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Influence of food, body size, and fragmentation on metabolic rate in a sessile marine invertebrate

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Abstract

Metabolic rates vary among individuals according to food availability and phenotype, most notably body size. Disentangling size from other factors (e.g., age, reproductive status) can be difficult in some groups, but modular organisms may provide an opportunity for manipulating size experimentally. While modular organisms are increasingly used to understand metabolic scaling, the potential of feeding to alter metabolic scaling has not been explored in this group. Here, we perform a series of experiments to examine the drivers of metabolic rate in a modular marine invertebrate, the bryozoan *Bugula neritina*. We manipulated size and examined metabolic rate in either fed or starved individuals to test for interactions between size manipulation and food availability. Field collected colonies of unknown age showed isometric metabolic scaling, but those colonies in which size was manipulated showed allometric scaling. To further disentangle age effects from size effects, we measured metabolic rate of individuals of known age and again found allometric scaling. Metabolic rate strongly depended on access to food: starvation decreased metabolic rate by 20% and feeding increased metabolic rate by 43%. In comparison to other marine invertebrates, however, the increase in metabolic rate, as well as the duration of the increase (known as specific dynamic action, SDA), were both low. Importantly, neither starvation nor feeding altered the metabolic scaling of our colonies. Overall, we found that field-collected individuals showed isometric metabolic scaling, whereas metabolic rate of size-manipulated colonies scaled allometrically with body size. Thus, metabolic scaling is affected by size manipulation but not feeding in this colonial marine invertebrate.

KEYWORDS
bryozoan, fragmentation, metabolic scaling, modularity, specific dynamic action

1 | INTRODUCTION

Metabolic rate is a useful indicator of the pace of life, potentially driving ecological and evolutionary processes at all levels of organization (Allen, Gillooly, & Brown, 2005; Brown, Gillooly, Allen, Savage, & West, 2004; Loreau, 2010; Sibly, Brown, & Kodric-Brown, 2012; West & Brown, 2005; but see Glazier, 2015). The rate at which organisms transform and use energy varies extensively among species, populations, and individuals of the same species (Burton, Killen, Armstrong, & Metcalfe, 2011; Konarzewski & Książek, 2013; White & Kearney, 2013). Some levels of this variation in metabolic rate are better understood than others. For example, ectotherms tend to have lower metabolic rates (after accounting for differences in mass) than endotherms, and larger species tend to have

lower mass-specific metabolic rates than smaller species (White & Kearney, 2013). Likewise, body mass is a strong predictor of metabolic rate within species (Brown et al., 2004; Huxley, 1932). Among individuals of the same size and living at the same temperature, however, variation in metabolic rate is less well understood (Burton et al., 2011; Konarzewski & Książek, 2013).

Organisms obtain energy from feeding, and food availability can therefore be considered a key factor affecting the life history of an individual (Stearns, 1992). Metabolic rate is highly affected by feeding, with individuals typically experiencing a rapid increase in metabolic rate after feeding. Upon reaching peak metabolism, metabolic rate decreases again to pre-feeding levels. This postprandial increase in metabolic rate is termed specific dynamic action (SDA; Rubner, 1902), and is significantly influenced by various factors including body size and temperature, and meal size, type, and composition (reviewed in Secor, 2009). In recent studies, SDA was found to contribute significantly to an animal's energy budget (McCue, 2006; McCue, Bennett, & Hicks, 2005; McCue & Lillywhite, 2002; Secor, 2009), with observed metabolic rates exceeding maximal metabolism during activity in some species (Andrade, Cruz-Neto, & Abe, 1997; Secor & Diamond, 1997; Secor, Hicks, & Bennett, 2000). Specifically, the factorial scope during SDA, which describes the magnitude of increase in metabolic rate after feeding (Secor, 2009), might therefore be a good indicator of the ability of an individual to alter its metabolic rate with changing feeding conditions (i.e., its phenotypic plasticity).

Intuitively, the ability of an organism to alter its metabolic rate with varying food availabilities might be particularly important for sessile invertebrates such as corals, mussels, and bryozoans, as these animals cannot escape rapidly changing environments. To date, few studies have investigated the factorial scope and the overall SDA response of sessile marine invertebrates, and even fewer studies have addressed these responses in colonial marine invertebrates (see Table S1). The factorial scope reported for these species ranges 1.38–6.55 (mean ± *SE* factorial scope across all marine sessile species: 2.44 ± 0.6, $n = 8$; Table S1), with observed SDA durations of between 10 and 384 h (mean ± *SE*: 153.96 ± 68.85 h, $n = 5$; Table S1). In comparison, across all marine non-sessile invertebrate studies, including semiaquatic species such as crabs, the factorial scope ranges 1.14–5.2 (mean ± *SE*: 2.25 ± 0.09, $n = 76$; Table S1). The durations of the SDA response in motile marine invertebrates ranges 4–1200 h (mean ± *SE* duration across all marine motile invertebrates: 103.49 ± 36.24 h, $n = 41$; Table S1). Interestingly, to date the only colonial organism for which the metabolic response after feeding was characterized is the coral *Astrangia danae* (factorial scope 1.87; Szmant-Froelich & Pilson, 1984).

Metabolic theories seek to understand and predict biological processes at all levels from individuals to populations, communities, and ecosystems (Brown et al., 2004; Nisbet, Muller, Lika, & Kooijman, 2000; van der Meer, 2006). The relationship between metabolic rate (*MR*) and body mass (*M*) is one of the most studied in biology, particularly since metabolic rate scales allometrically with body mass in most species according to the power function $MR = aM^b$, where a and b are scaling constants and where the fitted value of b is typically less than 1 (e.g., Burgess et al., 2017; Kleiber, 1932, Savage et al., 2004). Metabolic scaling provides an important insight into differences in metabolic efficiencies associated with body mass. Here, metabolic scaling might also be affected by food availability, indicating differences in metabolic efficiencies of different-sized individuals under varying feeding conditions. To date, no studies have formally investigated metabolic scaling in modular organisms under different feeding conditions. In ectotherms more generally, larger individuals typically exhibit a greater SDA response (e.g., Katersky, Peck, & Bengtson, 2006; Luo & Xie, 2008; Secor & Faulkner, 2002), which often results in steeper metabolic scaling approaching isometry in fed individuals (Secor, 2009). Glazier (2010) suggested that near isometric scaling of metabolic rate during SDA arises from the strong influence of volume-related, SDA-induced metabolic demand. In other species, however, no effect of body size was found (e.g., Boyce & Clarke, 1997; Grigoriou & Richardson, 2008). In colonial organisms (i.e., clonal organisms that are subdivided into functionally autonomous or semi-autonomous, multicellular modules, Vuorisalo & Tuomi, 1986), feeding differs from that in unitary organisms in the way that colonial animals take up and transform resources. Most studies indicate that feeding rates scale isometrically or superlinearly in colonial animals (e.g., Okamura, 1984, 1985; Pratt, 2005), whereas metabolic scaling is allometric in most species (Barneche, White, & Marshall, 2017; Burgess et al., 2017; Hartikainen, Humphries, & Okamura, 2014). Hence, as colonies increase in size, their capacity to capture food increases more quickly than the rate at which they expend energy. Under varying feeding conditions, colonies have been shown to shut down the number of actively feeding modules in response to extremely low or high food concentrations (Riisgård & Larsen, 2000). Thus, changes in metabolic scaling with varying feeding conditions can be anticipated as the number of actively feeding modules changes disproportionally across colony sizes. For example, when food is restricted, all modules in smaller colonies might be actively feeding, while only a small number of modules are active in larger colonies. These differences in the number of feeding modules across colony sizes, in turn, may result in a decrease in metabolic rates in larger colonies but not in smaller ones, constituting an overall shallower metabolic scaling under restricted feeding conditions. Whether metabolic scaling in colonial organisms varies with changing feeding conditions according to these hypotheses remains to be studied.

Most studies investigating the scaling relationship between metabolic rate and body mass must rely on natural variation in body size among individuals, and those investigations are potentially confounded by the effect of other traits such as age and nutrition that covary with body size (e.g., Calder, 1984; Schmidt-Nielsen, 1984). Colonial animals provide an opportunity to manipulate size independently of other factors, thereby minimizing potentially confounding effects (e.g., those associated with age). Size manipulation approaches in several recent studies show how size can be manipulated to test predictions of competing theories

(Barneche et al., 2017; Nakaya, Saito, & Motokawa, 2005; White, Kearney, Matthews, Kooijman, & Marshall, 2011; reviewed in Burgess et al., 2017).

Three types of scaling relationship between metabolic rate and body mass have been recognized: ontogenetic, static, and evolutionary scaling (e.g., Cheverud, 1982; Pélabon et al., 2013; White & Kearney, 2014). Ontogenetic scaling considers the relationship between metabolic rate and mass in the same individual through developmental time (e.g., Killen, Costa, Brown, & Gamperl, 2007). Static scaling considers the relationship between metabolic rate and mass among individuals of the same developmental stage within a species (e.g., Pettersen, White, & Marshall, 2015). Evolutionary scaling considers the relationship between metabolic rate and mass among individuals of different species, again at the same developmental stage (e.g., Savage et al., 2004). Distinguishing between these forms of metabolic scaling is particularly important when comparing models that have been proposed to explain scaling relationships (see White & Kearney, 2014). The main objectives of the present study are to investigate how size affects metabolic rate (i.e., metabolic scaling) in the marine colonial bryozoan *Bugula neritina*, and how size manipulations, feeding, and starvation affect estimates of metabolic scaling.

2 | MATERIALS AND METHODS

2.1 | Study species, size manipulation, and measurement of metabolic rate

Bugula neritina LINNAEUS 1758 is a colonial, arborescent bryozoan commonly found as part of the fouling community on artificial structures throughout the world. Adult colonies of *B. neritina* grow via asexual budding by producing new pairs of zooids (individual subunits) at the distal ends of the branches of the colony. Regular bifurcations give the colony an arborescent shape (Keough, 1989; Keough & Chernoff, 1987). Once colonies are sexually mature, zooids develop clearly visible brood structures known as ovicells, in which offspring are brooded (Woollacott & Zimmer, 1975).

We collected non-reproductive colonies of *B. neritina* from the Royal Brighton Yacht Club in Port Phillip Bay, Vic., Australia (−37.909, 144.986), between August and November 2017. We transported colonies to the laboratory and maintained them in aerated tanks in field-collected seawater at 19°C for up to 12 h prior to their use in experiments.

Because of the colonial nature of *B. neritina*, we were able to manipulate the size of non-reproductive colonies by cutting off the basal part of the colony, thereby creating two different treatments: size-manipulated and intact colonies (Figure 1). We measured colony size as the number of bifurcations, and size-manipulated colonies were derived from bigger colonies (e.g., we cut off the lower part of a colony that was six bifurcations in size to derive a size-manipulated colony that was five bifurcations in size). By doing so, size-manipulated and intact colonies used for experiments were of comparable size. Size-manipulated colonies were allowed to recover for 1 h before measurements.

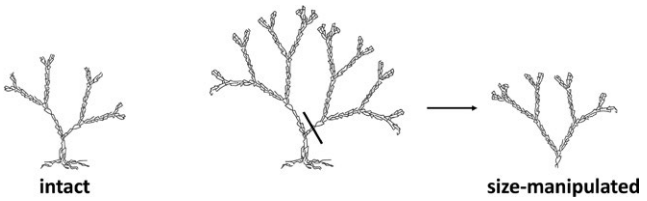

FIGURE 1 Schematic illustration of our fragmentation approach, allowing us to investigate the effect of size manipulation on the Routine metabolic rate and metabolic scaling in *Bugula neritina*. Importantly, by applying this size manipulation approach, intact and size-manipulated colonies were of comparable size, and the overall colony form was maintained

Based on comparisons of the average age of zooids in the size-manipulated and intact colonies, we found that our size manipulation approach did not alter the covariance between body size and age substantially, and was therefore an appropriate test of the effects of size manipulation on metabolic rate in this species. Importantly, and in contrast with the size manipulation approach recently applied for *B. neritina* by Barneche et al. (2017), the overall colony form was maintained in both treatments (for comparison, see Figure 1 and Barneche et al., 2017: fig. 1).

To determine metabolic rate, we measured the oxygen consumption rate ($\dot{V}O_2$, a commonly used proxy for metabolic rate) of individual colonies. Due to the presence of spontaneous activity such as expanding and retracting of the feeding structures during measurements, we defined metabolic rate as Routine MR (Mathot & Dingemanse, 2015). Before measurements of metabolic rate, we inspected colonies for epibionts such as amphipods and ciliates. We carefully removed any epibionts with a forceps and cleaned each colony using a soft-tipped paint brush. We placed individual colonies into 5-ml SDR glass vials (PreSens, Germany) containing sterilized, 0.2-μm filtered seawater (FSW) and a non-consumptive O_2 sensor spot. To prevent colonies from touching the sensor spot during measurements, we placed a small sheet of acetate diagonally between the sensor spot and the colony. Measurements of $\dot{V}O_2$ were conducted using 24-channel PreSens sensor dish readers (Sensor Dish Reader SDR2, PreSens, Germany), along with four controls (blank vials containing only seawater and acetate) per SDR reader. Prior to $\dot{V}O_2$ measurements, we calibrated the sensor spots with air-saturated (AS) seawater (100% AS) and seawater containing 2% sodium sulfite (0% AS). Measurements of $\dot{V}O_2$ were recorded in a darkened, constant-temperature room at 19°C over 3 h (for an example of the SDR outcome, refer to Figure S1).

We used the R package LoLinR (Olito, White, Marshall, & Barneche, 2017), which implements local linear regression techniques for estimating monotonic biological rates from time-series or trace data, to determine the optimal measurement interval (i.e., the most linear part of the measurement curve). We excluded the first 30 min of the 3-h measurement period (during which colonies might show oxygen consumption patterns that reflect recovery from handling procedures). As LoLinR only considers a fraction of the measurement curve, we additionally ran the program using different parts

of the curve, thus ensuring that we did not miss peak $\dot{V}O_2$. We used either the first half or the last half of the curve (after excluding the first 30 min of the overall measurement time) and compared the output to the results obtained from analysis of the whole measurement curve. Routine MR values calculated from the last half and the overall curve were very similar, but metabolic rates calculated from the first half of the curve were slightly lower (Figure S2). Those slightly lower MR values could be attributed to a delayed detection of small decreases in oxygen in the SDR vials, especially in measurements from smaller colonies. Nevertheless, these findings indicate that we indeed captured the maximum peak $\dot{V}O_2$ of *B. neritina*.

Using the LoLinR output, we calculated $\dot{V}O_2$ from the rate of change of O_2 saturation over time (m_a; in % per hour) as per White et al. (2011):

$$\dot{V}O_2 = -1\left(\frac{m_a - m_b}{100}\right) V\beta O_2$$

where m_b is the rate of change of O_2 saturation for control vials (% per hour), βO_2 is the oxygen capacitance of air-saturated seawater at 19°C (5.31 ml/L; Cameron, 1986) and V is the water volume (the volume of the animals was subtracted from the total vial volume of 5 ml). To convert $\dot{V}O_2$ (ml per hour) to metabolic rate (milliJoules per hour), we used the calorific conversion factor of 20.08 J/ml O_2 (Crisp, 1971).

2.1.1 | Ontogenetic versus static metabolic scaling (Experiment 1)

Barneche et al. (2017) have recently shown that metabolic rate scales with body size with an allometric scaling exponent of 0.72 in size-manipulated colonies of *B. neritina* at a slightly higher temperature (25°C) than the one we used in the present study (19°C). When collecting colonies of varying body sizes from the field, however, the ontogenetic stages of these colonies were unknown. Therefore, in order to estimate the contribution of ontogenetic variation to metabolic scaling in *B. neritina*, we conducted a field experiment in which we investigated and compared the ontogenetic and static scaling of metabolic rate in *B. neritina*.

We collected reproductive colonies of *B. neritina* at the Royal Brighton Yacht Club in November 2017 and induced spawning according to standard light-shock procedures: colonies were kept in darkened, aerated tanks at 19°C for 48 h and then placed in beakers filled with seawater and are exposed to bright light (Marshall, Bolton, & Keough, 2003). We then pipetted the released larvae in a drop of seawater directly onto two roughened A4 acetate sheets to induce settlement. Following settlement, we randomly assigned the acetate sheets to one of two PVC backing panels (570 × 570 × 6 mm), and suspended these panels 1 m below the water surface in a horizontal orientation, with the newly settled colonies on the underside of the panel facing the substrate, at the Royal Brighton Yacht Club (for a detailed description of the field deployment, see Marshall & Keough, 2009). After 3 weeks in the field, we brought the acetate sheets with colonies back to the laboratory to conduct metabolic rate measurements (we refer to these initial data as Measurement 1; see Section 2.1, above). We also counted the number of zooids and ovicells in each colony as a proxy for body mass, to avoid the inaccuracies inherent in weighing colonies attached to the acetate sheets. In *B. neritina*, the number of zooids and body mass are highly correlated ($r_{33} = 0.91$, $p < 0.0001$; Figure S3). Following measurements, we glued individual colonies back onto smaller squares of acetate sheet (55 × 55 mm), assigned each colony an identifying number, and deployed the colonies in the field again to allow them to grow. We then conducted further metabolic rate measurements and counted the number of zooids and ovicells 1 week (Measurement 2), 2 weeks (Measurement 3), and 3 weeks (Measurement 4) following the first measurement.

2.1.2 | Effects of starvation and size manipulation on Routine MR (Experiment 2a)

To investigate the effect of starvation and size manipulation on the Routine MR of *B. neritina*, we collected 60 colonies and assigned them to a size-manipulated treatment ($n = 29$) or an intact colony treatment ($n = 31$). We then acclimated the colonies in field-collected seawater at 19°C in a constant-temperature room for 3 h prior to the initial metabolic rate measurement. Following the first measurement, we estimated colony mass by blotting dry and weighing each colony to the nearest 0.01 g. We then incubated all colonies in 15 L of FSW in a big cooler box, with each colony placed inside a 60-ml glass jar completely submerged in the FSW. We then conducted metabolic rate measurements 24, 36, and 48 h following the initial metabolic rate measurement. We renewed the FSW daily.

2.1.3 | Disentangling the effects of starvation and laboratory conditions on Routine MR (Experiment 2b)

To test whether the Routine MR of colonies kept in the laboratory decreased as a response to starvation or to laboratory conditions more generally, we used a total of 35 colonies that were assigned to a fed treatment ($n = 16$) or a starved treatment ($n = 19$). Within the fed treatment, eight colonies were size manipulated, and eight colonies were left intact. Within the starved treatment, nine colonies were size manipulated, and 10 colonies were intact. As in Experiment 1, we acclimated freshly collected colonies in field-collected seawater at 19°C for 3 h prior to the first metabolic rate measurement. Subsequently, we weighed each colony and incubated colonies in the starved treatment in 60-ml glass jars containing 50 ml of FSW. Colonies in the fed treatment were incubated in 60-ml glass jars containing 50 ml of unfiltered seawater to which we added the green alga *Dunaliella tertiolecta* (Butcher; Australian National Algae Culture Collection; strain code CS-14) at a concentration of 10,000 cells/ml (based on measurements of optical density). We chose this alga because a previous cultivation study by Kitamura and Hirayama (1984) and our unpublished pilot studies showed that colonies of *B. neritina* consume and grow on this diet in the laboratory. We conducted metabolic rate measurements of colonies 24, 48, 72, 96, 120, and

144 h after the initial metabolic rate measurement. As in Experiment 1, we renewed the seawater and added algae to the colonies in the fed treatment after each metabolic rate measurement.

2.1.4 | Effect of size on specific dynamic action (Experiment 3)

To determine the effect of body size and size manipulation on the specific dynamic action (SDA) of *B. neritina*, we collected 56 colonies and assigned them to a size-manipulated treatment (n = 29) or an intact colony treatment (n = 27). We then incubated colonies in 15 L of FSW (each colony was placed in a 60-ml glass jar, as described in Experiment 1, for 24 h at a temperature of 19°C. Following an initial metabolic rate measurement to determine the baseline metabolism of starved colonies, we weighed each colony, returned them to seawater, and added the red alga *Rhodomonas salina* (Australian National Algae Culture Collection; strain code CS-692) to 15 L of FSW to approximate a concentration of 10,000 cells/ml (based on measurements of optical density). We chose this algal concentration because it supports the highest growth rates in colonies of *B. neritina* (based on Kitamura & Hirayama, 1984 and unpublished pilot studies). After adding algae, we collected water samples and fixed algae in a 2% Lugol solution. We then estimated the phytoplankton concentration by manual cell counts (using a Neubauer hemocytometer). The average phytoplankton concentration was ~11500 cells/ml. Colonies were fed for a total of 4 h, but we completely renewed the FSW supplemented with algae after 2 h. Following feeding, we rinsed all colonies in FSW for 1 h to remove excess algae, and then determined the peak $\dot{V}O_2$ of each colony. We then kept colonies in 15 L of FSW and conducted further metabolic rate measurements 16 and 24 h after feeding. We used these data to quantify the factorial scope of peak $\dot{V}O_2$ (calculated as peak $\dot{V}O_2$ divided by the baseline metabolism), based on the mean Routine MR of colonies before and after feeding, as described by Secor (2009).

2.2 | Statistical analyses

For statistical analyses, we used a repeated measures design analysis of co-variance (ANCOVA), with treatment (size-manipulated vs. intact colonies), feeding (fed vs. starved colonies), time (metabolic rate measurement points) and the number of zooids (Experiment 1) or colony mass (Experiments 2a,b and Experiment 3), and all their possible interactions as fixed effects and as a covariate. Routine MR and the number of zooids or mass were log transformed prior to analyses. We included colony ID nested within mass as a random factor. Model reduction was conducted by removing nonsignificant interactions if their inclusion did not improve the model fit (Quinn & Keough, 2002). We further conducted Wald tests for differences in the scaling exponents. Scaling exponents were derived using a log-transformed linear relationship as $\log_{10}(\text{Routine MR}) = b \times \log_{10}(\text{Mass}) + \log_{10}(a)$ (Experiment 2a,b and Experiment 3), or $\log_{10}(\text{Routine MR}) = b \times \log_{10}(\text{Zooids}) \times \log_{10}(\text{Ovicells}) + \log_{10}(a)$ (Experiment 1), respectively, if colonies were reproductive. In *B. neritina*, the number of zooids within a colony is linearly related to colony mass (Figure S3). Furthermore, scaling exponents were similar across experiments when using either the number of zooids or mass in regression analyses. All statistical analyses were conducted in R (R Core Team 2017) using the package lmerTest (Kuznetsova, Brockhoff, & Christensen, 2017).

3 | RESULTS

3.1 | Ontogenetic versus static metabolic scaling (Experiment 1)

Our estimates of ontogenetic and static scaling differed in field-collected colonies of *Bugula neritina*. Although metabolic rate throughout ontogeny scaled isometrically with the number of zooids at an exponent of 1.04, static scaling exponents ranged between 0.77 (Measurement 3) and 0.93 (Measurement 2). Static scaling exponents were not significantly different from 0.75 (Table 1; Figure 2).

3.2 | Effects of starvation and size manipulation on Routine MR (Experiment 2a)

We found an interaction between the size manipulation treatment and body mass, with larger size-manipulated colonies having a lower Routine MR than larger intact colonies (Table 2; Figure 3).

TABLE 1 Summary of scaling exponents (b) (±SE) and coefficients (a) for metabolic rate and mass (intact and size-manipulated colonies) or the number of zooids (ontogenetic and static scaling) in colonies of *Bugula neritina*, using a log-transformed linear relationship between metabolic rate and mass or number of zooids (see Section 2)

	n	Coefficient (a)	Scaling exponent (b) ± SE	p-value $b \neq 0$	p-value $b \neq 1$	p-value $b \neq 0.75$	R^2
Intact colonies	31	0.62	0.96 (± 0.079)	<0.0001	0.66	<0.05	0.84
Size-manipulated colonies	29	0.86	0.71 (± 0.071)	<0.0001	<0.001	0.58	0.79
Ontogenetic scaling	260	−0.97	1.04 (± 0.05)	<0.0001	0.48	<0.0001	0.82
Static scaling, 3 weeks old	65	−0.49	0.83 (± 0.1)	<0.0001	0.1	0.46	0.5
Static scaling, 4 weeks old	65	−0.61	0.93 (± 0.09)	<0.0001	0.42	0.06	0.61
Static scaling, 5 weeks old	65	−0.12	0.77 (± 0.12)	<0.0001	0.06	0.85	0.4
Static scaling, 6 weeks old	65	−0.1	0.81 (± 0.08)	<0.0001	<0.05	0.46	0.61

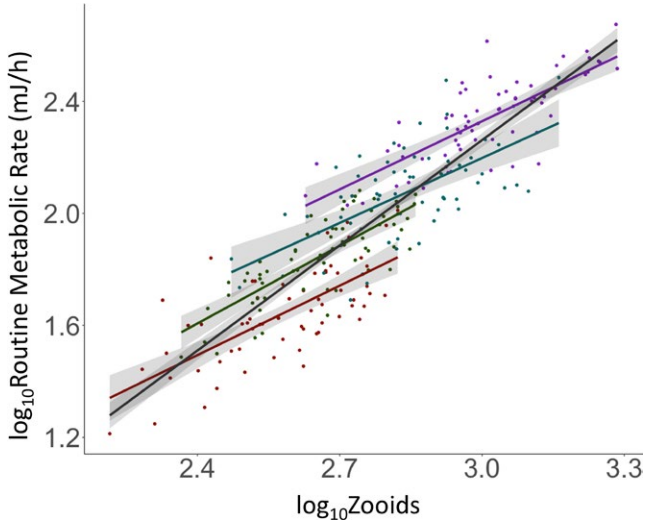

FIGURE 2 Relationship (log-transformed) between routine metabolic rate (mJ/h) and the number of zooids within a colony in *Bugula neritina*. The black line indicates the ontogenetic scaling relationship across developmental stages, while the colored lines indicate the static scaling at different developmental stages. Regression lines indicate scaling in colonies that are 3 weeks (red line), 4 weeks (green line), 5 weeks (blue line), or 6 weeks old (purple line). Regression lines were derived using a log-transformed linear relationship, where $\log_{10}$(Routine MR) = $b \times \log_{10}$(Zooids) × $\log_{10}$(Ovicells) + $\log_{10}(a)$; a and b are scaling exponents; "Zooids" and "Ovicells" refer to the number of zooids and ovicells, respectively, in a colony. Data points represent single colonies repeatedly measured over time. Gray areas indicate the 95% confidence intervals. Scaling exponents are presented in Table 1

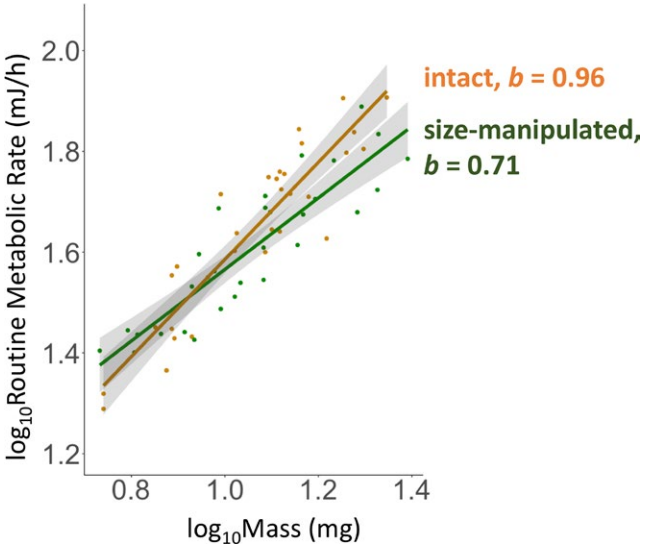

FIGURE 3 Relationship (log-transformed) between routine metabolic rate (mJ/h) and mass (mg) for freshly collected colonies of *Bugula neritina*. The green line indicates the scaling relationship of size-manipulated colonies, the yellow line indicates the scaling relationship of intact colonies. Regression lines were derived using a log-transformed linear relationship, where $\log_{10}$(Routine MR) = $b \times \log_{10}$(Mass) + $\log_{10}(a)$. Each data point represents a single colony. Gray areas indicate the 95% confidence intervals

TABLE 2 Repeated measures ANCOVA examining the effects of mass and treatment (size-manipulated vs. intact) on the Routine metabolic rate in colonies of *Bugula neritina* during starvation. Nonsignificant interactions were removed from the final model (Table S2)

	df	*F*	*p*
Between subjects			
$\log_{10}$(mass)	1	462.692	<0.0001
Treatment	1	7.906	0.007
$\log_{10}$(mass × treatment)	1	8.247	0.006
Error	56		
Within subjects			
Time	3	159.776	<0.0001
Treatment × time	3	3.214	0.024
Error	174		

The scaling exponent for intact colonies was $b = 0.96$ and did not differ significantly from 1, whereas size-manipulated colonies scaled at $b = 0.71$. The scaling exponent for size-manipulated colonies differed significantly from 1 (Table 1), and also differed significantly from the scaling exponent of intact colonies (Wald test; $p < 0.01$).

During starvation, the Routine MR in colonies of *B. neritina* decreased overall (Figure 4), and although the effect of colony mass was consistent, the effect of size manipulation changed over time (Table 2). Intact colonies had a higher mean Routine MR than size-manipulated colonies at time point T0 (freshly collected colonies). After 24 h, however, intact and size-manipulated colonies had reached similar mean Routine MRs, and metabolic rates decreased at similar rates in both treatments.

3.3 | Disentangling the effects of starvation and laboratory conditions on Routine MR (Experiment 2b)

We found that feeding (starved vs. fed) had a significant effect on the Routine MR of colonies over time (Figure 5; Table 3). Although the Routine MR of starved colonies decreased by 20%, the Routine MR of fed colonies remained constant over time. There was a significant interaction between mass and time (Table 3): the scaling exponent of the relationship between mass and Routine MR of both starved and fed colonies decreased over time. Notably, the interaction between mass and feeding was not significant, indicating that metabolic scaling was not significantly different between starved and fed colonies ($F_{1,31} = 2.303$, $p = 0.141$; Table S3), but there was a trend for starved colonies to have lower metabolic scaling exponents (Table 3). We did not detect any significant difference between size-manipulated and intact colonies, and the interaction between treatment and time was nonsignificant (Table 3). Therefore, for visualization purposes, we plotted metabolic scaling regression lines for both treatments combined (Figure 5).

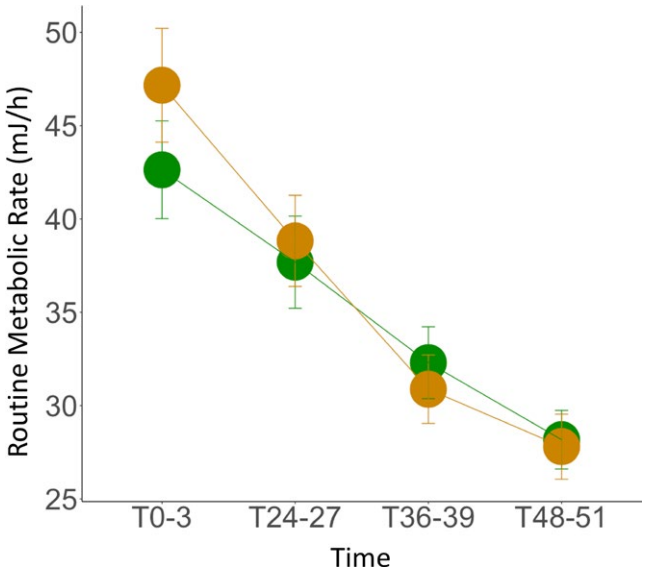

FIGURE 4 The change in mean routine metabolic rate (mJ/h) of starved colonies of *Bugula neritina* over time. Orange dots indicate the decrease in mean metabolic rate over time of intact colonies. Green dots indicate the decrease in mean metabolic rate over time of size-manipulated colonies. T0-3 depicts the mean metabolic rate of freshly collected colonies, T24-27, T36-39, and T48-51 represent the mean metabolic rate of starved colonies after 24–27, 36–39, and 48–51 h, respectively. Error bars indicate the standard error

3.4 | Effect of size on specific dynamic action (Experiment 3)

The Routine MR in colonies of *B. neritina* increased significantly after feeding (factorial scope = 1.43; Figure 6; Table 4). After 16 h, Routine MR was still elevated, but colonies reverted to their pre-feeding Routine MR 24 h after feeding (Figure 7). Interestingly, the scaling relationship between mass and Routine MR did not change over time (Table 4), indicating that the SDA response was similar across all body sizes. Also the effect of size manipulation did not change over time (Table 4). Size-manipulated colonies, however, had on average a higher Routine MR than intact colonies (Figure 7).

4 | DISCUSSION

Metabolic responses to varying feeding conditions are typically characterized by a decrease in metabolic rate during starvation, and an increase in metabolic rate after the ingestion of a meal (reviewed in Secor, 2009). Our findings are consistent with previous studies in marine invertebrates, in which metabolic rate changed with varying food availabilities (see Table S1). Under food deprivation, Routine MR decreased by 20% (Experiments 2a,b), and this response was independent of laboratory conditions (Experiment 2b). Upon feeding, metabolic rate increased significantly by 43% and remained elevated for 24 h before returning to pre-feeding levels (Experiment 3). Size manipulation, furthermore, had unanticipated effects on the metabolic scaling of *B. neritina*. Although ontogenetic scaling is isometric, size manipulation resulted in a shift to allometry (Experiment 1), which corresponds to the static scaling in this species (Experiment 2a).

Food availability can have significant effects on the phenotype of an organism. Palumbi (1984) showed that demosponges change their overall body structure to maximize feeding in highly turbulent environments. Similarly, colonies of *B. neritina* develop smaller feeding structures when growing in environments with high density of

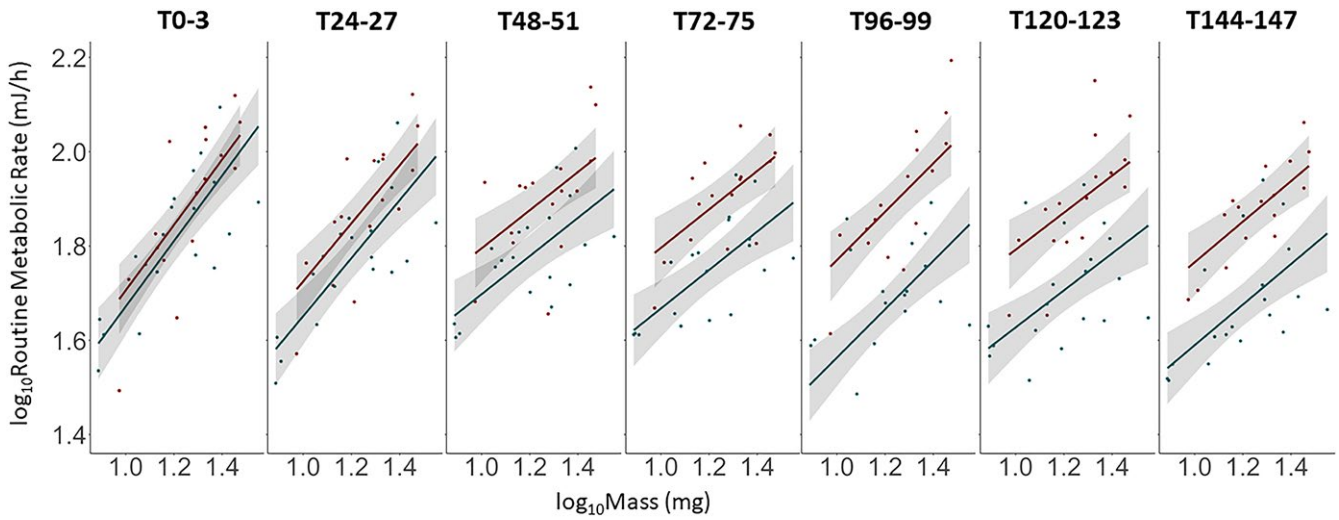

FIGURE 5 Predicted relationships (log-transformed) between routine metabolic rate (mJ/h) and mass (mg) of starved (blue lines) and fed (red lines) colonies of *Bugula neritina* over time. T0-3 depicts the metabolic rate of freshly collected colonies. T24-27, T48-51, T72-75, T96-99, T120-123, and T144-147 represent the metabolic rate of starved (blue points and lines) and fed (red points and lines) colonies after 24–27, 48–51, 72–75, 96–99, 120–123, and 144–147 h, respectively. Regression lines were derived using a log-transformed linear relationship, where $\log_{10}(\text{Routine MR}) = b \times \log_{10}(\text{Mass}) + \log_{10}(a)$. Each data point represents a colony repeatedly measured over time. Grey areas indicate the 95% confidence intervals

TABLE 3 Repeated measures ANCOVA examining the effects of mass, treatment (size-manipulated vs. intact), and feeding (starved vs. fed) on the Routine metabolic rate in colonies of *Bugula neritina*. Nonsignificant interactions were removed from the final model (Table S3)

	df	*F*	*p*
Between subjects			
$\log_{10}$(mass)	1	51.511	<0.0001
Treatment	1	2.735	0.108
Feeding	1	28.536	<0.0001
Error	31		
Within subjects			
Time	6	1.991	0.069
$\log_{10}$(mass × time)	6	2.347	0.033
Feeding × time	6	5.728	<0.0001
Treatment × time	6	2.022	0.065
Error	186		

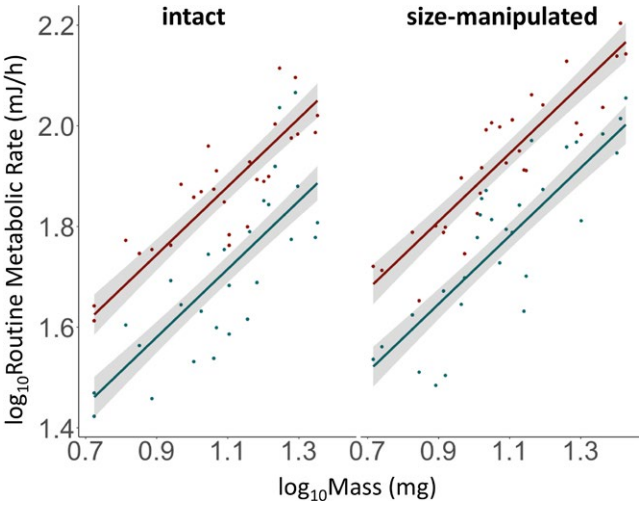

FIGURE 6 Predicted relationships (log-transformed) between routine metabolic rate (mJ/h) and mass (mg) of intact (left panel) and size-manipulated (right panel) colonies of *Bugula neritina* before (i.e., starved colonies; blue lines) and after feeding (red lines). Each data point represents a colony measured before (blue dots) and after feeding (red dots). Regression lines were derived using a log-transformed linear relationship, where $\log_{10}$(Routine MR) = $b \times \log_{10}$(Mass) + $\log_{10}(a)$. Grey areas indicate the 95% confidence intervals

TABLE 4 Repeated measures ANCOVA examining the effects of mass and treatment (size-manipulated vs. intact) on the Routine metabolic rate in colonies of *Bugula neritina* during SDA. Nonsignificant interactions were removed from the final model (Table S4)

	df	*F*	*p*
Between subjects			
$\log_{10}$(Mass)	1	242.607	<0.0001
Treatment	1	10.476	0.002
Error	53		
Within subjects			
Time	3	119.887	<0.0001
Treatment × time	3	2.403	0.069
Error	162		

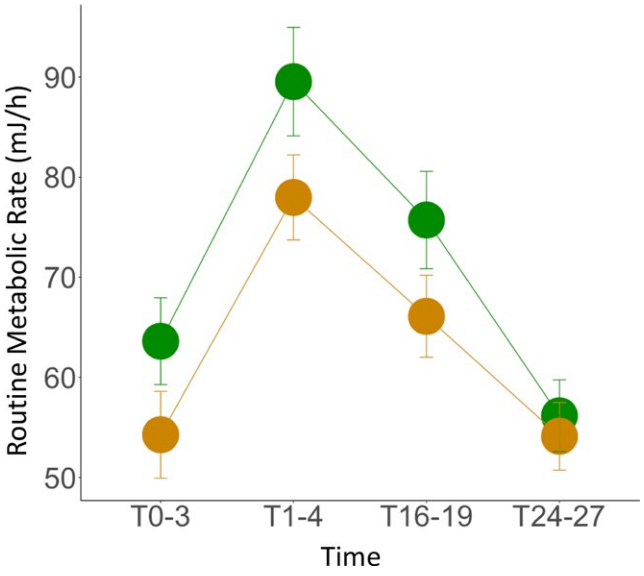

FIGURE 7 The change in mean routine metabolic rate (mJ/h) of colonies of *Bugula neritina* during specific dynamic action. Orange dots indicate the SDA response of intact colonies. Green dots indicate the SDA response of size-manipulated colonies. T0-3 depicts the mean metabolic rate of colonies that were starved for 24 h prior to measurements. T1-4 represents the mean peak metabolic rate of colonies 1–4 h after feeding. T16-19 and T24-27 are the mean metabolic rates of starved colonies 16–19 and 24–27 h after feeding. Error bars indicate the standard error

conspecifics (Thompson, Marshall, & Monro, 2015), and in such colonies the individual feeding rates are typically decreased (Amundsen, Knudsen, & Klemetsen, 2007; Damuth, 1981). In addition to this morphological plasticity, we show that metabolic rate changes with increased or restricted food availability. Importantly, this ability to alter metabolic rate can have implications for the life history of an individual (Stearns, 1992). In brown trout, for example, individuals that were best able to adjust metabolic rate had the highest growth rate under changing food availability (Auer, Salin, Rudolf, Anderson, & Metcalfe, 2015). Similarly, growth rate is positively correlated with the magnitude of the factorial scope during SDA in the common starfish, *Asterias rubens* (Vahl, 1984). Therefore, SDA is often used as an index of the energetic cost of growth or biosynthesis (Kiørboe, Munk, & Richardson, 1987; Wieser, 1994).

In *B. neritina*, Svensson and Marshall (2015) showed that food availability affects colony growth. Similarly, body size and fitness decrease with increasing conspecific densities (Allen, Buckley, & Marshall, 2008; Ghedini, White, & Marshall, 2017; Hart & Marshall, 2013). High conspecific densities, furthermore, result in decreased

individual metabolic rates along with decreased feeding rates (Ghedini et al., 2017). Here, reduced oxygen availabilities (Lagos, Barneche, White, & Marshall, 2017), or the presence of metabolites from conspecifics (Thompson et al., 2015), have been proposed to drive the observed decrease in metabolic rates. Our results, however, suggest that reductions in food availability alone (possibly associated with increased density) could drive these changes in metabolic rate.

Both the factorial scope and the duration of the overall SDA response vary among species (Secor, 2009). In comparison to other sessile marine invertebrates, we found that *B. neritina* had one of the lowest factorial scopes reported to date and the duration of the overall SDA response was lower than the median duration reported for other sessile marine invertebrates (see Figure 8). An organism's SDA is affected by various factors including meal type and size, and body size and temperature (Secor, 2009). For example, SDA in ectotherms living in colder environments is generally lower and lasts longer than in ectotherms in warmer environments (e.g., Peck & Veal, 2001). Although the factorial scope may be similar across all body sizes in some species (e.g., McGaw & Curtis, 2013), in most species the factorial scope increases with body size (e.g., Boyce & Clarke, 1997). The effects of meal type and size have been studied in several marine invertebrates (e.g., McGaw & Curtis, 2013; Rosas et al., 2001). Typically, an animal's factorial scope and duration increase with increased meal sizes and with meal types that are costlier to digest. In *B. neritina*, Kitamura and Hirayama (1984) found that colonies had the highest growth rate when fed with *R. salina* at a concentration similar to the one we used in the present study. Furthermore, when fed at very high algal concentrations, feeding activity in bryozoans decreases because the number of actively feeding zooids is reduced (Riisgård & Goldson, 1997). Thus, we are confident that the factorial scope reported here represents the upper limit for the postprandial increase in metabolic rate in *B. neritina*. Why the observed factorial scope in *B. neritina* is so low, however, cannot be easily explained by factors such as meal type or size, or body size or temperature.

In comparison with our study, Sigsgaard, Petersen, and Iversen (2003) found that the ascidian *Ciona intestinalis* exhibited one of the highest factorial scopes across all studied sessile marine invertebrates, and a comparably longer duration. Similarly, other sessile species, including species of molluscs, were found to have greater scopes and longer durations than *B. neritina* when fed with algae at both lower and higher temperatures (see Table S1). As far as we are aware, the only other colonial animal for which SDA has been characterized is the coral *A. danae* (Szmant-Froelich & Pilson, 1984). When fed a shrimp meal, colonies of *A. danae* exhibited a slightly higher factorial scope than that of *B. neritina*; the overall duration of SDA, however, was not reported (see Table S1). The factorial scope in *A. danae* was also low relative to other marine invertebrates (fifth lowest overall). Whether modularity (i.e., the fact that many small subunits take up and transform resources within a colony) is the cause of this relatively modest SDA response remains to be studied.

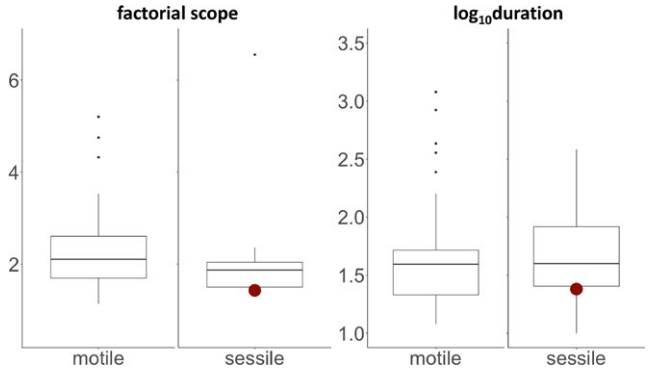

FIGURE 8 Factorial scopes and durations of specific dynamic action (SDA) in sessile and motile marine invertebrates, respectively (listed in Table S1). The red dot indicates either the scope or the duration of SDA in the colonial bryozoan *Bugula neritina*

Modular animals are useful for testing theories of metabolic scaling, as it is possible to manipulate their size and shape (reviewed in Burgess et al., 2017). In a colonial ascidian, Nakaya, Saito, and Motokawa (2003) found that metabolic scaling switched from allometry to isometry during the takeover stage of the colony, in which the zooids of the parent generation in a colony degenerate and zooids of a new generation develop in unison. Size manipulation, and also fusion of various colonies, however, did not affect the metabolic scaling in this species (Nakaya et al., 2005). White et al. (2011) did not find any differences in the allometric metabolic scaling between intact and size-manipulated colonies of the encrusting bryozoan *Hippoporina indica*. In the arborescent freshwater bryozoan *Fredericella sultana*, Hartikainen et al. (2014) showed that metabolic scaling in size-manipulated colonies is allometric. Similarly, allometric scaling has recently been demonstrated in size-manipulated colonies of *B. neritina* (Barneche et al., 2017). As we show here, metabolic scaling in field-collected intact colonies is isometric rather than allometric. It seems that the differences in metabolic scaling might be driven by unanticipated effects of size manipulation on metabolic rate in size-manipulated colonies. Within cheilostome bryozoans such as *B. neritina*, zooids are connected by pores in the interzooid walls (Best & Thorpe, 2001; Bobin, 1977; Lutaud, 1985; Mukai, Terakado, & Reed, 1997). Size manipulation might lead to leaking of nutrients, driving the differences in metabolic scaling between size-manipulated and intact colonies. Notably, both the size-manipulation approaches conducted by Barneche et al. (2017) and our approach (refer to Figure 1) reported similarities in the scaling of size-manipulated colonies. Although in their study, Barneche et al. (2017) cut off the tips of colonies to mimic natural predation, in our study we retained the upper part of the colony and discarded the stolon. As both approaches resulted in the allometric metabolic scaling of fragments, these findings indicate that variation in colony form is unlikely to drive the observed differences in the scaling. To fully understand the effects of size manipulation on metabolic rates and biological processes within *B. neritina* colonies, further studies are needed.

Overall, we find that neither feeding nor starvation alter metabolic scaling exponents in *B. neritina*. Size manipulation has unanticipated effects on metabolic scaling in this species. Although field-collected individuals of unknown age scale isometrically,

metabolic scaling in size-manipulated colonies is allometric, which corresponds with the static scaling of this species. There appears to be an unusually short SDA period and low scope in *B. neritina*. Whether this is a species-specific trait or one driven by coloniality is unclear at this stage, and we encourage further tests of SDA in other colonial marine invertebrates.

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CONFLICT OF INTEREST

All authors declare no conflict of interest.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

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