

RESEARCH ARTICLE

Functional Ecology



Predicting the effects of body size, temperature and diet on animal feeding rates

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Abstract

1. Consumption rates constitute a fundamental, yet relatively elusive quantity in ecophysiology and ecosystem ecology. Measuring consumption rates of highly mobile animals is often challenging, especially in the wild, which makes scientists rely on proxies such as bite rates. However, we still lack a theoretical framework that formally bridges these quantities.
2. Here we expanded a model based on the Metabolic Theory of Ecology to quantitatively characterise how consumption rates are related to bite rates, and predict how the latter should change with body size, temperature and diet. We test our predictions using mensurative experiments from eight populations of redlip blennies—genus *Ophioblennius*—across the Atlantic Ocean.
3. Bite rates scaled with body size according to our theoretical predictions. On the other hand, they increased at a faster-than-predicted rate with rising temperatures. This finding might be explained if the energetic content of *Ophioblennius* spp. diet—which is primarily composed by detritus across all populations—decreases with temperature. Yet, they seem to be consistent with the idea that populations adapted to warmer environments exhibit higher-than-expected grazing pressure on primary producers.
4. Current ocean warming is set to skew body size distributions towards smaller sizes, and our model indicates that the combined effects of smaller sizes and higher temperatures will increase mass-specific consumption rates, with direct implications for how energy flows through food webs.

KEYWORDS

bite rates, body size, consumption rates, diet, nutrients, reef fish, temperature

1 | INTRODUCTION

The amount of energy and nutrients consumed by individuals in order to grow, maintain bodily functions and reproduce constitutes an

important ecological function in natural ecosystems. Consumption rates thus constitute a centrepiece in the pursuit to link individual function to ecological processes at higher levels of organisation.

In food webs, consumption rates of organisms can control myriads of ecological processes, from net primary production (e.g. via biomass removal of primary producers and selected grazing by

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herbivores) to the recycling of energy and nutrients (e.g. by defecation of heterotrophic consumers; Estes et al., 2011; Hata & Kato, 2002; Roman & McCarthy, 2010; Schiattkatte et al., 2019; Taylor et al., 2006; Vanni, 2002). However, measuring consumption rates is often challenging—particularly in the wild (Garvey & Whiles, 2016). For slow-moving organisms, such as sea-urchins, consumption rates can be measured directly using standard methods (e.g. Carr et al., 2018). On the other hand, for highly mobile organisms, such as fishes, individuals need to be observed exhaustively to determine their feeding period, and later sacrificed analyse their gut content (e.g. Ferreira, Peret, et al., 1998; Garvey & Whiles, 2016; Wootton, 1997). Therefore, consumption rates need to be quantified indirectly, for instance, via functional response curves (Pawar et al., 2012), or by counting bite rates (i.e. number of bites on the substratum per fixed unit time; Bonnet et al., 2015; Ferreira, Peret, et al., 1998). This latter quantity has been notoriously used in behavioural studies and serves as an empirical proxy to consumption rates because it is much simpler to be tallied (e.g. Barneche et al., 2009; Longo et al., 2019). However, we still lack a theoretical framework that formally bridges bite rates with consumption rates and, in doing so, sets quantitative predictions about how bite rates vary with biotic and abiotic variables. Such a framework would constitute a fundamental step towards predicting the role of individuals in food webs.

By virtue of being an energy-intake rate, bite rates are expected to scale with individual body mass (Barneche et al., 2009; Medeiros et al., 2014). For example, studies focusing on terrestrial mammals (Pelletier & Festa-Bianchet, 2004), marine iguanas (Wikelski & Carbone, 2004) and reef fishes (Barneche et al., 2009; Floeter et al., 2005; Medeiros et al., 2014) suggested that bite rates scale negatively with increasing body size. These are at odds with the size scaling of consumption rates, which are positive and can be either hypo- or hyper-allometric depending on the dimensions of the preying environment (Pawar et al., 2012). These apparent discrepancies may be reconciled by considering how the volume of bites scales with body size. Doing so would formally allow the direct quantitative conversion between the two rates.

Bite rates are also expected to vary with abiotic variables, chief among which is temperature (Brown et al., 2004; Dell et al., 2013; Ferreira, Gonçalves, et al., 1998; Garvey & Whiles, 2016; Mendes et al., 2009). Within the natural temperature regime experienced by organisms, bite rates increase exponentially with environmental temperature (Barneche et al., 2009; Dell et al., 2013), perhaps suggesting that their temperature dependence might be proportional, or even indistinguishable, to the temperature dependence of metabolic and growth rates (Barneche & Allen, 2018; Barneche et al., 2014; Brown et al., 2004; Gillooly et al., 2001, 2002). However, consumer species adapted to warmer temperature regimes can exhibit grazing rates that are higher than expected from simple acute-exposure temperature performance curves (Schaum et al., 2018); or lower than expected, due to acclimation to the local thermal and environmental regime (Carr et al., 2018; Marshall & McQuaid, 2010). Resolving the actual temperature dependence of

bite rates (and therefore of consumption rates) is crucial, for example, to improve our ability to predict both the direct and indirect feeding impacts on ecosystems, as well as the impacts of climate change on population and extinction dynamics (Savage et al., 2004; Vasseur & McCann, 2005).

In addition to body size and temperature, the nutritional quality or energy content of diet is expected to play a role in explaining consumption—and by extension, bite—rates (Hood et al., 2005; Otto & Svensson, 1981; Sala et al., 2012; Wilson et al., 2003). The energy content of primary producers and sessile invertebrates is expected to be lower than mobile invertebrates and vertebrate animals (Cummins & Wuycheck, 1971; Harmelin-Vivien, 2002). Studies indicate that consumption rates can be lower when the nutritional quality of food is higher because metabolic requirements will be fulfilled faster. For example, herbivorous/detritivorous insect larvae may eat less often when plants exhibit higher N content (Otto & Svensson, 1981). Moreover, populations of Magellanic penguins may invest less time diving and searching for food when the nutritional quality of their prey is higher (Sala et al., 2012). On the other hand, studies have demonstrated that herbivorous reef fish feed more intensely when photosynthate concentration is higher in algae (Zemke-White et al., 2002).

Detritivorous species are particularly important in the recycling of organic matter in both aquatic (Schaus et al., 1997; Taylor et al., 2006) and terrestrial ecosystems (Seastedt & Crossley, 1984). In coral reef fishes, the often-observed high consumption rates of nominally detritivores have been associated with the low energy content of organic detritus and other primary producers when compared to animal protein (Mendes et al., 2018; Wilson et al., 2003). For instance, abundant crypto-benthic fishes generate a fundamental link to the maintenance of ecosystem-wide biomass by ingesting large quantities of detritus (Depczynski et al., 2007; Wilson et al., 2003). This group is generally characterised by species of small body sizes and is particularly abundant in tropical reefs (Brandl et al., 2018). While those features alone are expected to yield high biomass consumption, production and turnover (Allen et al., 2005; Brandl et al., 2019; Brown et al., 2004; Savage et al., 2004), quantitatively characterising the roles of individual body size, environmental temperature and prey type on consumption rates of detritivorous fishes is paramount to assess and predict their ecosystem function at both local- and macro-ecological scales.

In this study, we first develop a theoretical framework to link the size scaling of both consumption rates and bite rates. We then derive quantitative hypotheses and predictions regarding the size scaling and temperature dependence of bite rates, which are empirically tested using data from Atlantic reef fishes from the genus *Ophioblennius* (Perciformes: Blenniidae; Figure 1). We complement our discussions with laboratory diet analyses which accessed differences in diet composition across *Ophioblennius* populations. This is an ideal group to test our predictions because they encompass two orders of magnitude in body size (ranging between 0.6 and 84 g in our data), inhabit reefs spanning a water temperature gradient of 12°C (from 18°C in south Brazil to 30°C in

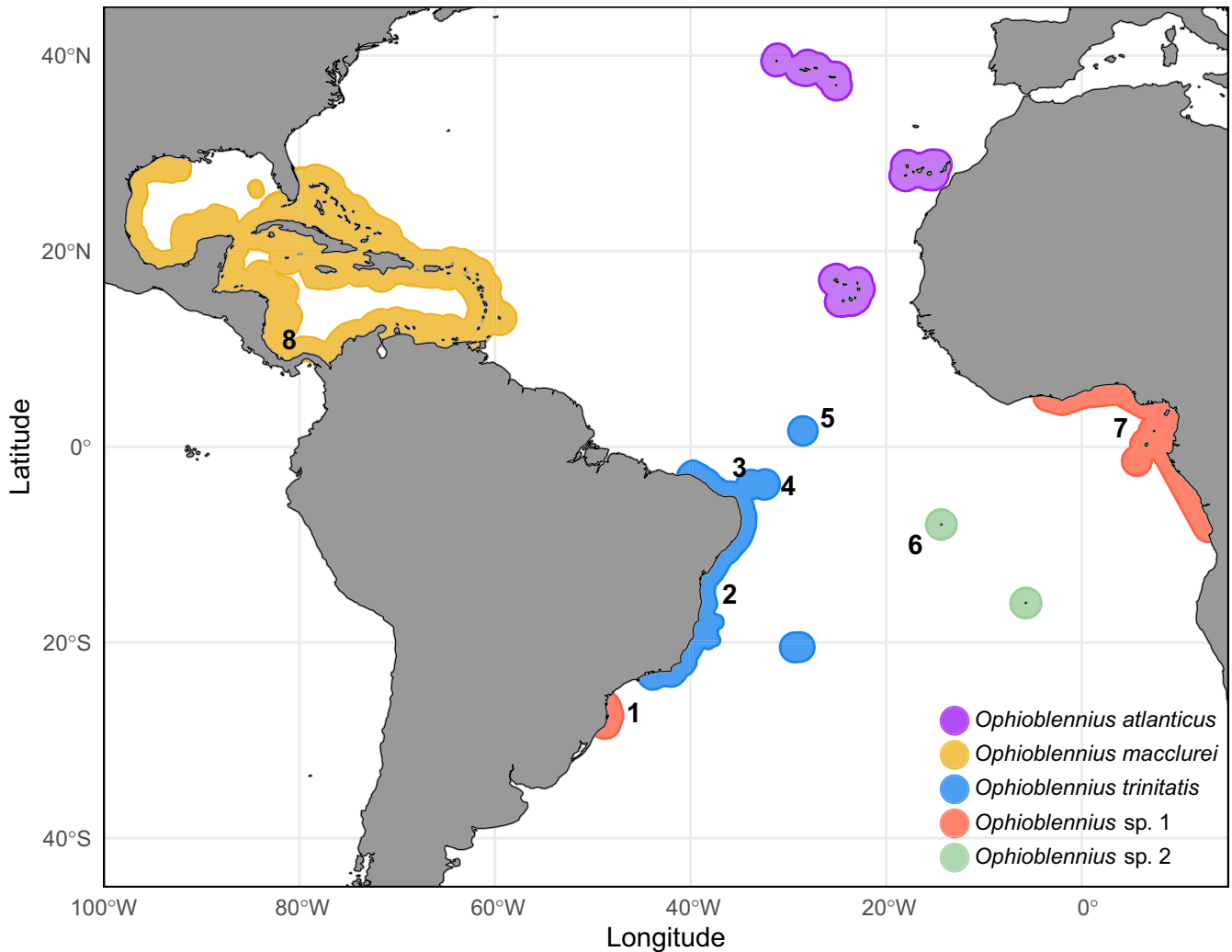


FIGURE 1 Distribution of five *Ophioblennius* species occurring in the Atlantic Ocean. 1: Santa Catarina State; 2: Salvador; 3: Rocas Atoll; 4: Fernando de Noronha; 5: St Peter and St Paul Archipelago (SPSPA); 6: Ascension Island; 7: Príncipe Island; 8: Bocas del Toro. See Table 1 for sampling details

equatorial oceanic islands). We conclude our study by discussing the potential implications of our findings in light of future ocean warming.

2 | MATERIALS AND METHODS

2.1 | Theory and hypotheses

2.1.1 | Hypothesis H1: Bite rates are expected to exhibit negative body size scaling with a power-law scaling exponent $-0.39 \leq \rho \leq -0.18$

Individual-level consumption rates, C_i (mm^3 of food minute^{-1}), like most physiological rates (Brown et al., 2004), are partly determined by the body size, M_i (grams), of the individual following a power function of the form:

$$C_i = c_0 M_i^\alpha, \quad (1)$$

where c_0 ($\text{mm}^3 \text{min}^{-1} \text{g}^{-\alpha}$) is a normalisation constant that is interpreted as the consumption rate of an individual whose body size is 1 g, and α is the dimensionless scaling exponent. Traditionally, bodies of theory such as the Metabolic Theory of Ecology (MTE; Brown et al., 2004) assumed that consumption rates exhibited the same size scaling of whole-organism metabolic rates. In such cases, α would take a value between 0.5 and 1, averaging at approximately 0.75 (Barneche et al., 2014). More recent developments have demonstrated that α can either be <1 (i.e. sublinear or hypo-allometric averaging at 0.85) or >1 (i.e. superlinear or hyper-allometric averaging at 1.06) if the individual forages, respectively, in two or three dimensions (Pawar et al., 2012).

Consumption rates can be directly determined by bite rates, F_i (bites per minute), if the average volume of the bite, V_i (mm^3/bite), is known:

$$C_i = F_i V_i, \quad (2)$$

We note that Equations 1 and 2 are developed in terms of food volume rather than energy; doing so implicitly assumes that the energy density

of ingested food (Joules/mm³) is constant throughout ontogeny. The volume of the bite is also expected to exhibit size scaling:

$$V_i = v_0 M_i^\delta, \quad (3)$$

where v_0 (mm⁻³ bite⁻¹ g^{-δ}) is a normalisation constant and δ is the dimensionless scaling exponent. Combining Equations 2 and 3 yields

$$F_i = f_0 M_i^\rho, \quad (4)$$

where $f_0 = c_0/v_0$ is the bite rate of an individual whose body size is 1 g, and $\rho = \alpha - \delta$. The scaling exponent of consumption rates of crypto-benthic detritivorous fishes is unknown. Based on Pawar et al. (2012), we could expect $\alpha \approx 0.85$ a priori because crypto-benthic fishes are expected to search for food on 2D surfaces. Although it is also possible that $\alpha \approx 1.06$ (or some other value in between) due to a number of factors not included in our simplified model. As we demonstrate in the Results section below, based on body size and mouth volume data, $\delta = 1.24$ on average, and, if we constrain $0.85 \leq \alpha \leq 1.06$ (Pawar et al., 2012), then our model predicts a mean scaling exponent, ρ , contained within the -0.39 to -0.18 interval. We note, however, that the model of Pawar et al. (2012) implicitly included the effect of bite-rate scaling, that is, it assumed that bite-rate size scaling is dimensionality independent. Our Equation 4 relaxes this assumption, and empirical evaluations of ρ will therefore serve as a benchmark against which deviations can be analysed to generate future directions and insights.

2.1.2 | Hypothesis H2: Bite rates are expected to exhibit the same temperature dependence of whole-organism metabolic rates with an activation energy $E_f \approx 0.6$ eV

Temperature is a fundamental driver of many physiological rates which determines myriads of ecological processes at higher levels of organisation, such as population growth, community biomass turnover and ecosystem carbon residency times (Allen et al., 2005; Barneche & Allen, 2018; Barneche et al., 2014; Brown et al., 2004; Savage et al., 2004). In general, physiological rates exhibit a positive exponential-like increase with increasing temperature within most of the natural range of temperatures experienced by an organism in the environment (i.e. below the optimum; Barneche & Allen, 2018; Barneche et al., 2014; Gillooly et al., 2001, 2002). Here we borrow MTE's model to empirically characterise such effects on bite rates as:

$$f_0 = f_0(T_c) e^{\frac{E_f}{k} \left(\frac{1}{T_c} - \frac{1}{T} \right)}, \quad (5)$$

where $f_0(T_c)$ is f_0 at an arbitrary standardising temperature T_c (Kelvin), E_f (electronvolts) is an 'activation energy'-like parameter that defines the rate of exponential increase, k is the Boltzmann constant (8.62×10^{-5} eV K⁻¹) and T is the environmental temperature (K). In fishes, the temperature dependence of metabolic rates is characterised by activation energies between 0.4 and 0.8 eV

(Barneche & Allen, 2018; Barneche et al., 2014; Brown et al., 2004). Previous theoretical work has demonstrated that the activation energies of consumer-resource interactions can be mechanistically predicted via ecological processes and are within the 0.4–0.8 eV range (Dell et al., 2013). Building on this finding, we therefore predict that $E_f \approx 0.6$ eV by assuming that bite rates will exhibit the same temperature dependence of metabolic rates.

2.2 | Testing hypotheses

2.2.1 | Hypotheses H1 and H2

The *Ophioblennius* genus encompasses seven crypto-benthic reef fish species (two of which are yet to be formally described), five of which occur in the Atlantic Ocean (Lastrucci et al., 2018; Muss et al., 2001). The genus is distributed across all tropical and subtropical Atlantic marine provinces, and each of the five species is endemic to a single province, with the exception of one species found in both south-western Atlantic (SWA) and the Gulf of Guinea (Lastrucci et al., 2018). Species in this genus are an ideal model to study feeding activity because they inhabit shallow reefs, are easy to observe and follow continuously, and are distributed along a range of environmental temperatures and reef types (Medeiros et al., 2014; Nursall, 1977).

We estimated the bites rates of four *Ophioblennius* species in eight locations of the Atlantic Ocean encompassing both oceanic and coastal reefs. Sampling occurred during daylight by snorkelling in shallow reefs (between 3 and 6 m, see Table 1 for details) from 10:00 to 15:00. Separate sampling periods for summer and winter were conducted in Santa Catarina (south Brazil) because this was the only location that exhibited seasonality in the sea surface temperature, which ranged from 14 to 29°C (Faria-Junior & Lindner, 2019).

In each location, we employed the 'focal-animal' method (adapted from Lehner, 1996), which entailed following one *Ophioblennius* individual for 3 or 5 min (depending on the location) while tallying its total number of bites in the substratum. Multiple individuals were observed across locations (total $n = 304$). To avoid possible interference in the feeding activity, the observer waited 1 minute before each observation for the fish to become accustomed to their presence, and subsequently followed the individual at a minimum distance of 2 m. Each individual was only sampled once. A bite was tallied when the fish hit the substratum with its jaw open, regardless of further ingestion (Longo et al., 2019). Considering that *Ophioblennius* individuals feed by taking several bites in quick succession between pauses (i.e. the 'foray' mode), each bite was counted individually as opposed to considering bursts of quick bites as a single bite each.

In addition to the number of bites, we recorded the sea surface temperature (°C) during observations using a dive computer (Mares® Puck Pro model)—please see the Supporting Information for comparisons with satellite data. Also, we visually estimated the total length S_i (cm) of each fish individual to the nearest 1 cm to calculate its body mass (M_i) through well-established relationships of the form $M_i = aS_i^b$ (Froese & Pauly, 2019).

TABLE 1 Species of *Ophioblennius* and sampled locations

Species	Location	Latitude	Longitude	SST	Depth	Bite	Diet	Intestine	Mouth volume
<i>O. macclurei</i>	Bocas del Toro	9°18'38"N	82°11'41"W	29.0	1.0	15	—	—	—
<i>Ophioblennius</i> sp1.	Principe Island	1°41'29"N	7°26'29"E	29.0	1.5	50	3	3	—
<i>O. trinitatis</i>	SPSPA ^a	0°55'01"N	29°20'44"W	27.7	8.0	36	12	18	—
<i>O. trinitatis</i>	Rocas Atoll	3°51'37"S	33°49'07"W	29.6	0.5	48	9	30	4
<i>O. trinitatis</i>	Fernando de Noronha	3°50'20"S	32°25'0.8"W	28.5	1.5	43	—	—	6
<i>Ophioblennius</i> sp2.	Ascension Island	7°53'33"S	14°22'51"W	24.0	1.0	16	—	—	—
<i>O. trinitatis</i>	Salvador	13° 0'13"S	38°32'03"W	27.0	2.0	65	17	17	8
<i>Ophioblennius</i> sp1.	Santa Catarina	27°47'09"S	48°30'28"W	24.5	3.0	31	9	7	5

Abbreviations: Bite, number of individuals whose bite rates were observed; Depth, maximum depth (m) at which sampling was conducted; Diet, number of specimens collected for the diet analysis; Intestine, number of individuals whose intestines were measured; Mouth volume, number of individuals from which we measured mouth volume; SST, Mean sea surface temperature (°C) during sampling.

^aSt Peter and St Paul Archipelago.

We combined Equations 4 and 5 on the natural log scale, and adopted a Bayesian hierarchical model to test the effects of body size and temperature on bite rates at the individual level, i :

$$\ln F_i \sim \mathcal{N}(\mu_i, \sigma).$$

$$\mu_i = \Delta \ln f_o(T_c)_{L_i} + \ln f_o(T_c) + \rho \ln M_i + \frac{E_f}{k} \left(\frac{1}{T_c} - \frac{1}{T_i} \right) + \beta \ln Y_i \quad (6)$$

$$\Delta \ln f_o(T_c)_{L_i} = \vartheta \sigma_{\Delta \ln f_o(T_c)}$$

$$\ln f_o(T_c) \sim \mathcal{N}(0, 1); \rho \sim \mathcal{N}(0, 1); E_f \sim \mathcal{N}(0, 1)$$

$$\sim \mathcal{N}(0, 1); \vartheta \sim \mathcal{N}(0, 1); \sigma_{\Delta \ln f_o(T_c)} \sim \Gamma(2, 0.1); \sigma \sim \Gamma(2, 0.1)$$

where \mathcal{N} and Γ , respectively, represent the normal (mean and standard deviation) and gamma (location and shape) distributions, ϑ is the vector of standardised location-level, L_i , deviations from $\ln f_o(T_c)$, $\Delta \ln f_o(T_c)_{L_i}$ comprises the actual location-level deviations from $\ln f_o(T_c)$, and $\sigma_{\Delta \ln f_o(T_c)}$ is the among-location hyper standard deviation of $\Delta \ln f_o(T_c)_{L_i}$ (please see the online Supporting Information for a model selection of random effects). In this context, $\ln f_o(T_c)$ represents a mean across locations. We preferred to estimate $\sigma_{\Delta \ln f_o(T_c)}$ among locations ($n = 8$ levels) rather than species ($n = 4$ levels) because the former had more grouping levels, thus permitting a better characterisation of hierarchical variance. The parameter β was added to account for the effects of log-transformed observation time (minutes), $\ln Y_i$. The model was implemented using the package *brms* (Bürkner, 2018) in R (R Core Team, 2019) to determine posterior distributions and associated 95% credible intervals (CIs) for the fitted parameters. The posterior distributions of model parameters (Table S1) were estimated using Hamiltonian Monte Carlo (HMC) methods by constructing four chains of 5,000 draws each, with 2,500 warm-up draws, so a total of 10,000 draws were retained to estimate posterior distributions (i.e. $4 \times [5,000 - 2,500] = 10,000$). Model convergence was deemed as achieved when the Gelman–Rubin statistic, \hat{R} (Gelman &

Rubin, 1992), was 1. We used Bayesian R^2 to estimate the amount of explained variation of each model (Gelman et al., 2019). Posterior predictive checks are provided in the Supporting Information (Figure S1).

To estimate the size scaling exponent of bite volume, δ (Equation 3), we also measured the upper-bound bite size (i.e. mouth volume) of multiple *Ophioblennius* individuals ($n = 23$) which were independently collected from the individuals observed to tally bite rates (see collection methods under *Complementary diet composition analyses* below). We opened the mouth of each collected specimen and carefully filled them with modelling dough until they were completely full while ensuring that the dough did not invade the oesophagus. Each dough was placed between two thick coverslips and kneaded with a microscope slide to a height of 1 mm such that the number of 1 mm² grids occupied by the dough on the petri dish represented the mouth volume in mm³ (Nunes et al., 2019). We measured the total length (cm) of the individuals, and then transformed length to body mass following the above-mentioned length–weight relationship (Froese & Pauly, 2019). We then transformed Equation 3 to the natural log scale to estimate the effects of size on individual mouth volume, V_i , using a Bayesian linear model:

$$\ln V_i \sim \mathcal{N}(\mu_i, \sigma)$$

$$\mu_i = \ln v_o + \delta \ln M_i \quad (7)$$

$$\ln v_o \sim \mathcal{N}(0, 1); \delta \sim \mathcal{N}(0, 1); \sigma \sim \Gamma(2, 0.1)$$

No hierarchical effects were included because we only had data from two species and four locations which prevented us from reliably estimating a hyper-variance. Fitting specifications followed the same procedure as described above for Equation 6. See Figure S2 for posterior predictive checks.

2.2.2 | Hypotheses evaluation criteria

We evaluated hypotheses H1 and H2 based on the region of practical equivalence (ROPE) around the null value of each parameter of

interest (Kruschke, 2018). We accepted a hypothesis if a parameter's posterior 95% highest density interval (hereafter 95% HDI) was fully contained within the ROPE. We rejected a hypothesis if a parameter's 95% HDI fell outside the ROPE. We considered having insufficient evidence to either accept or reject a hypothesis as the 95% HDI both overlapping and exceeding the ROPE. Ideally, a ROPE should be guided by both theoretical expectations and empirical knowledge (Kruschke, 2018). Thus, for hypothesis H1, we adopt a ROPE of $-0.5 \leq \rho \leq -0.01$ because of the inherent uncertainty contained in both δ (see Results below) and α (Pawar et al., 2012). For hypothesis H2, we consider a ROPE of $0.4 \leq E_f \leq 0.8$ eV because it contains many of the empirically observed temperature dependence estimates for fish metabolic rates (Barneche et al., 2014; Brown et al., 2004).

2.3 | Complementary diet composition analyses

The diversity and relative abundance of diet items for most *Ophioblennius* species and populations in the Atlantic Ocean remain unexplored. *Ophioblennius macclurei*, endemic to the Caribbean, constitutes an exception to this because it is known to feed almost exclusively on organic detritus (Randall, 1967). Other studies indicate that animal prey may also be ingested incidentally or in small quantities (Mendes, 2000); however, there are no quantifications of whether these proportions change among populations. We therefore quantified the proportion of different diet items across populations of the *Ophioblennius* spp. To do so, we collected adult individuals from two species in five Atlantic locations to evaluate gut content and mouth volume ($n = 50$ individuals). Individuals were collected with a hand spear, then immediately frozen—to cease enzymatic action that could degrade the gut content—and transported to the laboratory. We were not able to collect individuals from which we tallied bite rates.

In the laboratory, all individuals were measured and dissected, had their gut removed and were fixed in 10% formaldehyde. The fullness of each gut was visually estimated and assigned to one of four proportion bins according to the amount of food: 0.25 (almost empty), 0.5 (half full), 0.75 (almost full) and 1 (full; Nunes et al., 2019). The guts were sectioned in a petri dish under a stereomicroscope, where their content was separated and identified to the lowest taxonomic category possible (Nunes et al., 2019). The volume of each food item was then measured following the exact same procedure described above for the quantification of mouth volume.

We assessed the population-averaged importance of each food item, d , for all studied *Ophioblennius* populations. To do so, we calculated the feeding index, I_d (%) by relating feeding items' frequency of occurrence to the volume (Nunes et al., 2019):

$$I_d = \frac{O_d J_d}{\sum_{d=1}^n O_d J_d} \times 100, \quad (8)$$

where O_d (%) is the frequency of occurrence of food item d across all sampled guts from a given location, and J_d (%) is the volumetric index,

which is defined as the volume (mm^3) of item d summed across individuals relative to the summed volume of all n registered items.

3 | RESULTS

3.1 | Hypothesis H1

We observed substantial variation in bite rates among locations (Figure 2a). This variation was captured by our hierarchical modelling approach (Equation 6): specifically, our mean estimate of 0.65 for the standard deviation of the location-level deviation in normalised bite rate ($\sigma_{\Delta \ln f_0(T_c)}$) implies that bite rate varied by about 3.7-fold ($e^{2 \times 0.65}$) among locations after accounting for the effects of body size, temperature and observation time.

The model fit of Equation 6 also revealed that bite rates varied systematically with body size, temperature and observation time (Bayesian $R^2 = 0.39$; 95% HDI: 0.31–0.45; Table S1; Figure 2b). In agreement with hypothesis H1, the mass scaling exponent of bite rates, ρ , was substantially negative and its 95% HDI was contained within the ROPE -0.5 to -0.01 (mean = -0.18 ; 95% HDI: -0.27 to -0.10 ; Figure 2b). The model fit of Equation 7 revealed that the mass scaling exponent of mouth volume, δ , was substantially higher than 1, characterising a hyper-allometric relationship (mean = 1.24; 95% HDI: 1.15–1.33; Bayesian $R^2 = 0.98$; 95% HDI: 0.97–0.98; Figure 3; Table S2).

3.2 | Hypothesis H2

The mean temperature dependence of bite rates, which is characterised by the empirical activation energy E_f (Equation 6), was substantially steeper than the expected value of 0.6 eV (mean = 1.06 eV; Figure 2c), that is, bite rates were higher than expected at higher temperatures. However, we lacked sufficient evidence to either accept or reject hypothesis H2 because the 95% HDI (0.44–1.68 eV) fell both within and outside the ROPE 0.4–0.8 eV. Similar results were obtained using satellite-derived temperature data (Figure S3).

3.3 | Complementary diet composition analysis

We identified 11 diet items in the diet of *Ophioblennius* spp. Organic detritus, which was composed of morpnic and amorphous forms, was the most important item across all locations, with a mean feeding index, I_d , of 87.36% (ranging between 62.03%–98.59%; Figure 4). Algae and animal material were also found in the diet but in low proportions, indicating either unusual or accidental ingestion. We also found plastic in the stomachs for most of the locations (Figure 4). A complementary morphometric analysis revealed that *Ophioblennius* spp. exhibit primarily an omnivorous diet with detritivore tendencies (Figure S4).

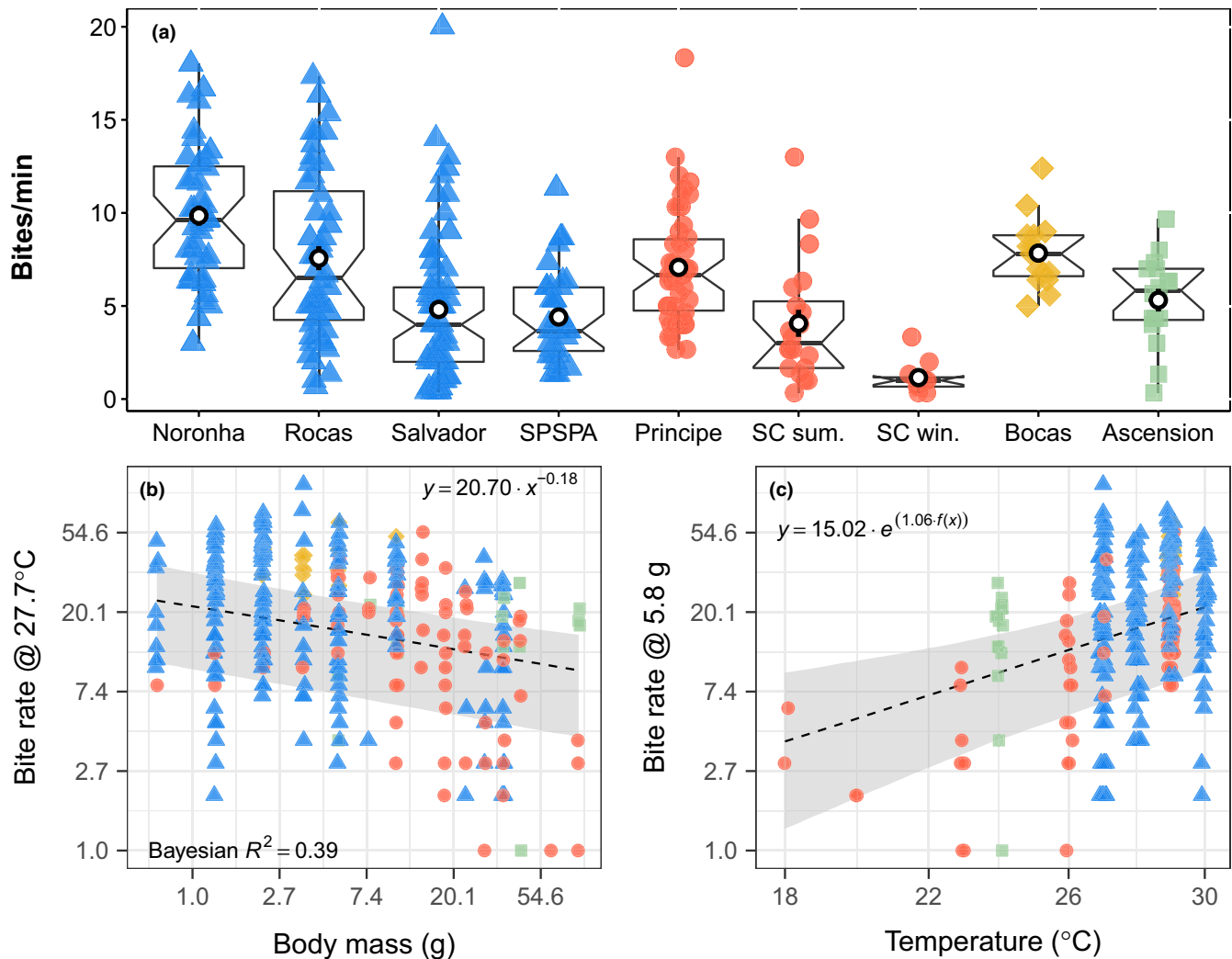


FIGURE 2 Variation in *Ophioblennius* spp. bite rates (bites on the substratum/minute) in the Atlantic Ocean across (a) locations, with (b) body mass and (c) and temperature. Each point corresponds to an individual bite-rate observation. In (a), black and white circles and black lines represent the mean number of bites and their standard error, respectively. Parameters in (b) and (c) were estimated using a Bayesian hierarchical model (Equation 6) and are listed in Table S1. Following Equation 6, the effect of temperature on bite rate in (b) was controlled by standardising the temperature measures, T (in K), to the mean temperature in the dataset, $T_c = 300.87$ K ($=27.7^\circ\text{C}$). In (c), the effect of body mass was controlled by standardising measures to the mean observed body size on natural log scale ($\ln(5.8)$ g). $f(x) = 1/k(1/T_c - 1/(x + 273.15))$ and assumes $T_c = 300.87$ K. Both (b) and (c) have been corrected for the mean observation time on natural log scale ($\ln(3.57)$ min). Colours and symbols represent different species: *Ophioblennius trinitatis* (blue triangles), *O. macclurei* (golden diamonds), *Ophioblennius*. sp.1 (red circles) and *Ophioblennius*. sp.2 (green squares)

4 | DISCUSSION

We developed a new model inspired by the Metabolic Theory of Ecology to quantitatively predict how individual bite rates scale with body mass and temperature. Although our model was put to the test using a specific clade of crypto-benthic reef fishes that is widely distributed across the Atlantic Ocean, its simplicity (based on body size and temperature alone) should make it general and applicable to most ectothermic animals for which bite rates can be tallied. We believe that our test data—which comprises a clade of sister species—may yield similar scaling estimates to those that would be obtained at the within-species level, which arguably is the baseline level of interest for these metabolic scaling

models. Thus, our study represents a good macroecological test of an MTE-inspired model at an ideal level of biological organisation. However, it is also important to note that, in our current dataset, temperature regime, species and population identity, and geographical location (and therefore other local environmental factors) are somewhat confounded, which is inevitable for an observation-based study such as ours. Laboratory experiments focusing on one species at a time should be able to control for these effects, and the findings reported here establish a benchmark against which said experiments can test the generality of our theoretical predictions.

In our test study group, the explanatory power of body size and temperature was modest ($R^2 = 0.39$), suggesting that additional

sources of variation are influencing bite rates. Yet, the negative size scaling of bite rates is consistent with previous studies focused on multiple groups of animals (Barneche et al., 2009; Pelletier & Festa-Bianchet, 2004; Wikelski & Carbone, 2004), and its estimated exponent, $\rho = -0.18$, matched our theoretical prediction from hypothesis H1. Moreover, based on the equality $\rho = \alpha - \delta$, and our result in which $\delta = 1.24$, the consumption rates should exhibit a hyper-allometric relationship, with a size scaling exponent $\alpha = 1.06$ (Figure 5). Such

value has been attributed to consumers foraging in 3 dimensions, that is fishes which are foraging not only on the reef substratum but also the water column (Pawar et al., 2012). Given that *Ophioblennius* spp. are primarily benthic 2D dwellers, this might suggest that the mouth-filling method used here generates an overestimate of the

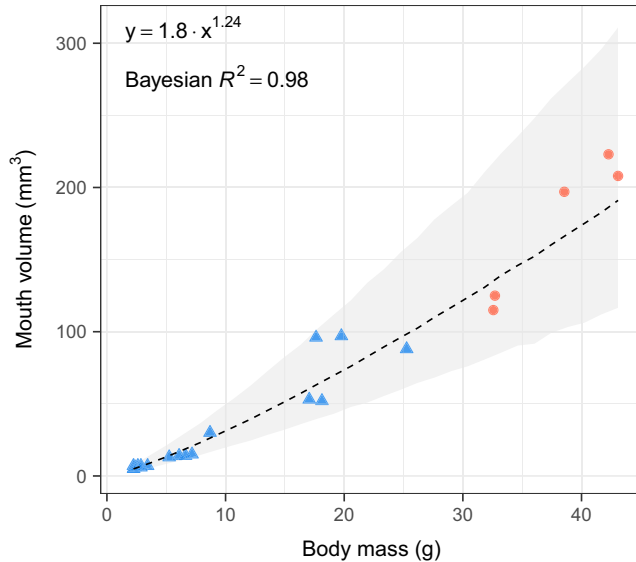


FIGURE 3 Scaling of mouth volume of *Ophioblennius* spp. with respect to body mass. Parameter estimates (listed in Table S2) were obtained using a Bayesian linear model following Equation 7. Colours and symbols as in Figure 2. Shaded polygon represents the Bayesian 95% credible intervals

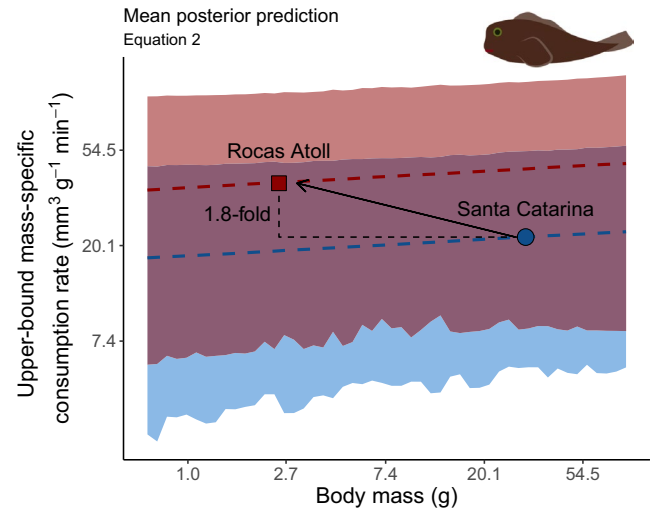


FIGURE 5 Mass-specific consumption rates of *Ophioblennius* spp. along their body size gradient. Consumption rates were calculated from the mean posterior predictions of both bite rates (Equation 6) and mouth volume (Equation 7), which yield consumption rates when multiplied (Equation 2). Blue line and circle depict the larger-bodied (30.5 g) population from the colder Santa Catarina shores (24.5°C); red line and square depict the smaller-bodied (2.5 g) population from the warmer Rocas Atoll (29.6°C). Dashed lines represent mean predictions, and shaded polygons represent Bayesian 95% credible intervals. *Ophioblennius* cartoon: ©Naomi Lastrucci 2020

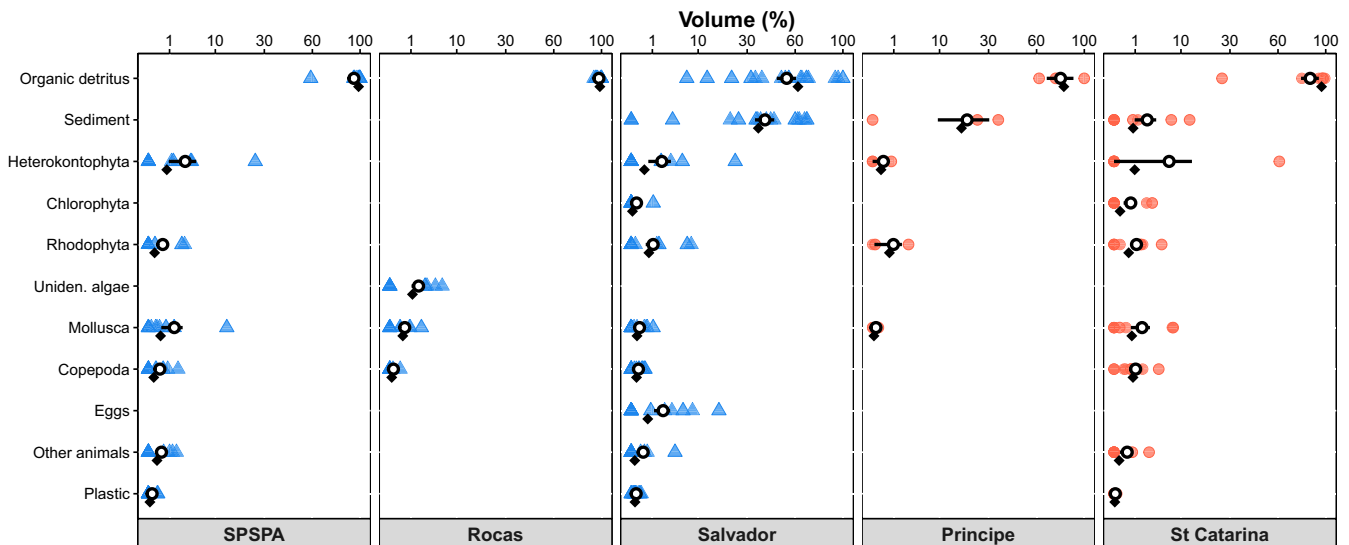


FIGURE 4 Diet composition of *Ophioblennius* spp. across five locations in the Atlantic Ocean. Points represent individuals and the volume (%) of a diet category in their gut. Black and white circles and black lines represent the mean volume and its standard error, respectively. Black diamonds represent the importance of each diet item at each location, as calculated using the feeding index, I_d (%). Locations: St Peter and St Paul Archipelago (SPSPA), Rocas Atoll (Rocas), Salvador, Principe Island (Principe) and Santa Catarina (St Catarina). Colours and symbols as in Figure 2

upper-bound mouth volume mass exponent, δ , and in reality $\alpha < 1$. On the other hand, the $\alpha = 1.06$ corollary could also represent an underappreciated facet of this clade's feeding behaviour. In fact, *Ophioblennius* spp. have been seen feeding on the water column for short periods of time (authors' personal observation). In either case—that is, 2D or 3D forager—our general model provides guidance to further investigate the feeding ecology of our test study group.

Environmental temperature is an important driver of metabolic rates in ectothermic animals, and therefore it should also directly affect consumption rates in predictable ways (Barneche et al., 2009, 2014; Brown et al., 2004; Bruno et al., 2015; Dell et al., 2013; Ferreira et al., 2019; Gillooly et al., 2001; Schaum et al., 2018). The positive relationship between temperature and bite rates observed here is qualitatively consistent with results from other studies focused on nominally herbivorous reef fishes (e.g. Barneche et al., 2009; Floeter et al., 2005; Mendes et al., 2009). However, contrary to our prediction in hypothesis H2, our mean estimate for the temperature dependence of bite rates in *Ophioblennius* spp. ($E_f = 1.06$ eV) indicates that fish are feeding at a much faster rate than what would be predicted if bite rates were primarily governed by metabolic rates alone. These results are consistent with the idea that populations adapted to warmer environments exhibit higher-than-expected grazing pressure on primary producers (Schaum et al., 2018).

Consistent with earlier accounts from *Ophioblennius macclurei* (previously cited as *O. atlanticus* by Randall, 1967), all *Ophioblennius* populations exhibited a diet that was dominated by detritus. Algae, plastic and other materials were less important, and possibly reflected accidental ingestion. Detritus is a common component found in the algal matrix, which is the main substratum in most rocky and coral reefs (Aued et al., 2018; Wilson et al., 2003) and is the preferential foraging ground of *Ophioblennius* (Medeiros et al., 2014). Detritus is composed of multiple animal and plant material degraded by microbial activity, a process that increases with higher temperatures (Carvalho et al., 2005; Wilson et al., 2003). This suggests that the nutritional value of detritus might change with the environment, and as such should affect the bite rates of detritivorous animals. We propose that future studies in this and other groups should assess the nutritional quality of all diet components, and in particular the detritus (Mendes et al., 2018), by directly measuring their energy density or the ratio between carbon and nitrogen (Wilson et al., 2003). The effect of food nutritional quality, and how it varies over ontogeny, can formally be incorporated into our model, and, when tested, could help explain additional variance in bite-rate data.

Additional non-exclusive mechanisms might explain part of the unexplained variance in the data. However, at this point we can only speculate about them. For example, our simplified model did not account for the mechanics of jaw movement; many properties of jaw mechanics are known to scale with body size and change with temperature (Gidmark et al., 2013; Huber & Motta, 2004; Turingan & Sloan, 2016; Wainwright & Shaw, 1999; Wainwright et al., 2000). Particularly, the mass scaling of bite rates could be influenced by the size scaling of jaw opening, whereby larger jaws (i.e. larger individuals) require more force/time for opening, which, in turn, might account for slower bite

rates (Huber & Motta, 2004; Wainwright & Shaw, 1999; Wainwright et al., 2000). Moreover, the thermal sensitivity of bite kinematics (e.g. gape velocity, time to peak gape) might differ from the canonical MTE expectation. That said, the Q10s estimated for these variables are generally lower than those predicted by MTE and the activation energy estimated in our study (Gidmark et al., 2013; Turingan & Sloan, 2016; Table S3). In addition to jaw mechanics and bite kinematics, the nutritional content of the detritus might be decreasing at warming temperatures (as observed in phytoplankton; O'Connor et al., 2009), and consequently fish might exhibit a faster-than-predicted bite rate to achieve their nutritional targets which are necessary to maintain bodily functions. Also, the energetic content (i.e. total calories) of the detritus might be decreasing with temperature (as seen in macrophytes Carvalho et al., 2005). We welcome future research measuring how jaw mechanics, bite kinematics and food nutritional/energy quality might predictably influence bite and consumption rates.

Ocean warming will affect the dynamics of energy transmission in ecosystems in non-trivial ways. Higher temperatures will shrink the average size of many fish species (Audzijonyte et al., 2020). In our own dataset, *Ophioblennius* populations from Santa Catarina in south Brazil (mean size = 30.5 g) had their bites recorded at 24.5°C, whereas populations from Rocas Atoll (mean size = 2.5 g) had their bites recorded at 29.6°C. Such a change in mean body size and temperature implies a 1.8-fold increase in mass-specific consumption rates (Equation 2, Figure 5). These differences take particular significance because small cryptobenthic detritivores such as *Ophioblennius* spp. are extremely abundant and comprise one of the most important sources of energy for larger predators in coral reef ecosystems (Brandl et al., 2019; Depczynski et al., 2007). Warming may decrease the carrying capacity of these populations via higher per-capita consumption rates, which could cascade onto lower carrying capacity for meso and top predators.

5 | CONCLUSIONS

Here we built upon and expanded existing ecological theory to predict how the bite rates—a widely employed quantity of feeding behaviour and energetic demand of animal populations—vary with body mass, environmental temperature and diet. In testing our predictions with laboratory data and field observations from a broad geographical range, we also quantitatively integrated bite rates with the more elusive consumption rates. Therefore, our model serves as a bridge between classic behavioural ecology and ecophysiology, and a means to better predict the effects of environmental change on consumers' feeding pressure. Alterations in energy flows through cryptobenthic fish will cascade through, and help shape the structure of future reef ecosystems.

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AUTHORS' CONTRIBUTIONS

L.T.N., D.R.B. and S.R.F. conceived the ideas and designed the study; L.T.N., N.S.L., J.A.C.C.N., C.E.L.F. and S.R.F. collected the bite-rate data and/or individuals for diet; D.R.B. developed the theory; L.T.N. and D.R.B. conducted the data analysis; L.T.N. and A.A.F. performed all the laboratorial analysis; L.T.N. and D.R.B. wrote the first draft of the manuscript, and all authors contributed substantially to revisions. All authors gave final approval for publication.

DATA AVAILABILITY STATEMENT

Data and R codes are publicly available in GitHub Repository (https://github.com/dbarneche/redlip_bites). When using the data or code from this paper, please cite it as: Nunes LT, Barneche DR, Lastrucci NS, Fraga AA, Nunes JACC, Ferreira CEL, Floeter SR (2021) dbarneche/redlip_bites: Accepted version of paper data and code of manuscript: Predicting the effects of body size, temperature and diet on animal feeding rates (*Functional Ecology*). *Zenodo*. <https://doi.org/10.5281/zenodo.5003045>.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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