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Metabolic scaling in modular animals

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Abstract. Metabolic scaling is the relationship between organismal metabolic rate and body mass. Understanding the patterns and causes of metabolic scaling provides a powerful foundation for predicting biological processes at the level of individuals, populations, communities, and ecosystems. Despite intense interest in, and debate on, the mechanistic basis of metabolic scaling, relatively little attention has been paid to metabolic scaling in clonal animals with modular construction, such as colonial cnidarians, bryozoans, and colonial ascidians. Unlike unitary animals, modular animals are structural individuals subdivided into repeated morphological units, or modules, each able to acquire, process, and share resources. A modular design allows flexibility in organism size and shape with consequences for metabolic scaling. Furthermore, with careful consideration of the biology of modular animals, the size and shape of individual colonies can be experimentally manipulated to test competing theories pertaining to metabolic scaling. Here, we review metabolic scaling in modular animals and find that a wide range of scaling exponents, rather than a single value, has been reported for a variety of modular animals. We identify factors influencing variation in intraspecific scaling in this group that relate to the general observation that not all modules within a colony are identical. We highlight current gaps in our understanding of metabolic scaling in modular animals, and suggest future research directions, such as manipulating metabolic states and comparisons among species that differ in extent of module integration.

Additional key words: allometry, body size, colonial animals, isometry, respiration

Individual metabolism, the "fire of life" converting energy into whole-organism biomass and activity, is a fundamental process of life (Kleiber 1961; Schmidt-Nielsen 1984). As a result, understanding the relationship between whole-organism metabolic rate and body mass, known as metabolic scaling, provides a powerful foundation to predict biological processes at the level of individuals, populations, communities, and ecosystems (Nisbet et al. 2000; Brown et al. 2004; Whitfield 2004). The majority of studies on metabolic scaling have, however, focused on unitary animals and, to a lesser extent, unicellular organisms, algae, and plants (Reich et al. 2006; Glazier 2010).

Relatively little attention has been paid to metabolic scaling in clonal animals with modular construction, such as colonial cnidarians, bryozoans, and colonial ascidians (Kearney & White 2012), which are important components of the living benthos in many aquatic environments. A distinguishing feature of modular animals is that an individual organism is subdivided into functionally autonomous (or semi-autonomous) modules that are physically and physiologically interconnected to varying degrees within a colony (Vuorisalo & Tuomi 1986). Such modular design and clonal growth permits greater flexibility in organismal size and shape relative to unitary body plans, and potentially permits indeterminate growth.

Current explanations for the way metabolism scales with body size are linked with resource

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uptake, usage, and transportation throughout the body (e.g., West et al. 1997; Banavar et al. 2010; Glazier 2010, 2014b; Kearney & White 2012). A modular design allows an individual to gather food resources across much of the body surface rather than from a single source, and this influences how energy and material resources are transported and used within the colony (Jackson & Coates 1986; Hughes 2005; Winston 2010). However, the extent to which metabolic scaling relationships of modular animals differ from relationships observed in unitary organisms remains unresolved. Modular animals have also been proposed as useful models to distinguish among competing theories for metabolic scaling (Kearney & White 2012), such as the West, Brown, and Enquist (WBE; West et al. 1997) model, or the Dynamic Energy Budget model (DEB; Kooijman 2010), because the size and shape of an individual organism can be experimentally manipulated (Nakaya et al. 2005; White et al. 2011). Studying body plans beyond a unitary design can increase our understanding of the causes of metabolic scaling, the extent to which general theories apply to all organisms, and the extent to which such scaling relationships have predictable consequences at higher levels of biological organization (Glazier 2014a).

Here, we explore aspects of the biology of modular organisms that inform the causes of metabolic scaling. We also summarize existing data on metabolic scaling in aquatic benthic modular animal species and compare their mean scaling relationship to that of benthic unitary animal species. Metabolic scaling relationships can be considered both within and among species, but we focus on intraspecific scaling relationships (i.e., among conspecifics of different sizes) and compare them among species. We start by providing an overview of metabolic scaling and why it is valuable to focus on modular animals. We summarize existing data and compare estimates of metabolic scaling between benthic modular aquatic species and benthic unitary aquatic species. Subsequently, we discuss why metabolic scaling might vary among modular animals and suggest ways in which modular taxa can be exploited in experimental designs to assess the causes of metabolic scaling. Although the definition of modularity varies (e.g., Harper 1977; Esteve-Altava 2016), our use follows previous authors (Jackson 1977; Jackson & Coates 1986; Vuorisalo & Tuomi 1986; Hughes 2005). We recognize that modularity can be defined at a hierarchy of biological levels (e.g., organelles within cells, or tissues and organs within multicellular individuals), but we focus on the situation in colonial invertebrates where modules are repeated morphological units that are functionally autonomous (or semi-autonomous), multicellular, and are physically and physiologically interconnected within a structural individual (Vuorisalo & Tuomi 1986; Glazier 2014a).

Overview of metabolic scaling

Although not always addressed, considerations of metabolic scaling must first define metabolism. Metabolism is often loosely defined as the process of converting energy and materials into living structures and activities, including cellular and tissue maintenance, growth, reproduction, movement, and thermoregulation (Brown et al. 2004; Glazier 2015). Most analyses measure the rate of oxygen uptake as a direct measure of aerobic respiration, but alternative techniques can include the measurement of heat production, carbon dioxide production, or heart rate (Speakman 1998; White & Kearney 2014). The measurement of heat production has the advantage of quantifying both aerobic and anaerobic metabolism. Because most studies of metabolism in modular animals quantified oxygen use, we focused only on aerobic respiration. The contribution of anaerobic pathways to metabolic flux is likely to vary among taxa, but is expected to be small.

The relationship between organismal metabolic rate and organism body mass has long been described by the power function $Y=aM^b$ (Krogh 1916; Kleiber 1932). The exponent b defines the scaling of metabolic rate (Y) with mass (M), and a is a scaling coefficient. When metabolic rate varies in direct proportion to body mass, $b=1$ and metabolic rate scales isometrically; when $b \neq 1$, the relationship between metabolic rate and body mass is allometric. Allometric metabolic scaling means that larger organisms have a different metabolic rate per unit mass than smaller organisms. The relationship between metabolic rate and body mass is one of the best studied of all biological principles and numerous studies demonstrate that the exponent b is often <1 in organisms ranging from unicellular microbes to multicellular plants and animals (Brown et al. 2004; Glazier 2010). The consistency in the relationship among species has been interpreted as evidence of a fundamental constraint by which ecological processes, at multiple functional scales extending from individuals to ecosystems, are governed (Brown et al. 2004; Glazier 2010). Nonetheless, despite decades of research on this topic, there is still debate over the precise value of b and the mechanisms determining its value (Dodds et al. 2001; White & Seymour 2003; Agutter & Wheatley 2004;

Kozłowski & Konarzewski 2004; Savage et al. 2004; Brown et al. 2005; Van Der Meer 2006; Glazier 2005, 2014a; Maino et al. 2014).

The principle behind whole-organism metabolic allometry most often considered is that, as organisms grow larger, the volume (hence mass) of cells liberating energy from food resources increases faster than the surface area across which metabolic resources and products are exchanged with the external and internal environment (Glazier 2014a). The primary differences between the mechanistic theories that explain metabolic allometry are their assumptions about the flow and partitioning of assimilated energy into, through, and out of an organism. The WBE model assumes that whole-organism metabolic rate is limited by the internal transport of resources through hierarchical, fractal-like, pathways that extend throughout the volume of the organism (West et al. 1997, 1999; Price et al. 2007). By contrast, DEB models focus on surface area to volume relationships that influence the capacity to take up and use food and oxygen (Kooijman 2010). An alternative theory, the Metabolic-Level Boundaries (MLB) model, proposes that surface area-related fluxes of metabolites and waste products are most influential on metabolic scaling under conditions of high metabolic activity, while volume-related resource demands have the strongest influence on scaling when metabolic activity is low (Glazier 2010, 2014b). The self-organized criticality hypothesis (*sensu* Nakaya et al. 2005) predicts that the pattern of metabolic scaling in extant organisms emerged, perhaps by chance, from the first organisms that achieved self-organized criticality. In this construct, organisms could increase in size without needing elaborate controlling structures to regulate the activities of self-organized components (see Nakaya et al. 2005 for more information). For aquatic invertebrates and algae, Patterson (1992a,b) hypothesized that metabolic scaling is a function of water motion and the delivery of metabolically important compounds via diffusion across a boundary layer between water and body tissue. These and many other mechanistic theories for metabolic scaling are discussed in detail elsewhere (Dodds et al. 2001; Kozłowski et al. 2003; Agutter & Wheatley 2004; Glazier 2005, 2014a,b; Van Der Meer 2006; Kearney & White 2012; White & Kearney 2014).

Most mechanistic theories for metabolic scaling attempt to explain when and why the scaling exponent for whole-organism metabolic rate, *b*, should be centered on 0.75 (West et al. 1997), or vary between 0.5 and 1 (Price et al. 2007; Glazier 2010; Kooijman 2010). Although the scaling exponent

often approximates 0.75 in interspecific comparisons of unitary organisms, a range of scaling exponents is observed in intraspecific estimates (Patterson 1992b; Clarke & Johnston 1999; Glazier 2005; Killen et al. 2010). Even though some patterns of variation in the scaling of metabolism have emerged (White & Seymour 2004; Glazier 2005; Killen et al. 2010; Ehnes et al. 2011), the functional drivers of this variation remain unclear, including the extent to which the variance reflects biological and physiological processes versus methodological limitations (McKechnie & Wolf 2004; White & Seymour 2004; White & Kearney 2014).

Metabolic scaling in modular animals

Modular animals differ from unitary animals in how individuals grow, and in how they acquire and distribute resources, so they are likely to be metabolically constrained in different ways. Many unitary organisms grow via a determinate pathway of development into a tightly canalized adult form ("assembly-line animals" *sensu* Blackstone 2007). For unitary organisms, food is acquired from a single mouth and distributed throughout the body from that single origin. In contrast to unitary organisms, modular animals are structural individuals subdivided into repeated morphological units, or modules, that are multicellular, functionally autonomous (or semi-autonomous), and physically and physiologically connected to varying degrees. In modular animals, growth is achieved by asexually adding modules, such as polyps or zooids. Modular animals, therefore, have a greater variety of strategies available to increase the interface between the external and internal environment and show great diversity in the way they store, distribute, and use acquired resources (Blackstone & Bridge 2005; Blackstone 2007).

Modular animals were originally thought to be the exception to the 2/3 or 3/4 rule of metabolic allometry when Hughes & Hughes (1986) demonstrated metabolic isometry in their seminal work on colonies of the marine bryozoan *Electra pilosa*. Isometric scaling in modular animals is expected if metabolic allometry occurs at the level of the module, rather than the whole colony. That is, while surface area to volume ratios, or transport system mechanics, impose metabolic allometry on the size of individual modules, colony growth that proceeds through the addition of identical modules of a fixed size will allow whole-organism biomass to increase without changing mass-specific metabolic rate (Hughes 2005). Under such dynamics, metabolic

rate should increase allometrically with module size (should module size vary), but whole colony metabolic rate should increase isometrically with the number of modules (colony size) (Muñoz & Cancino 1989). In some ways, this idea parallels that of the metabolic scaling models of Davison (1955) and Kozłowski et al. (2003) based on cell size.

Although the expectations for, and consequences of, metabolic isometry are clear, our review of the literature since Hughes & Hughes (1986) reveals that scaling exponents deviating from isometry have been reported for a variety of modular animals (Table 1). One explanation for allometric scaling in modular taxa is that although modular growth has often been represented as the addition of identical units to individual colonies (Hughes 2005), the units within colonies can vary in size, shape, state, and function. Even morphologically similar units differ in age, ontogeny, nutritional state, reproductive state, and position within the colony (Harvell 1994; Carter et al. 2010; Winston 2010). More extreme variation imposed by functional specialization can be found in many taxa. For example, in bryozoans, the avicularia, kenozooids, and ovicells function for either defense, cleaning, attachment, support, or reproduction (Silen 1977). In hydrozoans, dactylozooids and gonozooids are specialized polyps that function for defense and reproduction, respectively (Stokes 1974; Brusca et al. 2016). These different functions require different levels of resources, which must be acquired and distributed from feeding modules in the colony in an analogous way to the sharing of resources between different organs in unitary organisms. Whether whole colony metabolism increases allometrically or isometrically with the number of modules will, therefore, depend on how the state, arrangement, integration, and functional role of individual modules influences the uptake, supply, and use of metabolic energy (Glazier 2014a).

Another reason for interest in metabolic scaling in modular animals is that such organisms have been proposed as experimental systems for testing theories pertaining to metabolic scaling, because it is possible to manipulate their body size and shape (Nakaya et al. 2005; White et al. 2011; Kearney & White 2012; Barneche et al. 2017). Different mechanistic theories of metabolic scaling often make similar predictions for b (e.g., Price et al. 2007; White et al. 2011), such that testing of these theories requires manipulative experiments to establish cause-and-effect relationships between metabolic rate and body mass. The capacity to manipulate body size potentially allows experimental control of confounding effects (e.g., associated with age or nutritional status) that are associated with body size. Manipulations of body mass in most unitary organisms can only be achieved through progressive starvation or enhanced food rations (although see Oviedo et al. 2003). As Schmidt-Nielsen (1984:7) lamented, "it is regrettable that we cannot study the effects of scaling by building super-sized elephants." By contrast, in modular animals and sponges, biomass can be reduced by experimentally dividing a large individual into smaller units (Nakaya et al. 2005; Hart & Keough 2009; White et al. 2011). Furthermore, in some species, several smaller animals can be grown together to promote fusion, thereby experimentally increasing body size (Wulff 1986, 1991; Chadwick-Furman & Weissman 1995; Grosberg et al. 1996; Nakaya et al. 2005). Several recent articles have used such biomass manipulations on modular species that have a flat, two-dimensional growth form, thereby demonstrating how scaling exponents can be manipulated to test predictions of competing theories (Nakaya et al. 2005; White et al. 2011; Barneche et al. 2017). Such experimental techniques are valuable, but require care and knowledge of organism biology to ensure that manipulations affect size without unintentionally altering other aspects related to module variability, integration, or organization. For example, Hart & Keough (2009) experimentally fragmented colonies of the encrusting bryozoan *Watersipora subtorquata* and found that small fragments had different growth and reproduction compared to small colonies that had reached a similar size through uninterrupted growth from a larva (Hart & Keough 2009).

Empirical estimates

We compiled intraspecific estimates of the metabolic scaling exponent b from the literature for modular animals. Our collation of data should not be interpreted as a formal meta-analysis because both the paucity of suitable studies and the issues we raise below preclude such a formal analysis at this time. Furthermore, we have ignored pelagic colonial animals, such as siphonophores and salps (Hirst et al. 2014). We have also ignored sponges, which, although not modular or colonial animals, are characterized by clonal growth allowing diverse shapes and sizes as in modular animals (see Reiswig 1974; Barneche et al. 2017 for estimates of scaling exponents in sponges). The extent to which the factors we identify as influencing metabolic scaling in benthic modular animals are unique to this group still requires investigation.

Table 1. Estimates of the intraspecific metabolic scaling exponent b, from the equation $Y=aM^b$, describing the relationship between organism metabolic rate (Y) and body mass (M) reported in the literature for modular animals (plotted in Fig. 1A). The 95% confidence interval is provided when reported by the authors.

Citation	Phylum	Species	Growth form	Whole-organism size range	Estimate of scaling exponent b (95% confidence interval)	Conditions
Jokiel and Morrissey (1986)[a]	Cnidaria	*Pocillopora damicornis*	Erect branching		0.99	
Sebens (1987)[a]	Cnidaria	*Alcyonium siderium*	Erect lobed		0.88	
Vollmer & Edmunds (2000)	Cnidaria	*Siderastrea siderea*	Mound	~1–400 mg Dry mass	0.176 (0.12–0.24)[b]	
Hughes & Hughes (1986)	Bryozoa	*Electra pilosa*	Flat encrusting	0.05–100 mg Dry mass	~1	
Muñoz & Cancino (1989)	Bryozoa	*Cauloramphus spiniferum*	Flat encrusting	2–550 Zooids	0.83 (0.48–1.18)[b]	
Barnes & Peck (2005)	Bryozoa	*Isoseculiflustra tenuis*	Erect unilaminar branching	~7–250 mg AFDW	0.998 (0.78–1.21)[b] 0.964 (0.79–1.14)[b]	Winter Summer
		Kymella polaris	Erect bilaminar branching	~10–200 mg AFDW	1.125 (0.88–1.37)[b] 0.974 (0.56–1.39)[b]	Winter Summer
		Camptoplites bicornis	Erect bush-like branching	~5–200 mg AFDW	0.835 (0.70–0.97)[b] 0.836 (0.71–0.96)[b]	Winter Summer
White et al. (2011)	Bryozoa	*Hippoporina indica*	Flat encrusting	7.9–194.9 mg Wet mass	0.47 (0.36–0.58)	
Hartikainen et al. (2014)	Bryozoa	*Lophopus crystallinus*	Flat encrusting caterpillar-like	~2–50 Zooids	1.19[c]	
		Cristatella mucedo	Flat encrusting (fan shaped)	0.5–5 mm Diameter	1.12[c]	
		Fredericella sultana	erect branching	~1–200 Zooids	0.61[d]	
Barneche et al. (2017)	Bryozoa	*Hippopodina iririkiensis*	Flat encrusting	~18–114 mg Mass	0.72 (0.29–1.14) 0.24 (−0.17 to 0.66)	10°C 25°C
		Bugula neritina	Erect bush-like branching	~3.5–319 mg Mass	0.42 (0.27–0.57) 0.72 (0.58–0.84)	10°C 25°C
		Bugula stolonifera	Erect bush-like branching	~0.7–92 mg Mass	0.68 (0.48–0.87) 0.65 (0.5–0.81)	10°C 25°C
Nakaya et al. (2003)	Chordata	*Botrylloides simodensis*	Flat encrusting	0.0848–3.25 g Wet mass	0.799 (0.74–0.859) 0.95 (0.894–1.01)	Ordinary state Takeover state
Nakaya et al. 2005	Chordata	*Botrylloides simodensis*	Flat encrusting	0.0636–3.56 g	0.751 (0.677–0.825)	Before manipulation
				Wet mass	0.828 (0.788–0.868)	After size manipulation
					0.825	Before division
					0.819	After division
					0.77	Before fusion
					0.898	After fusion

[a] Estimates of scaling exponents come from those calculated in Patterson (1992b).
[b] 95% confidence interval (CI) calculated from standard error (SE) reported by the author (95% CI ~1.96 × SE).
[c] Authors report exponent not significantly different from 1, but significantly different from 0.86 and from 0.67.
[d] Authors report exponent significantly different from 1 and 0.86, but not significantly different 0.67.
AFDW, ash-free dry weight.

Eleven studies reported 29 intraspecific estimates of b in 16 modular animal species (which included colonial cnidarians, bryozoans, and colonial ascidians; Table 1; Fig. 1). When using the median value of b per species, values of b for modular animals had a mean of 0.79 (0.66–0.93, 95% confidence interval) (Table 2) and a median value of 0.83 (Fig. 1). The scaling exponents reported to date ranged from 0.176 in a coral (Vollmer & Edmunds 2000) to 1.19 in a bryozoan (Hartikainen et al. 2014) (Table 1). The authors of the latter study report that the exponent was not significantly different from 1, but was significantly different from 0.75 and 0.67. All estimates of b (Table 1) that were >1 were not statistically different from 1 in the articles reporting these estimates.

For comparison, we also compiled intraspecific estimates of the metabolic scaling exponent b for benthic aquatic unitary animals (Supporting information, Table S1). The data include those compiled in table 5 of the appendix in Glazier (2005), supplemented by additional studies from our literature search. Fifty studies reported 320 intraspecific estimates of b in 71 benthic aquatic unitary animal species (Fig. 1; Table S1). When using the median value of b per species, values of b for unitary animals had a mean of 0.65 (0.62–0.69, 95% confidence interval) (Table 2) and a median value of 0.66 (Fig. 1). The mean value of b for unitary species was not significantly different from the mean value of b for modular species (Welch two-sample t-test, $t=1.95$, df$=17.15$, p$=0.07$). The estimates of b for modular animals were fewer and more variable than those for unitary animals (Levene's test for homogeneity of variances, with Keyes–Levy adjustment after removing the outlier of $b=0.176$ for *Siderastrea siderea*, Z$=5.56$, p$=0.02$; Fig. 1). Comparisons of b between unitary and modular species in the same phylum were not possible because of the limited data available (Table 2). More generally, phylogenetically corrected comparisons of b between unitary and modular species are complicated by the fact that only cnidarians and chordates contain numerous modular and unitary species (although there are few sister taxa). By contrast, almost all bryozoans are modular species (the exception being a few unique and relatively unknown species in the genus *Monobryozoon* that exist as a single autozooid), and other phyla contain only unitary species (Table 2). Despite the obvious caveats for inferences based on compilations of relatively sparse data (in the case of modular animals), comparisons without correcting for the lack of independence due to shared evolutionary
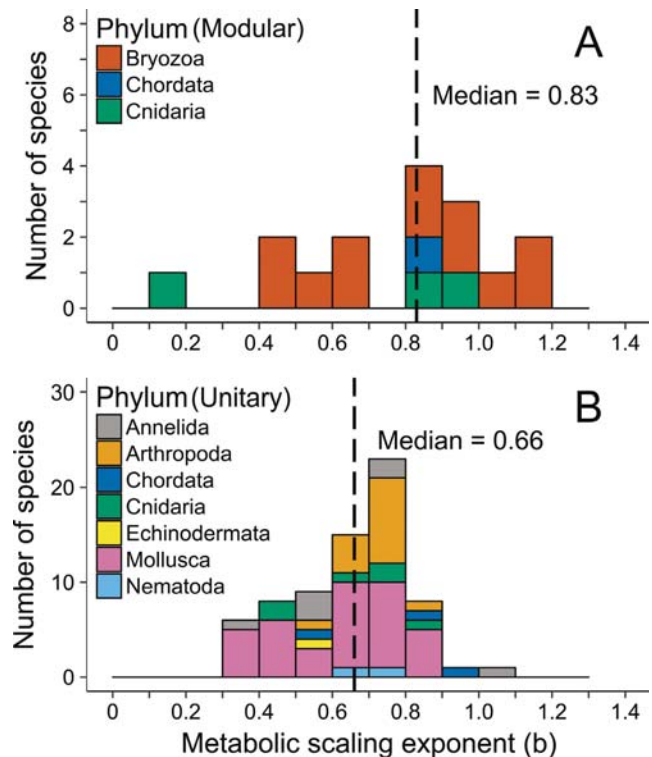

Fig. 1. Distribution of metabolic scaling exponent b from the equation $Y=aM^b$, describing the relationship between organism metabolic rate (Y) and body mass (M) reported in the literature for modular (**A**) ($n=16$ species) and unitary (**B**) ($n=71$ species) aquatic benthic invertebrates. Data for modular taxa come from Table 1. Data for unitary animals reported in Table S1. The median b per species was used to create this plot.

histories among lineages, and comparisons of measurements that include many sources of variance, these data are useful in identifying trends that can be used to generate hypotheses about how intrinsic and extrinsic factors might alter intraspecific metabolic scaling among species.

Why do estimates of metabolic scaling vary among modular animals?

Even though some fraction of the variability in Figure 1 might reflect methodological, or other non-biological sources of, variation, there are also likely many important biological causes for the variation. Measurements of metabolic rate commonly integrate a wide variety of functions performed by organisms. Biological sources of variation in metabolic scaling might therefore be related to differences in activity levels, growth rate and integration among parts of an individual, growth form, and the presence of photosynthetic endosymbionts.

Table 2. Mean estimate of the intraspecific metabolic scaling exponent b, from the equation $Y=aM^b$, describing the relationship between organism metabolic rate (Y) and body mass (M) for modular and unitary animals in each phylum.

Phylum	Classification	
	Modular	Unitary
Annelida		0.64 (0.47–0.81) (n=7)
Arthropoda		0.72 (0.68–0.76) (n=15)
Bryozoa	0.82 (0.67–0.96) (n=12)	
Chordata	0.82 (n=1)	0.78 (0.55–1.01) (n=3)
Cnidaria	0.68 (0.18–1.18) (n=3)	0.66 (0.53–0.79) (n=6)
Echinodermata		0.60 (n=1)
Mollusca		0.61 (0.56–0.66) (n=37)
Nematoda		0.72 (0.67–0.77) (n=2)
All Phyla	0.79 (0.66–0.93) (n=16)	0.65 (0.62–0.69) (n=71)

Means were calculated using the median value of b per species. Numbers in parentheses indicate the 95% confidence interval. n, number of species.

Metabolic state: resting versus active

Measurements of aerobic respiration are most common in analyses of metabolism, but not all measurements are directly comparable because the activity status of the organism affects respiration. Activity affects respiration through aerobic scope, which is the difference between basal metabolism (the lowest resting metabolism) and maximum metabolism, as occurs during greatest activity. The scaling exponent b depends on metabolic state (i.e., the degree of activity), which can be inferred, in a relative sense, from the intercept (i.e., elevation) of the scaling relationship (Glazier 2010). In unitary animals, it is generally accepted that exponents <1 characterize resting metabolic rates, whereas exponents approach 1 under maximal metabolic demand (Glazier 2010). This may suggest that allometric scaling of resting metabolic rate with b <1 creates opportunities for energetic savings in larger animals, without compromising peak performance (Glazier 2005).

Previous studies have assessed the effects of metabolic state by comparing the scaling relationships of active versus inactive birds, mammals, and insects

(Glazier 2010). In these taxa, it is relatively easy to diagnose active versus resting states because active individuals are usually flying or running. Many groups of modular animals, however, do not have such visual cues to their activity status, and it is much more difficult to assess activity level in most modular animals. Furthermore, modules may be uncoordinated in their active state, further complicating the assessment of their metabolic rate on a gradient from basal to maximum metabolic rate. For example, the metabolic rate of modules should be higher in bryozoans when lophophores are extended with their cilia beating to feed (i.e., an energy-requiring process), compared to when the lophophores are retracted into the cystid (i.e., the difference between active and resting metabolism).

Most analyses of interspecific metabolic scaling consider basal, or resting, metabolism (White 2011), yet the type of metabolism, in terms of resting or active, is often overlooked in studies of modular animals (Nakaya et al. 2003). Fluctuations in metabolic state and aerobic scope, however, are potentially important drivers of variation in b, both within and among species (Glazier 2010). Therefore, there is considerable value in identifying unequivocal criteria for an operational definition of resting in modular animals.

Integration of modules within colonies

The degree to which parts of a colonial organism are physically or physiologically integrated is likely to influence the pattern of metabolic scaling. If modules are physiologically similar and independent, whole colony metabolic rate is expected to be the product of the metabolic rate per module and the total number of modules, and therefore should scale isometrically. Although modules are typically not as tightly codependent as tissue and organs in unitary organisms, the more that modules are physiologically dependent on each other, the more metabolic scaling relationships can be expected to scale allometrically as in unitary organisms. For example, the colonial ascidian *Botrylloides simodensis* shows allometric metabolic scaling ($b=0.80$, 95% CI 0.74–0.86) when zooids share an integrated transport system, but isometric metabolic scaling ($b=0.95$, 95% CI 0.89–1.01) when zooids function more independently (Nakaya et al. 2003). One interpretation of these data focuses on interactions between zooids. In botryllid ascidians, such interactions temporally cease during approximately weekly takeover phases. The takeover phase occurs because the production of asexual zooids is synchronous, and when the next

generation of zooids starts to grow, the previous generation of zooids is resorbed (Milkman 1967; Nakaya et al. 2003). In the ordinary phase, zooids are arranged in clusters of rings (rosettes), where the excurrent siphon of each zooid opens into a common atrial opening, permitting a more powerful ejection of water than could otherwise be achieved by the excurrent siphon of a single zooid (Milkman 1967; Mukai et al. 1978; Nakaya et al. 2003) (similar to excurrent chimneys in encrusting bryozoans, Von Dassow 2006). During the takeover phase, interactions among zooids cease because the common drainage system of zooid clusters is disrupted, and the hearts in each zooid no longer cooperate to move blood through the common vascular network to which each zooid is connected. Such changes in resource sharing, from high integration to low integration, could explain the transition from allometric to isometric metabolic scaling.

Establishment and maintenance of resource-transport systems may incur high energetic costs, and, therefore, such systems are an important aspect of integration among modules that is fundamental to understanding variation in metabolic scaling in modular animals. For example, during the takeover phase in *B. simodensis*, Nakaya et al. (2003:1112), point out that "... cells of the growing zooids would show strong metabolic demand and reach maximum metabolic rate." Counterintuitively, the elevation of the regression line of metabolism on colony size declines substantially during the takeover phase, suggesting a lowered metabolic rate (Nakaya et al. 2003:fig. 6). Nakaya et al. (2003:1112) attribute this to an artifact: "Because the mass of the degenerating parent generation is large, it causes the overall specific metabolic rate to decline...." One could, therefore, summarize the life cycle of *B. simodensis* as alternating between an ordinary phase, with high integration allowing a resting metabolic rate, and a takeover phase, with low integration, and high metabolic rate. In the former phase, allometric exponents may be <1, while in the latter phase they are ~1.

The insights generated by Nakaya et al. (2003) can illuminate other examples of metabolic scaling in modular invertebrates. In cnidarians, for instance, some taxa employ only cilia in their transport systems, while other taxa exhibit primarily muscle-driven flow (Harmata et al. 2013). As a consequence, these taxa differ strikingly in colony integration. In some colonial octocorals, cilia-driven flow moves fluid continuously throughout the colony, and flow is simultaneously bidirectional, with polyps serving as "roundabouts" (*sensu* Harmata et al. 2013).

Metabolic demands of transport are evenly distributed among polyps in this design, as is resource acquisition, as these colonies are essentially autotrophic with respect to carbon, and dependent on their *Symbiodinium* symbionts (Harmata et al. 2013). Conversely, some colonial hydroids employ primarily muscle-driven flow within their transport systems (Dudgeon et al. 1999; Blackstone 2001; Harmata et al. 2013). Polyp contractions are stimulated by feeding, and food-rich fluid is driven from large feeding polyps in the center of colonies to colony edges that largely lack feeding polyps. Additionally, new modules initially are unable to feed until fully developed, so they require active or passive transport of food resources from older polyps to distal polyps. Flow to the periphery is sequentially bidirectional, meaning that feeding is concentrated in the center of the colony, which fuels the higher metabolic demands of polyps at the colony edge (Dudgeon et al. 1999; Blackstone 2001; Harmata et al. 2013).

Other examples may conform to this pattern of resource flow to the colony periphery. For example, in cheilostome bryozoans, metabolites are transported through a conducting system of hollow epithelial tissue (the funiculus), which runs from the gut throughout the zooid, and is associated with communication pores in the interzooid walls that physiologically connect zooids (Brusca et al. 2016). The transport system is compartmentalized by polarized plugs in the pore plate that promote peripheral movement of metabolites. In most encrusting bryozoans, primary modules at the edge of the colony typically bud new primary modules, so the metabolic costs of new modules at the growing edge include growth in addition to assimilation (feeding) and maintenance. In the bryozoan *Membranipora membranancea,* transport of carbon isotope tracer (^{14}C) was consistently unidirectional toward peripheral zooids, regardless of whether localized feeding through experimental microinjection occurred in center or edge locations (Miles et al. 1995). Higher metabolic rate in peripheral modules compared to central modules is expected to result in metabolic scaling exponents that depend on the extent of module integration. The DEB theory predicts that *b* will vary from 0.5 (if the transport of metabolites is slow relative to growth) to 1 (if the transport of metabolites is fast relative to growth) (White et al. 2011). This expectation was realized for the fast-growing encrusting bryozoan *Hippoporina indica,* in which *b* was 0.5 (White et al. 2011). A scaling exponent of 0.5 is also expected if the number of actively growing zooids on the

periphery increases with area to the power of 0.5, as it does in isomorphic shapes (Glazier 2014a). However, in *H. indica,* and in many other bryozoans (*M. membranancea* being one exception), older central modules produce ovicells, in which case their metabolic rate does not just include maintenance, so the assumption of higher metabolic rate in peripheral modules compared to central modules is not straightforward.

The ascidian example of metabolic scaling in a modular taxon (Nakaya et al. 2003, 2005) can be used to make predictions concerning the scaling of metabolic rate in other taxa. Colonies consisting of less-integrated modules should exhibit relatively high and stable metabolic rate, and their scaling exponents for metabolism should be ~1. Colonies with a greater degree of integration among modules, such as the hydroids in which muscle-driven flow is stimulated by feeding (Dudgeon et al. 1999; Blackstone 2001; Harmata et al. 2013), may only intermittently exhibit a resting metabolic rate. Therefore, measurements of metabolism during feeding are likely to reveal allometric scaling exponents <1, and perhaps even close to 0.75.

Growth form and three-dimensional morphologies

Morphology could explain variation in *b* by mediating the perimeter length to colony area ratio of the colony, thereby creating surface area across which the relative frequency of modules with differing metabolic rates can vary (Davies 1980). In flat, encrusting, two-dimensional growth forms approximating a disk with homogenous height, and a radius much greater than their height, surface area scales roughly in proportion to volume, promoting isometry. Some colonies that form erect, three-dimensional morphologies grow as sheet-like structures, which is in some ways similar to growth in two-dimensional encrusting morphologies. For example, the tissue of most colonial scleractinians occurs as a thin sheet over the surface of a mineral skeleton, so they should share similar surface area to volume ratios of live tissue with some flat two-dimensional morphologies. Likewise, upright, three-dimensional morphologies in some bryozoans can occur as a result of effectively one- or two-dimensional budding of zooids as uniserial (one zooid buds another end on) or multiserial (zooids bud others laterally and distally) growth, and as flat unilaminar (zooids on one side) or bilaminar (zooids on both sides) sheets. For organisms with sheet-like growth, these differences in organismal shape will lead to differences in perimeter length to colony area ratios, the

net effect of which will be variation in metabolic rates of edge versus central modules, and ultimately in the pattern of metabolic scaling (Patterson 1992b; Barnes & Peck 2005; Glazier 2014a; Hartikainen et al. 2014; Hirst et al. 2014; Glazier et al. 2015). Finally, erect, three-dimensional morphology may require increased metabolic demands, relative to encrusting growth forms, to increase structural strength to resist drag forces from water movement.

Colony morphology mediates the way that modules are spatially arranged and can result in among-module interference for resources (i.e., self-shading). Three-dimensional morphologies, therefore, are expected to show scaling exponents departing to a greater extent from the expectation of isometry relative to flat, two-dimensional, encrusting growth forms. In three-dimensional colonies, the capacity for modules to capture food (e.g., phytoplankton or zooplankton) typically varies among positions within a colony and with water flow (Okamura 1984; Sebens et al. 1997). Colony shape can also create drag causing lower water flow speeds around and within arborescent colonies that generate thicker boundary layers above the organismal tissue, especially in interstitial spaces among branches (Patterson 1992a; Hoogenboom & Connolly 2009). Such effects alter the microenvironment adjacent to the tissue relative to the ambient seawater, potentially causing modified conditions for O_2, CO_2, and pH (Patterson & Sebens 1991; Reidenbach et al. 2006; Chan et al. 2016). For example, as colonies of the scleractinian *Pocillopora verrucosa* grow larger, the branches become thicker and more clustered, and metabolic rate per unit surface area of tissue declines (Edmunds & Burgess 2016). For branching colonies, particle capture is lower for central compared with peripheral branches (McFadden 1986; Kim & Lasker 1997), particularly on branch apices (Sebens et al. 1997), or higher in peripheral modules under low water flow but higher in central modules under high water flow (Okamura 1984). In corals, the spaces among branches can develop largely stagnant seawater that quickly is depleted of food and metabolic resources (Chang et al. 2009). These effects can be augmented by variation in module density and tissue thickness within colonies (Wang-praseurt et al. 2016). Self-shading of resource capture is even apparent in modular organisms adopting flat sheet morphologies, where exposure to laminar and unidirectional flow results in high particle capture for modules on the leading edge of the colony, whereas modules behind them have impaired capture success (Buss 1979; Okamura 1985). Sharing resources among modules through an

effective transport system can ameliorate the effects of self-shading, particularly for morphologies that have high surface area to planar area. However, source and sink dynamics within a colony could also cause whole colony metabolism to scale with a lower exponent. Comparisons of metabolic scaling in three freshwater bryozoans are consistent with the expectation for increased allometry in more erect three-dimensional morphologies (Hartikainen et al. 2014). In the two species with flat, two-dimensional growth forms, metabolism scaled isometrically with size, but scaled allometrically ($b = 0.6$) in a species producing upright, arborescent colonies (Hartikainen et al. 2014).

Growth rate affects metabolic scaling (Glazier 2005, 2014a; Glazier et al. 2015). For example, DEB theory predicts that colony growth rate modifies the extent to which flat two-dimensional colonies exhibit isometry (White et al. 2011). This prediction arises if metabolic rate in peripheral modules is higher than in central modules, where metabolism in the former includes growth and maintenance, and in the latter includes only growth. For example, a circular growth form is predicted to exhibit increased allometry as the difference in metabolic rate in peripheral versus center modules increases, and to exhibit decreased allometry with slower colony growth (White et al. 2011). For colonies with a similar growth rate, expansion of the periphery into lobes leads to the prediction of a scaling exponent closer to isometry, because such growth increases the perimeter relative to that of a circle of similar area (White et al. 2011; Glazier 2014a). Based on this prediction, White et al. (2011) suggested that the isometric exponent found by Hughes & Hughes (1986) for *E. pilosa* might also have reflected the lobed and flattened morphology of this species. However, the prediction that growth rate should modify the extent to which encrusting two-dimensional colonies exhibit isometry applies only if there are no central polymorphic zooids (such as ovicells) that rely on resource capture from other zooids in the colony. Such polymorphic zooids may increase metabolic rate of central zooids, and remove the growth-driven differences in metabolic rate between peripheral versus center modules, making it difficult to interpret the cause of scaling.

Interestingly, the two species of flat bryozoan studied by Hartikainen et al. (2014), *Lophopus crystallinus* and *Cristatella mucedo*, may have maintained isometry by maintaining metabolic homeostasis in actively growing, peripheral modules as well as in non-growing, central modules. However, this outcome may have been achieved in different ways in the two species. *Cristatella mucedo* is unusual in that it produces a flat and elongated morphology, in which zooids are produced at the edge on either side of a central strip of degenerating zooids, that Hartikainen et al. (2014) described as a "caterpillar-like" morphology. These colonies increase in length without increasing in width, maintaining similar metabolic rates among modules because most modules remain as peripheral as the colony grows. Colonies of *L. crystallinus* (also a phylactolaematous bryozoan) have a flat, fan-like morphology, in which budding of new zooids is orientated in a single direction resulting in a larger distal zone of active zooids and a smaller proximal region of degenerating zooids. Because of frequent fission, *L. crystallinus* potentially exhibits similar metabolic rate in peripheral versus center modules. Colonies of *L. crystallinus,* generally occur at sizes in which the metabolic discrepancy between peripheral and central polyps is sufficiently small to support functional isometry.

The role of symbionts

Many modular organisms, across multiple different invertebrate groups, form symbioses. Photosynthetic symbiosis involving nutrient exchange, such as occurs between corals and dinoflagellates from the genus *Symbiodinium*, could be expected to decrease the reliance on transport networks that circulate resources between modules, because energy is harvested from sunlight through photosynthesis within cells scattered throughout the colony. When photosynthetic symbionts are present within tissues of integrated modules, the scaling of metabolism with colony size potentially might be independent of surface area to volume constraints, and not reliant on fractal circulation networks that underpin some explanations for allometric scaling (e.g., West et al. 1997). At present though, there are insufficient data to test whether b varies between symbiotic and non-symbiotic corals.

If the proportional contribution of symbiont biomass to holobiont biomass remains the same over all sizes, and the rate at which host resources are converted into symbiont and host biomass is the same, symbionts are unlikely to influence metabolic scaling. Increases in the proportional contribution of symbiont biomass to holobiont biomass, or changes in the rates at which host resources are converted into symbiont and host biomass across different host sizes, however, could provide a situation in which symbionts alter metabolic scaling in hosts (Poulin & George-Nascimento 2007; Robar et al.

2011). While the metabolic rate of symbionts may be modulated by the metabolic rate of the host, as symbionts rely on nitrogen and phosphorus derived from the host, metabolic rate of the host may increase with more symbionts, because they can directly supply the fuel and oxygen necessary for aerobic metabolism (Edmunds & Davies 1988) and moreover can lead to an oversupply of carbon relative to nitrogen and phosphorus. For instance, symbiotic corals in shallow water can release ~40–50% of their photosynthetically fixed carbon daily (e.g., Crossland et al. 1980; Muscatine et al. 1984), and such oversupply suggests measured metabolic rates of some reef corals are likely to be above basal levels. However, the proportional contribution of symbionts to host metabolic rate as host biomass increases is unresolved. Furthermore, photosynthetic symbiosis involving nutrient exchange might prevent consistent measures of metabolism, as well as alter patterns of scaling, in hosts if the symbiosis is mutualistic under some conditions, but parasitic in other conditions (Lesser et al. 2013; Shantz et al. 2016).

The additional resources supplied through translocation of carbon from photosynthetic symbionts to the host might counteract the effects of self-shading that can limit resource acquisition for modules at branch bases or colony centers, thereby providing a more even distribution of resources across the colony. Consequently, morphologies with high tissue surface area relative to planar areas (e.g., branching and foliose) should occur more frequently in symbiotic compared to non-symbiotic taxa in the same taxonomic group (e.g., Coates & Jackson 1987). To explore this pattern, we compiled data describing the colony morphology and photosynthetic symbiont association of 1234 scleractinian corals (see Appendix S1 and references therein; data primarily sourced from Wallace 1999; Cairns 2000; Veron 2000; Huang 2012, www.coraltraits.org). These data indicate that 84% of non-symbiotic species are solitary (e.g., *Flabellum* spp.), and only 16% develop branching, encrusting, or massive morphologies (e.g., *Solenosmilia variabilis*). By contrast, 94% of symbiotic species produce branching, columnar, encrusting, foliose, or massive colonies, and the morphological diversity observed among symbiotic species is larger than in non-symbiotic species (Fig. 2). Symbiosis is associated with changes in the magnitude and diversity of nutritional resources available to the host, as well as differences in colony morphologies, leading to contrasting predictions about how metabolism should scale with colony size. Photosynthetic symbiosis can be expected to favor isometric scaling if it frees colonies from constraints associated with resource uptake and circulation. On the other hand, the development of complex three-dimensional colony morphologies associated with symbiosis may increase variation in resource uptake between modules within colonies, and in fact counteract the benefits of symbiosis, leading to allometric scaling with b influenced by colony shape and growth rate.

Environmental context

Scaling is not immutable for any one Bauplan, functional group, or species, and is likely to vary in systematic ways as a result of environmental conditions. Of these conditions, potentially the most important are seawater flow and temperature, which provide first principle means by which b can be changed. Seawater flow is expected to drive variation in scaling relationships because it has interactive effects with organism shape and size, thereby mediating the overall effect of flow (as evaluated by the Reynolds number, Re, which is the ratio of inertial to viscous forces acting on the fluid as it moves past the organism) on organism mass transfer (as measured by the Sherwood number, Sh) (Patterson 1992a,b). Under certain assumptions, a given increase in flow speed and/or colony size should increase the flux of metabolic products according to $Sh=aRe^b$ (Patterson 1992a,b). Together, covariation in Re and Sh is expected to drive allometric scaling of metabolism, with exponents varying in predictable ways depending on organism size, shape, and flow regime (Hoogenboom & Connolly 2009).

Seawater temperature also should have direct and predictable effects on the metabolism of poikilotherms, at least until the threshold temperature is reached. Such variation will alter the elevation (a) of scaling relationships, and might promote changes in the relative importance of the surface area (i.e., $b=\frac{2}{3}$) and mass (i.e., $b=1$) limits to scaling relationships as a function of the magnitude of metabolism (Glazier 2010, 2014b). Temperature variation might also influence metabolic scaling coefficients (Barnes & Peck 2005, Glazier 2010, 2014a; White et al. 2011; Barneche et al. 2017). The DEB theory predicts that metabolic scaling exponents should be higher (more isometric) in cooler temperatures, such as higher latitudes or in winter months, because of slower growth (White et al. 2011). The MLB hypothesis predicts that metabolic scaling exponents should be higher in cooler temperatures because of decreases in metabolic rate (Glazier 2010, 2014a).
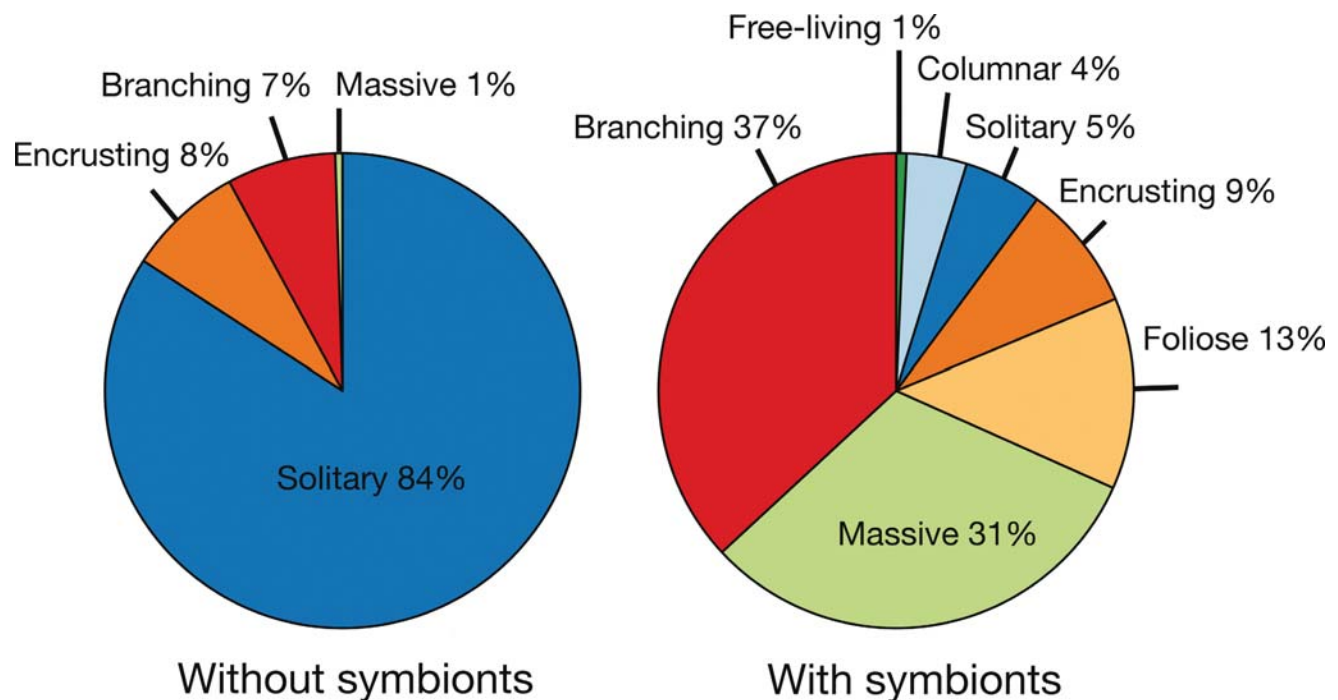
Fig. 2. Relative frequencies of colony morphologies for scleractinian coral species, **(A)** without photosymbionts and; **(B)** with photosymbionts (including both obligate and facultative associations). "Encrusting" refers to polyps forming a thin layer over existing substratum; "branching" refers to the production of upright, bifurcating branches from an encrusting base; "columnar" refers to production of thick, non-bifurcating branches; "massive" refers to production of an approximately hemispherical skeleton and includes colonies with some encrusting areas, "foliose" refers to the production of laminae that may be horizontal or vertically oriented; "free-living" refers to morphologies that are colonial but not attached to the substratum; and "solitary" refers to single polyps, which may be either attached or free-living (see Appendix S1 and references therein; data primarily sourced from Wallace 1999; Cairns 2000; Veron 2000; Huang 2012, www.coraltraits.org).

Future directions

As other researchers have also noted, future experimental analyses of metabolic scaling in modular organisms will be more valuable than additional analyses of statistical relationships between metabolism and body size (Glazier 2005, 2010, 2014a; Nakaya et al. 2005; White et al. 2011; Kearney & White 2012; Barneche et al. 2017). Carefully designed experiments with modular taxa can allow explicit tests of the mechanisms hypothesized to cause variation in metabolic scaling in ways that are difficult, or impossible, in unitary organisms. The issues detailed in the preceding sections make it clear that many questions pertaining to the causes and consequences of variation in metabolic scaling remain to be resolved. Two issues we consider to be important in designing experiments and making comparisons are discussed below.

Manipulate metabolic states

Metabolic or physiological state (i.e., resting vs. active state) is a potentially important source of variance driving variation in metabolic scaling exponents in modular animals. While inferences can be made about metabolic state from variability in estimates of the elevation of scaling relationships in multiple studies (Glazier 2010), more definitive insight must come from organisms that are quantitatively exercised (e.g., running mammals or flying insects) (Glazier 2014b). For unitary organisms whose functional biology is well understood, it is relatively easy to determine what factors induce metabolic demand, and when such organisms are resting. Conversely, the functional biology of many colonial organisms remains poorly characterized and this impedes assessment of activity levels.

Potential means to address the issue of metabolic or physiological state include the use of standardized conditions under which metabolism is measured. For example, a fixed starvation period determined through titration of metabolism against time to identify the inverse asymptote of metabolism can be used to understand metabolic state, and potentially to identify a state under which resting metabolism can operationally be defined. Metabolic

uncouplers (Blackstone 2003) have potentially insightful roles in studying scaling of maximal metabolic rate and aerobic scope. The well-characterized mitochondrial metabolic states (Chance & Williams 1956) may provide another opportunity to understand aerobic scope and scaling. One could induce a minimal metabolic rate (state 2 [after Chance & Williams 1956]) in an organism through starvation (Jacobson et al. 2016), and also induce maximal metabolic rate (state 3) using chemical uncouplers of oxidative phosphorylation (Blackstone 2003). By characterizing these endpoints and measuring where the unmanipulated metabolic rate lies between them, stronger insights into the nature of metabolic scaling could be obtained. Under conditions of maximal metabolic demand, scaling exponents can approach 1 (Glazier 2010). This may suggest that resting metabolic rate confers beneficial energetic savings for larger animals, without compromising the capacity for aerobic scope (i.e., peak performance). If so, resting metabolic rate could be viewed as an adaptation derived by tightly integrated unitary animals to facilitate larger sizes. Understanding whether, and when, modular animals display this kind of adaptation will be a key result of such studies.

Define and measure module integration

Objective comparisons between organisms with respect to degree of integration require a closer consideration of what is meant by integration. Situations where modules are integrated versus not integrated may only be clear in some taxa (e.g., Nakaya et al. 2003). An overall evaluation of the degree of integration within modular organisms should include these variables: the coordination of rapid whole-organism responses to external stimuli; the degree to which loss of parts impedes whole-organism performance; differential importance of parts to overall functioning (i.e., division of labor); regeneration of lost parts; and efficiency of resource-transport networks in subsidizing portions of the organism that are not directly involved in resource acquisition (for sponges, Hartman & Reiswig 1973; Wulff 2006, 2010). By including all of these variables in an evaluation of integration, it should be possible to make objective, and biologically meaningful, comparisons of the degree of internal integration among organisms sharing a modular design. Defining the extent to which modular organisms differ in the degree of integration would provide the means to experimentally test how regeneration or division of labor influences metabolic rate. While the multidimensional nature of the concept of integration makes it unlikely that a single classification scheme can be devised that would be appropriate for all taxa, relative integration among species could be considered.

Conclusions

Metabolic scaling varies among modular animals. Although some fraction of this variability might be a product of methodological variation, we contend that variability in intraspecific scaling exponents for modular animals is an important part of the biological signal, and not simply a component of the residual variance to be ignored as noise. Therefore, there is more to be gained by embracing the variation in intraspecific metabolic scaling exponents among species and attempting to explain it based on organism biology, rather than seeking a single value of b, from which departures in empirical value are measured (Glazier 2010, 2014a). This has important implications for the need to scale-up organismic studies to predict community and ecosystem responses to climate change and ocean acidification (Brown et al. 2004; Pandolfi et al. 2011; Bruno et al. 2015).

Modular animals differ in their degree of internal integration, growth form, association with photosynthetic symbionts, environmental sensitivity (e.g., water flow and temperature), and physiology. The multiple causes for variation in metabolic scaling can be studied with consideration of modular biology and careful application of suitable experimentation. An advantage of studying metabolic scaling in modular organisms is that whole-organism size can be experimentally increased or decreased. A lingering limitation, however, is that it is still difficult to experimentally alter the size of individual modules, so manipulating this aspect of the size of modular animals suffers a constraint similar to studies based on manipulating the size of unitary organisms. Nonetheless, metabolic rate may not always be equal in all repeated modules of similar size, and not all modules have the same metabolic requirement or access to resources. Therefore, a colonial modular design does not guarantee freedom from allometry. This has important implications, both in understanding the biology of metabolic scaling and in the ecology and evolution of modularity. It is worth emphasizing that despite limited available data, variation in b emerges among modular taxa, highlighting the need to explain variation in metabolic scaling.

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Supporting information

Additional Supporting information may be found in the online version of this article:

Table S1. Estimates of the metabolic scaling exponents for unitary aquatic benthic invertebrates. These data include those compiled by Glazier (2005), supplemented by additional studies from our literature search.

Appendix S1. Data and references for colony morphology and photosynthetic symbiont association for 1234 scleractinian corals.