruz-Rivera and Hay 2000, Schindler and Eby 1997, McIntyre et al. 2008, Evans-White and Halvorson 2017). Furthermore, compensatory feeding is promoted by the positive correlation between diet quality and absorption efficiency; consumers with low N or P diets tend to have low absorption efficiencies of these elements (Pandian and Marian 1985, Halvorson et al. 2017a, Jochum et al. 2017).

On coral reefs, fishes represent a large part of the consumer biomass and play an essential role in recycling nutrients. In recent years, excretion rates have been studied extensively (Allgeier et al. 2014; Allgeier et al. 2016; Francis and Côté 2018), but less is known about the rate and quality of coral reef fish egestion. Fish feces could likely represent an important food source for certain reef fishes (Bailey and Robertson 1982, Rempell 2022, Robertson 1982) and invertebrates (Pinnegar and Polunin 2006). Yet, little quantitative data exists on the rates of defecation, the consumption of feces, and nutritional properties of feces (but see Rempel et al. 2022, Bailey and

Robertson 1982). While bioenergetic models can be used to estimate rates of egestion, a lack of information on absorption efficiencies may create biased estimates of nutrient fluxes. To date, bioenergetic models applied to coral reef communities use constants for element-specific absorption efficiencies (e.g., Allgeier et al. 2014, Schiettekatte et al. 2020), which hampers their accuracy for quantifying egestion rates.

Here, we quantify the rate and nutritional quality of egestion for a wide range of reef fishes. Specifically, we examine the C, N, and P concentrations of the stomach contents and feces for 51 common coral reef fish species from 15 families collected around Mo'orea, French Polynesia. We estimate element-specific absorption efficiencies for each species and link absorption efficiency to each species' stomach content and intestine surface area. Then, combining our data with historical observational data on defecation and consumption rates (Robertson 1982), we infer potential coprophagic links among our study species. Finally, we parametrize bioenergetic models at the species and community levels to compare estimated nutrient fluxes in excretion and egestion.

Methods

Data collection and processing

We collected fishes around Mo'orea, French Polynesia across 62 sites distributed in the lagoon and outer reef (Appendix S1: Figure S1). We targeted 51 common species from 15 fish families: Cirrhitidae, Zanclidae, Balistidae, Holocentridae, Chaetodontidae, Acanthuridae, Labridae, Aulostomidae, Mullidae, Serranidae, Pomacentridae, Pomacanthidae, Lethrinidae, Tetraodontidae, and Monacanthidae (see Appendix S1: Table S1). In total, we collected 620 individuals using spear fishing between 9:45am and 2:30pm between 2017 and 2019 (Appendix S1: Table S1). Fishes were pithed immediately upon capture and transported to the laboratory at the Centre de Recherches Insulaires et Observatoire de l'Environnement (CRIOBE) on ice. In the laboratory, fishes were measured, weighed, and dissected to expose the full alimentary tract. Samples of ingested material were taken from the stomach and hindgut. For fishes that do not have a stomach (e.g., Labridae), a sample from the esophagus or foregut was taken. When the foregut or hindgut were empty, no sample was collected.

Samples were frozen for at least 24 hours, then freeze-dried for at least 24h prior to transport to the CRIOBE in Perpignan, France. After lyophilization, samples were ground to a fine powder using a homogenizer. Homogenized samples were then sent to the University of Michigan Biological Station for the estimation of carbon (C), nitrogen (N), and phosphorus (P) concentrations . Ground samples were analyzed for %C and %N content using a CHN Carlo-Erba elemental analyzer (NA1500) and %P using dry oxidation-acid hydrolysis extraction

followed by a calorimetric analysis (Allen et al. 1974). Elemental content was calculated based on dry weight.

We determined ash contents of stomach contents and feces by combustion at 450 °C in a muffle furnace for at least 6h. The ash content was calculated by dividing the weight of the sample after combustion by the dry weight of the sample before combustion. Since the material was too limited for both nutrient and ash content analysis, we determined the ash content for a subset of samples to calibrate our data. Ash contents for missing species were estimated using information from the literature or based on an average estimate for each trophic guild (see Appendix S1: Table S2).

We divided the study species into six trophic guilds, based on Parravicini et al. (2020) (Appendix S1: Table S2):

1 detritivores (and microvores): species primarily feeding on detritus or microorganisms);

2 herbivores: species primarily feeding on autotrophs;

3 invertivores (including microinvertivores, macroinvertivores, and sessile invertivores): species feeding on Asteroidea, Bryozoa, Cirripedia, Porifera, Annelida, Arachnida, Hemichordata, Nematoda, Peracarida, Nemertea, Mollusca and Echinodermata, and Tunicata;

4 corallivores: species primarily feeding on Anthozoa and Hydrozoa;

5 planktivores: species mainly feeding on zooplankton, cyanobacteria and Harpacticoida.

6 carnivores: species primarily feeding on Actinopterygii, Cephalopoda, Decapoda, and Stomatopoda.

While detritivores (and microvores) and herbivores are combined in Parravicini et al. (2020), we categorized *Acanthurus pyroferus*, *A. olivaceus*, *Ctenochaetus striatus*, and *Chlorurus spilurus* separately as detritivores in accordance to previous literature and due to the considerable nutritional difference between algae and detritus/microbes (Choat et al. 2002, Eagle and Jones 2004).

Finally, to examine the occurrence of potential coprophagous behavior, we extracted the data from Robertson (1982), which describes the consumption of feces by fishes in a diverse coral reef fish assemblage in Palau, an island in the western Pacific. For each species in the study, we extracted: (1) whether a species was considered a coprophage or not based on the author's observations, (2) the total number of defecation events observed per species, and (3) the proportion of those defecation events where feces were consumed by another fish species. To obtain the raw defecation data format, we transformed the summary data presented in the paper (i.e. the total number of defecation events and the proportion of those defecation events where feces were consumed) to binary data where each data point is a single defecation event. For example, a species with 200 defecation events with 75% of those observations including coprophagy would result in 150 data points with coprophagy and 50 data points without coprophagy. We then combined this data with our species-level estimates of stomach and feces nutrient content, resulting in 14 overlapping species between Robertson (1982) and this study. This combined data was used for further analysis.

Data analysis

All data were analyzed using Bayesian analysis with *rstan* (Carpenter et al. 2017) or *brms* which uses Stan, a C++ package to perform full Bayesian inference (Burkner 2017). The posterior distributions of model parameters were estimated using Hamiltonian Monte Carlo (HMC) methods by using four chains of 2,000 samples, including 1,000 samples as a warm-up. Thus, a total of 4,000 draws were used to estimate posterior distributions. The convergence and fit of the models were verified by examining the Rhat, parameter trace plots, and posterior prediction plots.

Estimating diet and stomach content for C, N, and P

We predicted the average food and feces content for C, N, and P by fitting a Bayesian regression model for each species with *rstan* (Carpenter et al. 2017). We fitted the data to a student-t distribution to decrease the influence of outliers:

$$x_{i,k} \sim student\left(nu_{i,k}, mu_{i,k}, sigma_{i,k}\right), \quad (1)$$

where i is either stomach content or feces, k is the element, $x_{food,k}$ and $x_{feces,k}$ are measures of the elemental content from ingesta in the stomach and the hindgut respectively (in % of dry mass), nu is the degrees of freedom, mu is the average elemental content (in % of dry mass), and $sigma$ is the standard deviation of the distribution. We used the following weakly-informative priors based on a realistic range of elemental contents:

$$mu_{i,n} \sim normal(5,5), mu_{i,p} \sim normal(1,1), mu_{i,c} \sim normal(30,30),$$

$$sigma_{i,c} \sim cauchy(0,5), sigma_{i,n} \sim cauchy(0,1), sigma_{i,p} \sim cauchy(0,0.5),$$

$nu_{i,k} \sim gamma(2,0.1)$The model resulted in 4,000 estimates for each parameter.

Pairwise comparisons between gut content and feces nutrients

To asses how gut content N% and P% relate to the feces N% and P% of other species we used the median species-level estimates from the above-mentioned model and calculated the difference between feces nutrients and stomach contents for all species pairs (n = 2550). Further, we summarized species pairs into pairs of trophic guilds by taking the median of the difference between feces nutrients and stomach contents.

Estimating absorption efficiencies

Using the above-mentioned samples of stomach content and feces C, N, and P (%), we estimated the absorption efficiency (a_k) for each element (k). Even if stomach content and feces were often taken from the same individuals, we could not assume that the food items in the stomach are the same as the digested material in the feces. Therefore, we considered the samples to be independent, and we used the iterations of the modeled averages of stomach content and feces elemental contents per species. We calculated the absorption efficiency for each iteration using the following formula that uses ash content as a proxy for the unassimable part of the gut content (in % of dry mass) (Montgomery 1980):

$$a_k = 1 - \left(\frac{ash_{food}}{ash_{feces}} \frac{mu_{feces,k}}{mu_{food,k}}\right) \quad (2)$$

For each parameter above, we then calculated the mean, standard deviation, and 95% and 50% credible intervals. Even though a proportion of the total P is likely to be a part of ash and may be absorbed by the gut wall, these values are so low in comparison with the high ash contents so this bias has negligible impact on the calculation.

Probability of coprophagy

To assess the relationship between the probability of being a coprophage and the N and P content in diet (*D*), we fitted Bayesian binomial models:

$$y_{cop,k} \sim Bernoulli(eta_k),$$

$$logit(eta) = b0 + b1D_k, \quad (3)$$

where *k* is the nutrient (N or P), *eta* is the expected probability of being a coprophage, *b0* is the intercept, *b1* is the slope, and y_{cop} is the probability of being a coprophage. We fitted similar models to relate the probability of feces consumption with the nutrient content of feces. We then use these models to predict the probability of each species being a coprophage, as well as the probability of feces consumption for all 51 species. From the model predictions, we report the species that are likely to partake in coprophagy (based on a threshold of 0.5) and the species that are likely to have its feces eaten by other fishes (based on a threshold of 0.5).

Regression with absorption efficiency

Finally, we tested (1) whether the absorption efficiency differs across C, N, and P and (2) whether the elemental content of the stomach contents (*D*) and intestinal surface area can predict absorption efficiency (*a*). The species-level intestinal surface area, extracted from Ghilardi et al.

(2020), and the median biomass per species were used to calculate the biomass-corrected intestinal surface area per species. We first fit a Bayesian model using *brms* to estimate the average absorption efficiency per element by including species as a random effect and element (C, N, and P) as a dependent variable with uninformative priors (Burkner 2017).

We then fit the following Bayesian model using the R package *brms* with uninformative priors (Burkner 2017):

$$a_k \sim student(mu_k, sd_k, nu_k),$$

$$mu_k = b0_k + b1_k D_k + b2_k log\left(\frac{intestinesurface}{weight}\right), (4)$$

where k is the element (C, N, or P), $b0$ is the intercept, $b1$ is the slope of the diet elemental content (D_k), $b2$ is the slope of the natural log-transformed intestinal surface area per fish body weight, mu is the expected value, and nu is the degrees of freedom parameter. To incorporate the uncertainty of absorption efficiencies, a_k represents the average estimates for each species and sd is a vector of standard deviations per species. Similarly, the uncertainty around the species-level estimate of D_k is incorporated by handling D_k as a parameter with a strong prior inside the model (i.e. $D_k \sim$normal(D_{k_mean}, D_{k_sd})) (Stan User's Guide Version 2.30). Incorporating uncertainties around the absorption efficiency and diet content nutrient% means that more confident estimates have a higher impact on the model fit.

Bioenergetic modeling

We ran bioenergetic models for each species at their median measured body size to predict the N and P fluxes in excretion and egestion using the R package *fishflux* (Schiettekatte et al. (2020)).

These models were parametrized with the elemental concentrations of stomach contents and absorption efficiencies estimated in the present study. We replaced negative and extremely low (<0.1) absorption efficiencies with the predicted values from the predictive regression model mentioned above (Equation 4). For all other parameters, we used values from the literature (Schiettekatte et al. (2022)). We then calculated the ratios between egestion and excretion for N and P and the N:P ratio (i.e. release ratios).

Finally, in order to exemplify the potential contribution of egestion at community level, we estimated P fluxes for the fish assemblages of the outer slope of Mo'orea. We chose to provide a case study for P because the absorption efficiency of P tends to be the lowest across species and it is an important limiting nutrient in coral reefs. We used visual census data from 2009 to 2016 for 13 sites, recorded as a part of the CRIOBE long-term monitoring program. During each census, a single diver swam along a 25 m transect and counted all fishes within a 2 m belt. All fishes were identified to the species level, and their length was estimated to the nearest 1 cm. Each transect covered an area of 50 m^2, except 2 sites which covered an area of 100 m^2 each. A total of 235 species were observed across years and sites. For each individual in the community, we ran the bioenergetic model and predicted P fluxes in consumption, excretion, and egestion. To do so, we used parameters provided by Schiettekatte et al. (2022) and replaced diet CNP concentrations and absorption efficiencies with values estimated in this study. The 51 species included in this study represented 70% of the total fish biomass. For the remaining uncommon species (n = 184), we used the median diet CNP content and absorption efficiency per trophic guild. After running the bioenergetic models, we summed individual estimates of P consumption, excretion, and egestion to approximate the total fluxes per trophic guild per square

meter. Furthermore, for the 51 species included in our study, we predicted the probability of feces consumption based on the P% content in the feces using the previously fitted model (Equation 3). For the remaining, rarer species in the community, we used the median probability of feces consumption per trophic guild. We interpret the estimated probability of feces consumption as the proportion of the feces that would be consumed. To be conservative, we did not consider species that had predicted probabilities of feces consumption lower than 0.5. We then estimated the amount of P from egestion that is consumed by any coprophagous fishes by multiplying the predicted probability of consumed feces by half the daily egestion rates. This calculation rests on the assumption that fishes release half of their daily egestion while close to the reef. Since the metabolism and digestion of fishes is higher when they are active, these estimates of coprophagy are conservative. Finally, we averaged values across all sites and years and standardized the excretion and egestion rates of each trophic group by the total amount of P consumed by all fishes

Results

Elemental stoichiometry of stomach contents and feces

Species-level elemental composition estimates from fish stomach contents varied remarkably across species (Figure 1, Appendix S1: Figure S2, Table S3). The C content of stomach contents varied 4.5-fold from 10.0% for *Acanthurus pyroferus* to 45.5 % for *Myripristis berndti*, and the C content of fish feces varied 2.7-fold from 15.5 % for *Acanthurus pyroferus* to 41.5% for *Chromis xanthura*. The N content of stomach contents varied 12.9-fold from 0.9% for *Acanthurus pyroferus* to 11.5 % for *Aulostomus chinensis*, and the N content of fish feces varied 8.2-fold from 1.1 % for *Acanthurus olivaceus* to 9.0% for *Forcipiger flavissimus*. The P content of stomach contents varied 27-fold from 0.1% for *Ctenochaetus striatus* to 2.7 % for *Cephalopholis urodeta*, and the P content of fish feces varied 10-fold from 0.2 % for *Ctenochaetus striatus* to 2.0% for *Chromis xanthura*. We found a remarkably low difference between stomach content and feces compositions for many species (Figure 1). For C and P, the feces composition is rarely lower than half of the stomach content. For N, 14 species have a feces composition that is lower than half compared to the stomach content. Carnivorous fishes tend to have the highest P% in stomach content and feces.

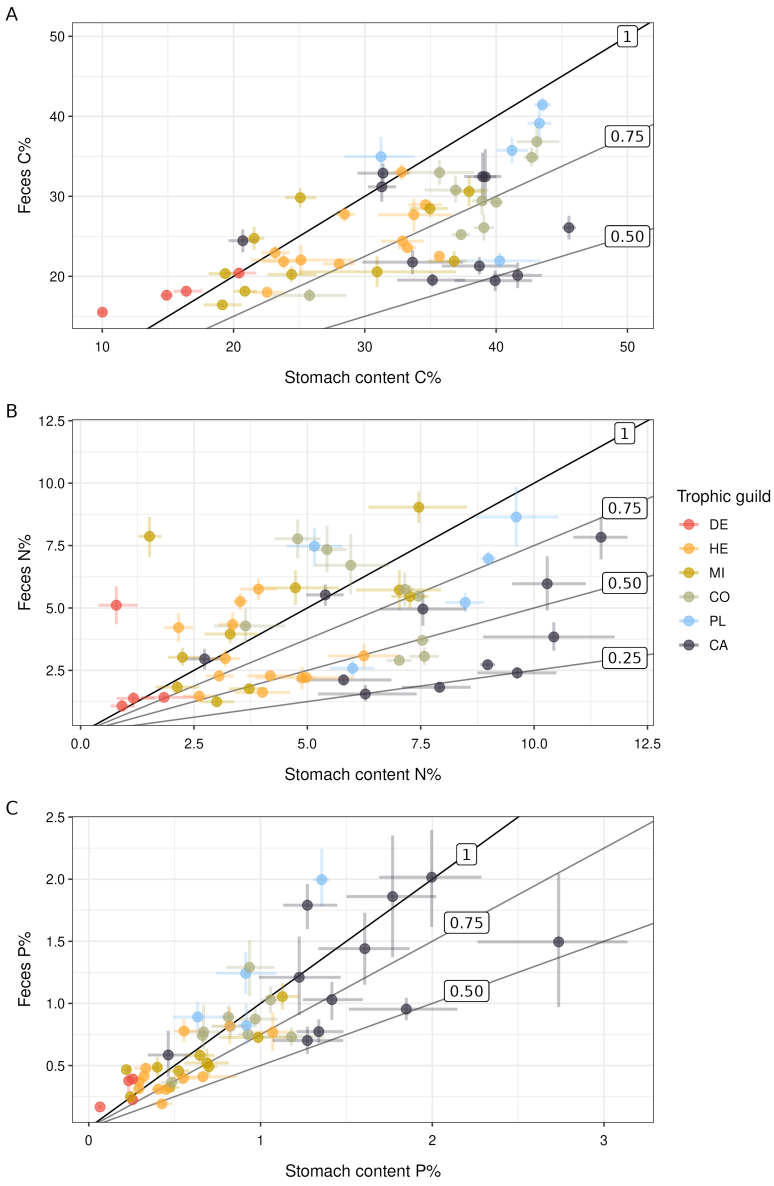

Figure 1. The estimated average (A) carbon, (B) nitrogen, and (C) phosphorus contents of stomach contents and feces from each study species. Errorbars indicate the 50% credible intervals. Lines indicate the ratio of the elemental content of the stomach contents and feces. DE = detritivores, HE = herbivores, MI = mixed invertivores, CO = corallivores, PL = planktivores, CA = carnivores.

Comparing the percentage of N and P from stomach contents and feces across all species, we find that fish feces from higher trophic levels often have a higher N or P content compared to the stomach content of fishes of lower trophic levels (Figure 2A,B; Appendix S1: Figure S3). For example, detritivorous and herbivorous fishes ingest food with a much lower nutrient concentration compared to the feces of other trophic groups. For N, corallivorous and planktivorous fishes have a higher N content in their feces compared to the diet of lower trophic groups. Planktivores and carnivores have the most P-rich feces. For 677 pairwise comparisons (26.6%), the stomach content N% is lower than the feces N%, and for 915 pairwise comparisons (35.9%), the stomach content P% is lower than the feces P% (with credible intervals of 75%). Further, by coupling our compositional data with observational data in the literature (Robertson 1982), we find that the probability of being a coprophage can be predicted by the N% or P% found in the stomach content. Thus, the lower the nutrient content in the diet, the higher the chance of being coprophagous (Figure 3C,D). The effects of nutrient content in the diet from the binomial regressions are -5.86 (-15.49 - -1.18 95%CI) and -8.63 (-17.90 - -2.51 95%CI) for N and P, respectively. Based on these relationships, we estimate that 28 out of our 51 study species (54.9%) could be coprophagous (based on a probability higher than 50%). Furthermore, the probability of feces consumption by coprophagous fishes can be predicted by N% or P% in the feces (Figure 3E,F). The slopes of the beta regressions are 1.54 (1.29 - 1.78 95% CI) and 2.61 (2.07 - 3.17 95% CI) for N and P, respectively. We estimate that 40 of our 51 study species (78.4%) produce nutrient-rich feces that have a higher than 50% probability to serve as a food source for other fishes.

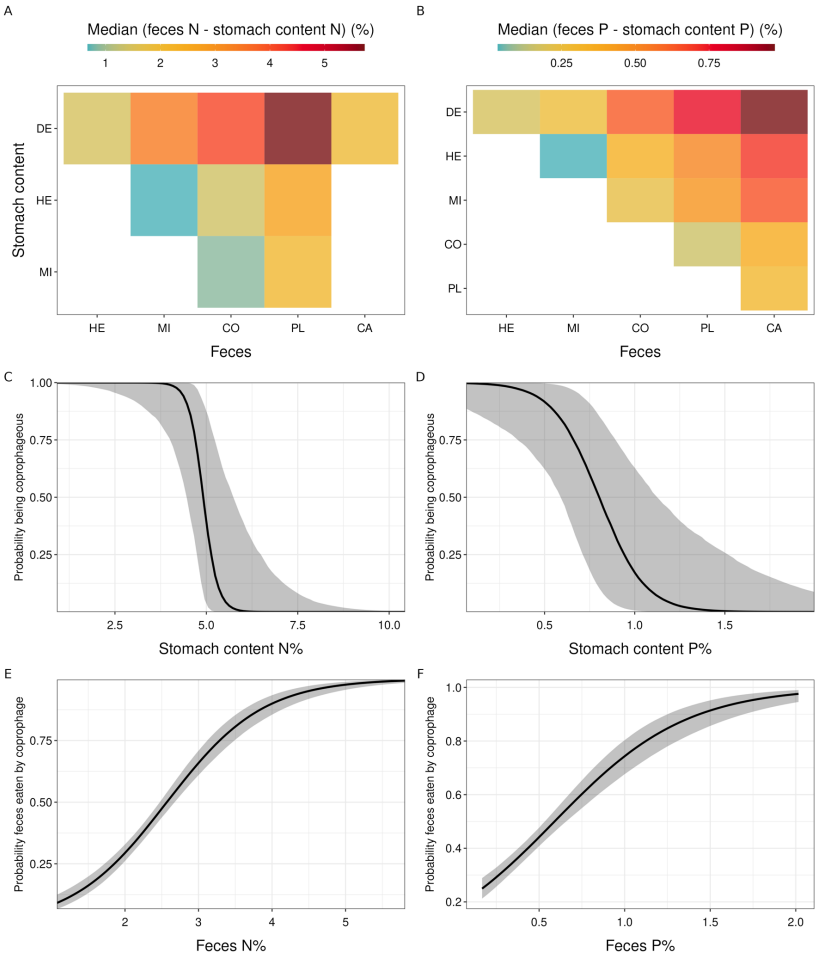

Figure 2. (A,B) Heatplots illustrating pairs of trophic guilds where the N% or P% of feces in one trophic guild is higher than the stomach content of another trophic guild. The color scale represents the median difference between the feces and stomach content per pair of trophic guilds. Only differences higher than zero (i.e., where feces nutrient % of a trophic group is higher than the stomach content nutrient % of another group) are shown. DE = detritivores, HE = herbivores, IN = invertivores, CO = corallivores, PL = planktivores, CA = carnivores. (C,D) Fitted probabilities of being coprophagous based on stomach content N and P composition. (E,F) Fitted probabilities of feces consumption based on fecal N and P composition.

Absorption efficiencies

We estimated element-specific absorption efficiencies for all species by combining our composition data with ash content data to account for total absorption per element (Appendix S1: Table S4). We first estimated the average absorption efficiency per element. N absorption efficiency tends to be the highest (average: 0.53; 95% CI: 0.46- 0.60), followed by C absorption efficiency (0.44; 0.37-0.51) and P absorption efficiency (0.40; 0.32-0.47). For each element, we then explored the relationship between absorption efficiencies and stomach content and relative intestine surface area (Figure 3). We found that absorption efficiency increases with stomach content for C (average slope: 0.013; 95% CI: 0.004-0.046), N (0.076; 0.052-0.10), and P (0.429; 0.249-0.626). Biomass-corrected intestine surface area also has a positive effect on absorption efficiency for N (0.078; 0.041-0.122) and P (0.089; 0.016-0.169), but not for C (0.008; -0.061-0.099).

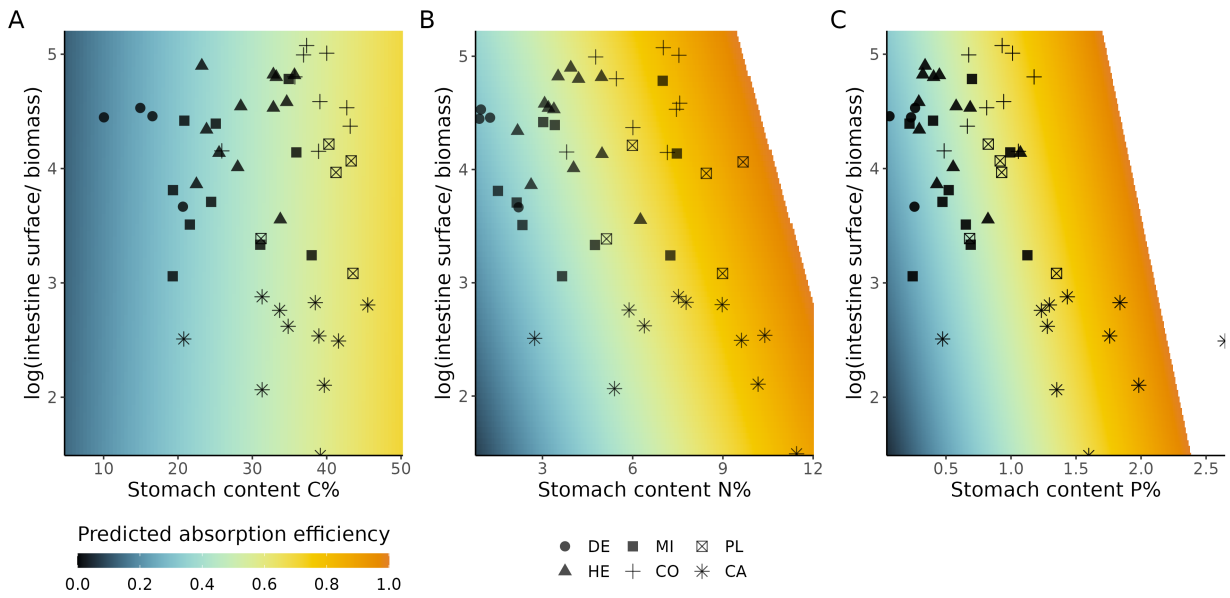

Figure 3. Fitted absorption efficiencies across trophic guilds across ranges of elemental contents of the stomach contents and intestinal surface area for carbon (A), nitrogen (B), and phosphorus (C). Color gradient indicates the predicted absorption efficiency for each element. Points show the fish species. The median biomass and intestine surface area were used to calculate the biomass corrected intestine surface area per species (as reported in Ghilardi et al. 2020).

Egestion rates

Using the estimated stomach content elemental composition and absorption efficiencies , we applied bioenergetic models for 51 species at their median size, and estimated the daily N and P fluxes for excretion and egestion. We then calculated the log release ratios (egestion/excretion) for N, P, and the N:P ratio. A positive release ratio indicates that N, P, or the N:P ratio is higher in egestion compared to excretion. With the exception of *Chaetodon citrinellus*, *Epibulus insidiator*, *Chromis xanthura*, and *Epinephelus merra*, the log release ratio was consistently higher than zero for P, indicating that there is more P flux through egestion than through excretion. For N, there was more N flux in egestion compared to excretion for 29 species. The trophic groups for which N excretion estimates exceeded egestion estimates were mostly carnivorous and corallivorous species (Figure 4). Consequently, the N:P ratio of excretion tended to be higher than the N:P ratio of egestion for most species (43 species).

For the case study on P fluxes at the community level for the outer reefs around Mo'orea (Figure 5), 65.3% of total consumed P is released in egestion compared to 13.5% released in excretion. This can be explained by the high density of detritivores and herbivores on reefs around Mo'orea, which egest 37.4% of the total consumed P, although their feces have low concentrations of P.

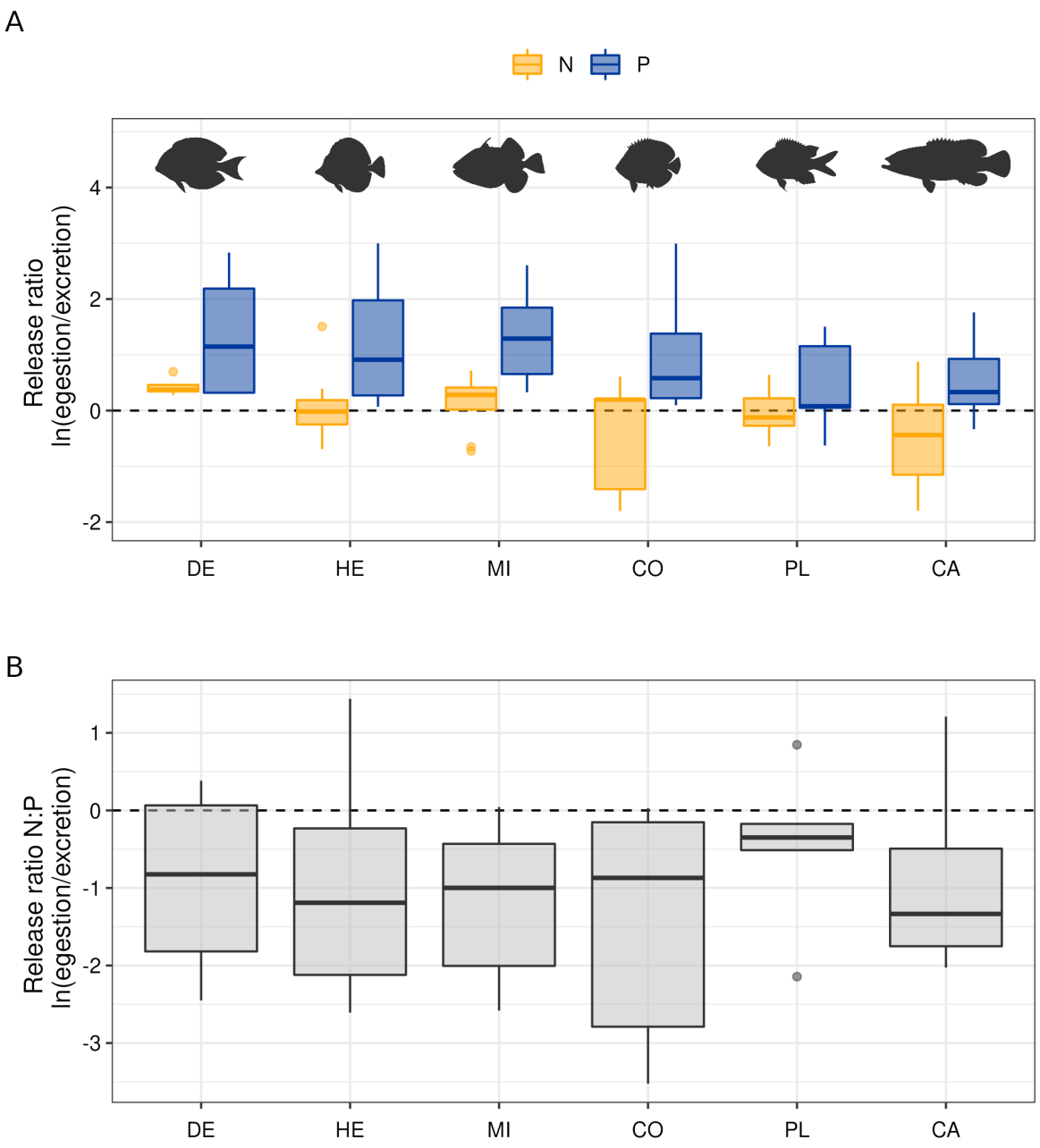

Figure 4. Release ratios (i.e., natural log-transformation of egestion divided by excretion) for (A) N and P and (B) the N:P ratio per trophic guild. DE = detritivores, HE = herbivores, MI = mixed invertivores, CO = corallivores, PL = planktivores, CA = carnivores.

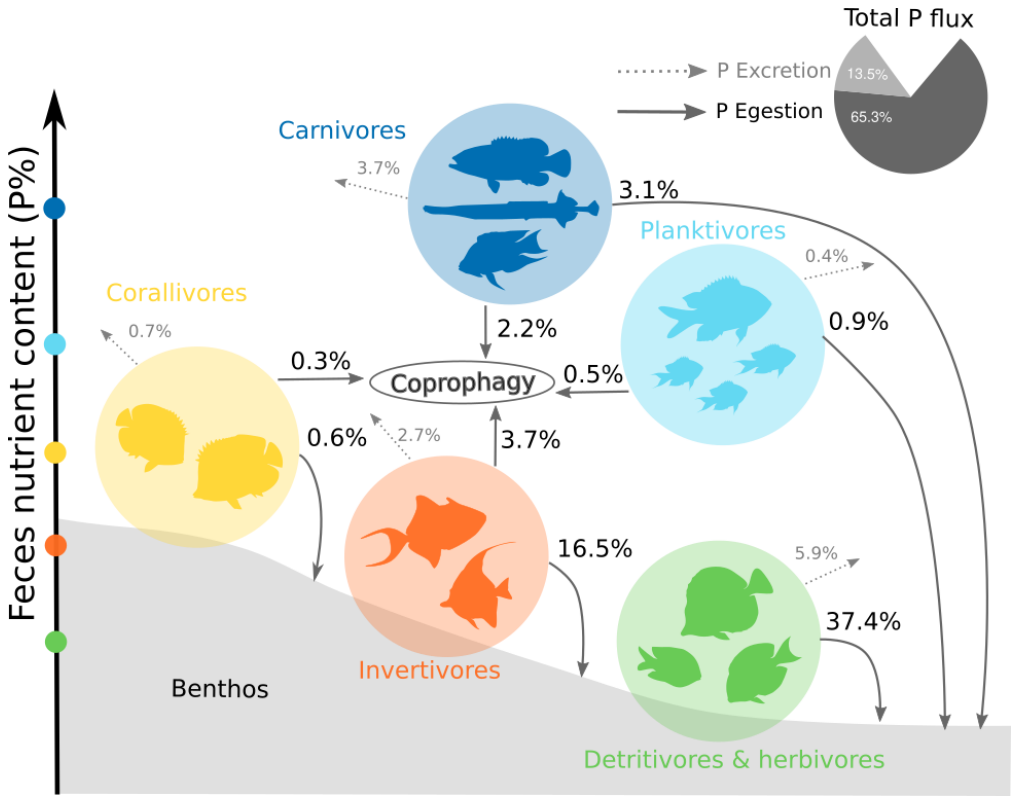

Figure 5. Phosphorus (P) fluxes in egestion and excretion across trophic groups in Mo'orea. Egestion flows to the benthos or coprophages. Feces consumption rates were determined by multiplying egestion rates of individual fishes by the predicted probability of feces consumption. All P fluxes are standardized by dividing each amount by the total amount of P consumed by the entire fish community on a daily basis. The 'missing' piece in the pie graph represents the proportion of P allocated to production.

Discussion

Across a wide range of coral reef fishes in 15 families, we show that elemental concentrations decrease remarkably little from stomach contents to feces. This is likely due to low absorption efficiencies, resulting in considerable amounts of energy and nutrients being egested. While it is commonly assumed that excretion is the primary source of animal-mediated nutrient fluxes in aquatic ecosystems, our results suggest that most coral reef fishes egest more N and P than they excrete, shedding light on the important role of egestion for nutrient cycling on coral reefs. Further, the quality and quantity of fish egesta varies greatly depending on trophic guild. Our study highlights the need for incorporating animal egestion alongside excretion in assessments of ecosystem functioning and food web structure (Atkinson et al. 2017, Halvorson et al. 2017b, Halvorson and Atkinson 2019).

We provide the first estimates of carbon (C), nitrogen (N), and phosphorus (P) concentrations of fish feces for 51 coral reef fish species in Moorea. Only two previous studies have analyzed the composition of coral reef fish feces across multiple species. Palau, Bailey and Robertson (1982) found an average N concentration of 1.52% for *Zebrasoma scopas*, which is slightly lower but within the credible range of our average (2.21 %). *Z. scopas* feed primarily on red algae, which can vary 4-fold in N concentration (Montgomery 1980). Similarly, Crossman et al. (2005) reported relatively low N concentrations in the feces of *A. lineatus* (1.44%) and *A. olivaceus* (0.34%) in the northern Great Barrier Reef as compared to our study (2.97% and 2.98%, respectively). The values reported in both studies are based on proteins or amino acids (Bailey and Robertson 1982, Crossman et al. 2005), and we converted these protein concentrations to total N using the standard conversion factor of 1:6.25 (N:protein). However, algae can have high

and variable concentrations of non-protein nitrogen substances, so the conversion we made from protein estimates by Bailey and Robertson (1982) and Montgomery (1980) are likely to underestimate the total N concentration (Lourenço et al. 2002). Thus, our estimated values align with the limited data available from previous studies.

We found remarkably low and variable reductions in elemental concentrations between stomach contents and feces and low absorption efficiencies across species. As expected, N absorption efficiencies are higher than C and P since N-rich protein is more digestible than other C-rich compounds such as carbohydrates and lipids (Montgomery 1980, Pandian and Marian 1985, Crossman et al. 2005). Further, absorption efficiency increases with the nutient concentrations of the food. This positive relationship exists in other animals (e.g., Jochum et al. 2017), and it has been suggested for total absorption efficiencies in fishes (Pandian and Marian 1985). This means that fishes with a high-N diet assimilate N more efficiently than those with an N-poor diet, and consequently, the maintenance of fish homeostasis must occur through the release of already assimilated nutrients (i.e., excretion). Furthermore, the positive effect of intestine surface area on N and P absorption suggests that intestinal surface area is an evolutionary strategy to increase the absorption of limiting elements (Ghilardi et al. 2021).

Absorption efficiencies varied across trophic guilds. Carnivorous fishes have the highest absorption efficiencies, which is likely because animal material is easier to digest than plant material and more nutrient-rich (Kozlovsky 1968, Pandian and Marian 1985). However, one exception was the carnivore *Cheilinus chlorurus*. This species feeds primarily on hermit crabs around Mo'orea (Casey et al. 2019), so the high proportion of $CaCO_3$ from shells in its diet may explain the low N and P percentages in their stomach. For corallivores, which had the second

highest absorption efficiency, this could be driven by their N-rich diet and their long intestines (Berumen et al. 2011, Ghilardi et al. 2021). In addition, the highly specialized feeding niche of many coral-feeding chaetodontids (Berumen and Pratchett 2008) may have boosted their nutrient absorption efficiencies since the digestive organs and gut microbiomes of specialized feeders are well adapted to specific prey items. In contrast to corallivores, planktivorous fishes exhibit fairly low absorption efficiencies despite having N-rich diets. Their feeding behaviour, which capitalizes on abundant zooplankton at incoming tides, along with a high food intake, may satisfy their daily needs even with low absorption efficiencies (Hamner et al. 1988). As expected, detritivorous and herbivorous fishes had generally low absorption efficiencies, but within herbivores, absorption efficiencies were remarkably variable. Absorption efficiencies for herbivorous coral reef fishes have been reported to range between 17.4% and 97.2% for protein and 5.3% and 80.2% for lipids and carbohydrates (Crossman et al. 2005). Herbivorous fishes have specialized digestive strategies linked with differences in diet, even though they are often designated as a single trophic category (Brandl et al. 2015; Crossman et al. 2005). Our results suggest that these differences are reflected in their digestive dynamics as well. In addition, especially for herbivores, the fish gut microbiome may play a large role in digestion and resulting absorption efficiencies (Miyake et al. 2015). Overall, our results emphasize the high variability of absorption efficiencies among but also within trophic groups.

Notably, we found several negative absorption efficiencies, mostly for N and P. Specifically, 6%, 25%, and 20% of our 51 study species had negative estimated absorption efficiencies for C, N, and P, respectively. For some detritivorous acanthurids (e.g., *Ctenochaetus striatus*), negative absorption efficiencies can be explained by their gizzard-like stomach in which they retain

inorganic material to grind down dietary food particles (Crossman et al. 2005; Horn 1989). The presence of inorganic material probably resulted in an underestimation of food quality, thus yielding negative assimilation efficiencies. For these species, it may be better to sample putative food sources from the environment rather than stomach contents. For other taxa, explanations are less straightforward. The higher P in the feces of some planktivores compared to their stomach contents could be caused by a high density of bacteria with low C:N:P stoichiometry, a high proportion of indigestible invertebrate exoskeleton (chitin) in their planktonic prey, or selective absorption of C and N-containing compounds (Geesey et al. 1984). Planktivores could also occasionally supplement their diet with P-rich food items such as fish feces (Pinnegar and Polunin 2006; Rempel et al 2022). Another possible explanation would be that after death, some cells of the fish gut degrade quickly adding body nutrients to feces sample even if fishes were kept cool and were dissected within hours after death. Finally, some negative absorption efficiencies may result from low sample sizes of both nutrient and ash contents. Most species for which we found negative absorption efficiencies had a sample size lower than ten and sample sizes were low for ash content for most species We suggest future studies should aim for a higher sample size. Overall, species that consistently feed on a single taxonomic group (e.g., piscivorous groupers) had less variable food stoichiometry and may thus require less replicates (e.g., *Cephalopholis argus*). Conversely, species that ingest a wide range of taxa (e.g., some herbivorous fishes, planktivores, and omnivores) may require a higher number of replicates to obtain reliable estimate of assimilation efficiencies.

The low absorption efficiencies of fishes with nutrient-poor diets necessitate an increased feeding rate or diversification of their diet to obtain sufficient N and P for growth and

homeostasis. For example, herbivores feed on nutrient-poor algae, thus displaying a large mismatch between the food elemental concentrations and the ideal elemental composition needed for maintenance and growth (Schiettekatte et al. 2020). While these fishes increase the absorption efficiency of limiting elements to ameliorate their existing nutrient imbalances (Sterner and George 2000), low absorption efficiencies remain common in these species. Except for a single study on herbivorous terrestrial invertebrates, which compensated for a limiting element by altering absorption efficiency (Clissold et al. 2010), feeding on nutrient-rich resources is a common approach to make up for low-nutrient diets across many taxa. Indeed, this feeding strategy has been demonstrated in freshwater invertebrates (Evans-White and Halvorson 2017), insects (Jochum et al. 2017), snail grazers (Liess 2014), and marine amphipods (Cruz-Rivera and Hay 2000). On coral reefs, nutrient-rich feces of nominally carnivorous, planktivorous, and corallivorous fish species provide an ideal additional food source for species that typically feed on nutrient-poor foods such as algae or detritus. Aside from providing a valuable source of nutrition, coprophagy has the additional benefit of increased availability and accessibility to the consumer in most fish communities.

Our results highlight the role of fish egestion for system-wide nutrient cycling. A logical consequence of low absorption efficiencies is that nutrients may be released more abundantly through egestion instead of excretion, especially for P, resulting in feces with low N:P ratios. Similar findings have been reported for marine invertebrates (Halvorson and Atkinson 2019) and terrestrial vertebrates, in which urine contains little P but a high concentration of N, while feces contain most of the P (Sitters et al. 2017). Consumption of P-rich feces is common among coral reef fishes, and some prey (e.g. plankton) may pass through three fish stomachs before reaching

the benthos (Rempel et al 2022; Robertson 1982). Similarly, feces that are not consumed in the water column are probably consumed by invertebrates in reef crevices (Pinnegar and Polunin 2006), thus fueling another sector of the coral reef food web. In contrast, nutrient poor feces from herbivores or detritivores are rarely consumed directly; rather, they are decomposed by microbial communities (Halvorson et al. 2017b). Depending on the N:P ratio, these feces may exhibit an uptake of dissolved N or P, suggesting that decomposing feces can serve as a nutrient sink (Halvorson et al. 2017b). Overall, very little is known about the diverse fates of fish feces in coral reef ecosystems, and future research should address the various pathways by which fish feces affect nutrient cycling and ecosystem functioning.

To understand the interaction strengths in food webs, we need to estimate the amount of elements and energy flowing through each interaction, which necessitates a quantification of consumption rates. Some studies have attempted to recreate complex food webs for coral reef fishes (e.g., Bascompte et al. 2005; Casey et al. 2019; Pozas-Schacre et al 2021), but food web models do not take variation of absorption efficiencies into account, which may introduce substantial bias. Further, coprophagic links are not explicitly included in food web models, even though they may represent an important food source (Rempel et al. 2022; Robertson 1982). For example, *Naso vlamingii* consumes up to 200 planktivore fecal pellets per hour during periods of high feeding activity (Robertson 1982), suggesting that coprophageous links play a substantial role in energy and nutrient transfers. While we predicted that more than half of our study species could notably contribute to the diet of other fishes through their nutritious feces, these estimates should be further validated through observational studies on fish behavior (e.g., Rempel et al. 2022 ; Robertson 1982). Bioenergetic models represent a useful tool to estimate multiple

individual-level pathways of elements, and absorption efficiencies are important parameters to include (Schiettekatte et al. 2020). Due to a lack of data, it is common to use constants from the literature (e.g., 0.8 for N and C absorption efficiency, and 0.7 for P absorption efficiency) rather than values measured in the field (Allgeier et al. 2015; Kraft 1992; Schiettekatte et al. 2020; Schiettekatte et al. 2022; Schindler and Eby 1997). Our results illustrate that these values are not adequate approximations for coral reef fishes, which exhibit remarkable variability in their absorption efficiencies. In fact, of the 51 species included in our study, these constant values are only accurate for 1 species for C absorption efficiency, 10 species for N absorption efficiency, and 10 species for P absorption efficiency. Collecting and curating physiological data across species and locations will greatly enhance the parameterization of ecosystem models and our understanding of these complex systems. Future studies combining in-depth field observations on feeding, defecation, and coprophagic behavior and mesocosm experiments with realistic food items will improve estimates of absorption efficiencies.

Data on feces quality and quantity can be used to investigate pathways by which human impact may disrupt coral reef ecosystem functioning. Fishing selectively targets large fishes that occupy high trophic levels (Graham et al. 2017). The local depletion of large predators or planktivores not only affects prey populations and decreases excretion (Allgeier et al. 2016), but it potentially removes an important food source for coprophagous fishes. Likewise, communities that are dominated by detritivores and herbivores, which is the case on reefs around Mo'orea (Munsterman et al. 2021), have a high incidence of nutrient-poor egestion. Finally, coral loss and reduced structural complexity cause declines of planktivores, large carnivores, and corallivores (Brandl et al. 2016; Darling and D'agata 2017; Graham and McClanahan 2013) , and this may

lead to decreased nutritional quality of feces in fish communities. As such, system wide elemental fluxes can change on reefs with shifting fish assemblages, with unknown consequences for ecosystem processes. Our findings highlight the critical role of fish feces as a nutrient vector. Further research that quantifies the quality and fate of these feces is necessary to delineate how changes in community structure affect ecosystem functioning through trophic interactions, nutrient translocation, and microbial activity.

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