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Economies of scaling: More evidence that allometry of metabolism is linked to activity, metabolic rate and habitat

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ABSTRACT

Organismal metabolic rates influence many ecological processes, and the mass-specific metabolic rate of organisms decreases with increasing body mass according to a power law. The exponent in this equation is commonly thought to be the three-quarter-power of body mass, determined by fundamental physical laws that extend across taxa. However, recent work has cast doubt as to the universality of this relationship, the value of 0.75 being an interspecies 'average' of scaling exponents that vary naturally between certain boundaries. There is growing evidence that metabolic scaling varies significantly between even closely related species, and that different values can be associated with lifestyle, activity and metabolic rates. Here we show that the value of the metabolic scaling exponent varies within a group of marine ectotherms, chitons (Mollusca: Polyplacophora: Mopaliidae), and that differences in the scaling relationship may be linked to species-specific adaptations to different but overlapping microhabitats. Oxygen consumption rates of six closely related, co-occurring chiton species from the eastern Pacific (Vancouver Island, British Columbia) were examined under controlled experimental conditions. Results show that the scaling exponent varies between species (between 0.64 and 0.91). Different activity levels, metabolic rates and lifestyle may explain this variation. The interspecific scaling exponent in these data is not significantly different from the archetypal 0.75 value, even though five out of six species-specific values are significantly different from that value. Our data suggest that studies using commonly accepted values such as 0.75 derived from theoretical models to extrapolate metabolic data of species to population or community levels should consider the likely variation in exponents that exists in the real world, or seek to encompass such error in their models. This study, as in numerous previous ones, demonstrates that scaling exponents show large, naturally occurring variation, and provides more evidence against the existence of a universal scaling law.

1. Introduction

Allometric scaling of metabolic rates with body mass is an extensively studied phenomenon (Kleiber, 1932; Rubner, 1883; Schmidt-Nielsen, 1984; Zeuthen, 1953). Metabolic rate (R) follows a power law relationship to body mass such that:

$$R = aM^b$$

where M is body mass, a is a mass-independent normalization constant (the mass coefficient) that varies according to metabolic activity level, and b is a scaling exponent (Kleiber, 1932; Krogh, 1916). The value of b, or whether there is a consistent value between taxa, has been the particular subject of ongoing debate (Agutter and Wheatley, 2004). Rubner (1883) suggested that the value should be two-thirds (0.667), due to geometric ratios of surface area to volume of three-dimensional objects and the need for endotherms to regulate heat produced by metabolism. However, Kleiber (1932) noted a value approximating 0.75 in a study on birds and mammals (the origin of the so-called '3/4-power law'). It was also noted that this 3/4-power law apparently applied to many other taxa, including ectotherms (Hemmingsen, 1960). Similar 'quarter-power' scaling relationships have been observed for a variety of biological and ecological processes including mitochondrial densities (West et al., 2002), population growth rates (Savage et al., 2004b), and developmental timing (Gillooly et al., 2002). The apparent ubiquity of quarter-power relationships led to the conclusion that scaling must have a common underlying mechanistic origin (Savage et al., 2004a). West et al. (1997) proposed a physical basis for the value of 0.75, based upon the fractal nature of resource distribution networks in living organisms (the WBE model), a model subsequently supported through further theoretical refinement (e.g. Banavar et al., 1999, 2010) and empirical data (e.g. Riveros and Enquist, 2011; Savage et al., 2004a). Such models

Abbreviations: MLB, Metabolic Level Boundaries hypothesis; WBE, West, Brown, Enquist model; MTE, Metabolic Theory of Ecology.

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have been broadened to encompass whole ecosystem level processes, such as in the 'Metabolic Theory of Ecology' (MTE) (Brown et al., 2004), which attempts to explain broad ecological trends from metabolic rates (and hence body mass) in individual component organisms.

Recently the '3/4-power law', and the WBE model in particular, has come under increasing criticism (Bokma, 2004; Darveau et al., 2002; Dodds et al., 2001; Suarez et al., 2004; Symonds and Elgar, 2002; White and Seymour, 2003), particularly due to its inherent broad assumptions (Agutter and Wheatley, 2004; Savage et al., 2008), and the numerous examples of observed deviations of *b* from 0.75 (see Glazier, 2005). In a comprehensive review, Glazier (2005) showed that just over 50% of intraspecific studies found exponent values significantly different from 0.75 across a range of taxa. Additionally, some species that appear to follow the 0.75 model do not possess the circulatory or resource distribution networks upon which it is based (Glazier, 2005, 2006). While some of the apparent deviations from the 0.75 model may be attributed to ecological factors affecting metabolism or methodological error, several authors have suggested that it is more likely that the value of 0.75 is in fact an interspecies 'average' of different, naturally occurring allometric scaling values and that no 'universal' scaling law exists (Agutter and Wheatley, 2004; Bokma, 2004; Brey, 2010; Duncan et al., 2007; Glazier, 2006; Riisgård, 1998; Seibel, 2007; Suarez et al., 2004; White, 2011).

A potentially unifying approach has been proposed by Glazier (2005, 2010), in the form of the metabolic-level boundaries (MLB) hypothesis. This model incorporates aspects of several competing models and may explain much of the observed variability in scaling relationships. The MLB hypothesis describes how observed values of *b* often fall between theorized boundary values of two-thirds (0.667) and one (1.0). The former is when surface-area limits affect fluxes of resources, heat and waste products (essentially Rubner's (1883) two-thirds mass-to-volume ratio model); the latter when volume limits on energy use and power production dominate. It explains how *b* varies when supply exceeds metabolic demand, and when metabolic demand exceeds supply. Where *b* falls on the spectrum between these boundaries depends on several factors, including metabolic rate, activity and ecological factors.

The nature of metabolic scaling relationships is important for a number of reasons. It is of fundamental importance to the development of life, as scaling exponents of less than one describe a process of increased efficiency in metabolism with greater body size. An allometric scaling exponent of less than one means that as organisms get larger, either through ontogenetic or evolutionary development, they possess a relatively lower metabolism and so require relatively fewer resources per unit body mass. In the presence of adequate resources this provides an incentive for organisms to grow larger (although there may be other physiological, environmental or ecological factors which do the contrary). Furthermore, the scaling exponent describes the ecological relationship between organisms of different size in a community, and differences in the value of *b* may affect resource partitioning, competition and other community interactions both within and between species (Ohlberger et al., 2011). If the scaling exponent is not a fixed value but plastic, extrinsic factors such as environmental change may cause it to alter, with potential consequences for intra- and interspecific community dynamics. Finally, in ecological studies and models the commonly accepted allometric scaling value of 0.75 is routinely used to standardize and extrapolate metabolic rates of species to larger population or community levels (e.g. Brose et al., 2006; Harper and Peck, 2003; Lebsack, 1975; Seibel and Drazen, 2007). Even a small difference in the value of the scaling exponent can cause profound error in such models (Finn et al., 2002; Riisgård, 1998).

Differences in body mass are commonly larger between species than within species, so comparative studies have tended to focus on interspecific analyses. Comparative intraspecific studies of metabolism can clarify the extent of variation in *b* away from the classic models, even among closely related, functionally similar organisms. The tendency of theoretical models to focus on interspecific analyses may obscure the natural variation in *b* between species (Glazier, 2010). It is important to extend knowledge about scaling relationships to as wide a range of taxa as possible to facilitate full understanding of potential variation in allometric relationships.

The present study examines the metabolic scaling relationships among a group of closely-related, functionally similar marine species with the aim of determining whether scaling relationships differ significantly. Where differences are observed, we examine these patterns in light of ecology, lifestyle and other extrinsic factors with reference to recent theory.

2. Materials and methods

2.1. Study species

Polyplacophoran mollusks (chitons), are exclusively marine, characterized by their eight articulating shells (or valves), and represent an ancient molluscan lineage that is morphologically constrained in extant taxa (Sirenko, 2006). They are found in every ocean and in some regions may be the dominant intertidal grazing mollusk (Otaiza and Santelices, 1985; Smith and Otway, 1997). In such regions they control the structure of the algal biomass and therefore wider community structure (Dethier and Duggins, 1984; Gaines, 1985; Paine and Vadas, 1969; Stebbins, 1988). The full contribution of chitons to energy budgets and nutrient cycling in marine ecosystems is not yet understood, and quantifying their metabolic rates is a first step in determining their function in coastal food webs. Numerous chiton species are often found inhabiting the same locality (Kangas and Shepherd, 1984; Murdoch and Shumway, 1980; Piercy, 1987). The fauna in the eastern Pacific is particularly diverse (Fitzgerald, 1975), and here chiton species demonstrate the greatest variation in body mass (MacGinitie and MacGinitie, 1968; Slieker, 2000). The species examined in this study demonstrate wide variation in maximum body mass, and broadly co-occur, inhabiting distinct but overlapping ecological niches (Piercy, 1987). The species selected for this work are also phylogenetically constrained and all represent a single taxonomic family, Mopaliidae. As such they represent an excellent model system to examine how allometric scaling of metabolic rate may vary between closely related, functionally similar marine ectotherms, and whether the differences may be associated with lifestyle and ecological traits.

Six species were chosen based on common co-occurrence in rocky shore habitat, differing lifestyles, and variation in body mass (Table 1). *Katharina tunicata* (Wood, 1815) is a large, common species found on moderately exposed rocky shores where it feeds on large-leaf algae, especially *Ulva* and *Hedophyllum* (Dayton, 1975; Eernisse et al., 2007; Rostal and Simpson, 1988). *Cyanoplax dentiens* (Gould, 1846) is also very common, but often overlooked as it has a very small maximum body size in comparison to other co-occurring species (Eernisse et al., 2007). It is also commonly found on exposed rock surfaces where it grazes mainly on diatoms (Piercy, 1987). *Mopalia lignosa* (Gould, 1846) and *Mopalia muscosa* (Gould, 1846) are two species which grow relatively large and are generalist algal grazers on more sheltered surfaces and under boulders (Eernisse et al., 2007; Piercy, 1987). All four of these species are found throughout the intertidal into the shallow subtidal. *Tonicella lineata* (Wood, 1815) is generally found in the lower intertidal and shallow subtidal and feeds almost exclusively on encrusting coralline algae (Andrus and Legard, 1975; Barnes and Gonor, 1973; Demopulos, 1975). *Placiphorella velata* (Carpenter MS, Dall, 1879) is usually subtidal but occurs in the low intertidal, and is one of the most unusual chitons. While other species may ingest animal matter incidentally in the course of grazing (Barnawell, 1960), *P. velata* is an ambush predator, using its extended anterior girdle to trap

Table 1
Ordinary least square (OLS) linear regressions summary data; mass coefficient a (± SE) and allometric scaling exponent b (± 95% CI) for the interspecific regression of all six species plus that for each species. The last three columns indicate if b differs significantly from the commonly proposed value in the '3/4 power law' (0.75; West et al., 1997) and theoretical boundary limit values from the MLB hypothesis (0.667 and 1.0; Glazier, 2010).

Species	R	Mass coefficient a (± SE)	Scaling exponent b (± 95% CI)	0.667	0.75	1.0
All (Interspecific)	0.96	0.183 (±0.008)	0.73 (±0.03)	<0.05	NS	<0.05
Cyanoplax dentiens	0.96	0.520 (±0.106)	0.91 (±0.10)	<0.05	<0.05	NS
Tonicella lineata	0.97	0.251 (±0.027)	0.86 (±0.08)	<0.05	<0.05	<0.05
Mopalia lignosa	0.95	0.190 (±0.020)	0.69 (±0.11)	NS	NS	<0.05
Mopalia muscosa	0.99	0.182 (±0.013)	0.64 (±0.08)	NS	<0.05	<0.05
Katharina tunicata	0.99	0.195 (±0.006)	0.87 (±0.03)	<0.05	<0.05	<0.05
Placiphorella velata	0.97	0.145 (±0.010)	0.91 (±0.10)	<0.05	<0.05	NS

amphipods and small crustaceans. However, it is sedentary, and even in captivity may remain motionless for a number of weeks (McLean, 1962).

2.2. Specimen collection and maintenance

Ontogenetic series of specimens for each species were collected from the intertidal at sites around Bamfield, Vancouver Island, British Columbia, August 2011, including two *P. velata* specimens. Additional *P. velata* and *T. lineata* specimens were collected by SCUBA divers from Sanford Island, near Bamfield at approximately 10 m depth. Specimens were stored in a sea-table with flow-through seawater, and cleaned under magnification to remove encrusting fauna and flora, and left to recover before transport to the University of British Columbia, Vancouver where they were housed in perforated containers in a sea-table in re-circulating, aerated seawater (12 °C, salinity 30 ppt) and allowed to acclimate. Specimens had been starved for a minimum of seven days before experiments commenced.

2.3. Respiration experiments

Fiber-optic oxygen probes (FOXY systems, Ocean Optics, Dunedin, Florida) were calibrated at the start of each day using the same seawater in which specimens were housed and subsequently analyzed. Oxygen concentrations of experimental water were checked periodically using a Hach HQ10 dissolved oxygen meter accurate to 0.2 mg L^{-1} and found to be within this error range of calculated air-saturated values for the experimental conditions of temperature, pressure and salinity (8.92 mg L^{-1}; calculated according to Benson and Krause (1984)). Probes were calibrated for 0% oxygen using a chamber filled with flow-through nitrogen gas. Probes were allowed to stabilize in each of these calibration media for approximately 30 min before calibrations were set. Calibrations were checked after each trial, however no trials required adjustment for probe drift.

Shortly before experiments, each specimen was again gently cleaned using a soft brush and placed in a cylindrical Perspex respirometry chamber and allowed to attach to the internal surface of the unsealed chambers while under water. Chamber volumes ranged from 20 ml to 300 ml. Small stir bars were inserted, and chambers were sealed and fitted with a fiber-optic oxygen probe connected to a PC recording module. Chambers were placed in a tank containing circulating water brought from the storage sea-table to ensure constant temperature. The tank was situated above magnetic stirring plates. Each chamber was arranged so the stir bar rotated, but did not touch the specimen. Two to six trials were run simultaneously.

Oxygen tensions were recorded at intervals of 1 s down to a minimum of 50% of air-saturated conditions, taking approximately 2–10 h depending on the specimen. The chamber was then removed, dried externally and total mass determined. The specimen was removed, blotted dry on tissue paper and weighed. The chamber was emptied, dried and reweighed to determine internal water mass. Seawater mass was converted to volume according to Fofonoff and Millard (1983), using the calculated seawater density at the appropriate temperature and salinity.

Some specimens were recorded more than once, but allowed several days recovery in individually labeled containers in the sea-table. Only one trial per individual specimen was used for subsequent analysis.

To quantify any contribution of microbial organisms to oxygen consumption, six control trials were conducted using chambers containing only seawater, and a correction based on this was applied to all experimental data. Microbial action accounted for approximately 20% to <0.001% of total O_2 depletion depending on specimen size and chamber volume.

Total dry mass (DM) in grams was determined for all specimens after drying at 60 °C for a minimum of two days until constant mass was achieved. Specimens were then incinerated at 500 °C for 2 h in a muffle furnace and reweighed to establish shell and ash mass, and this was subtracted from DM to determine ash-free dry tissue (AFDT) mass. Masses were determined on a Mettler Toledo precision analytical balance accurate to six decimal places for DM less than 0.8 g and to five decimal places for DM 0.8 g to 3.4 g. Specimens with DM over 3.4 g were measured on an AE Adam balance accurate to four decimal places. The same balance used to determine DM was subsequently used to determine ash and shell mass for the same specimen.

2.4. Data analysis

Oxygen consumption rates (VO_2) ($mgO_2\ h^{-1}$) were determined for each specimen by averaging the rate of uptake over the period in which oxygen was reduced from 95% to 85% of air-saturated conditions. VO_2 and AFDT masses were log-transformed and a linear ordinary least squares (OLS) regression analysis was performed on the log-transformed data to determine coefficient (a) and scaling exponent (b) values. OLS regressions were performed both on a per-species (intraspecific) basis and on the entire dataset (interspecific). An ANCOVA analysis was performed on the resulting intraspecific OLS regressions.

Oxygen consumption rates (VO_2) were used to calculate mass-specific oxygen uptake using AFDT mass (mVO_2) ($mgO_2\ h^{-1}\ g^{-1}$), and a mean of these calculated per species. One-way ANOVA analysis was performed on these data, with post-hoc Tukey multiple comparisons.

In addition to mean mVO_2, an additional metric to estimate and compare metabolic levels (L_m) was calculated according to the method described by Killen et al. (2010), this being the predicted mass-specific metabolic rate at the midpoint of each species' regression line in log space.

All statistical analyses were implemented in R (R core development team, 2011). All tests of significance were performed with $\alpha = 0.05$, and all measurements of variability are standard error (SE). Regression exponents (b) are reported with ±95% confidence intervals (CI).

3. Results

The interspecific (total average) scaling exponent b for the six chiton species examined is 0.73 (±0.03 95% CI), a value not

significantly different from 0.75. The interspecific mass coefficient *a* is 0.183 (±0.008 SE) $mgO_2\ h^{-1}$ (R = 0.96) (Table 1).

Intraspecific variation in mass between the smallest and largest specimens examined within each of the six species ranges from 18-fold to 361-fold (Table 2). The interspecific mass range is 1373-fold between juvenile *C. dentiens* (0.003 g AFDT) and full-grown adult *K. tunicata* (4.428 g).

In the intraspecific regressions, there were significant differences in the values of the exponent *b* between the six species (Table 1; Fig. 1) (ANCOVA, $F_{1,5} = 3.87$, $p = 0.003$). Values of *b* ranged from 0.64 (±0.08 95% CI) in *M. muscosa* to 0.91 (±0.10 95% CI) in both *P. velata* and *C. dentiens*. Post-hoc tests reveal that the species can be separated into two groupings with non-significantly different *b* values; *M. lignosa* and *M. muscosa* ($p = 0.64$), and the remaining four species ($p = 0.75$).

When compared to the commonly proposed value in the '3/4 power law' (0.75; West et al., 1997), all species but one (*M. lignosa*) possess *b* values significantly different from 0.75 (Table 1). When compared to the boundary limit values of 0.667 and 1.0 proposed in the MLB hypothesis (Glazier, 2010), two species (*M. lignosa* and *M. muscosa*) possess *b* values not significantly different from 0.667, and two species (*C. dentiens* and *P. velata*) possess *b* values not significantly different from 1.0.

Mass-specific uptake rates (mVO_2) were significantly different between the six species (Fig. 2a) (ANOVA $F_{5,152} = 92.83$, $p < 0.0001$). *C. dentiens* has by far the highest mVO_2 of the six species. This species also has the smallest maximum body mass, however the mass-independent metric *a* (Fig. 2b; Table 1) and mid-point mass metabolic rate L_m (Fig. 2c), are also higher than in other species suggesting this is not solely attributable to body mass. By contrast, *P. velata* has a much lower mVO_2 than the other species, again not solely attributable to body mass as shown by the lower *a* and L_m values of this species in comparison to others. These are the two species that also demonstrate the highest scaling exponent values. The two species that show the next highest *b* values, *T. lineata* and *K. tunicata*, are those with the second highest and second lowest mean mVO_2 respectively, and this pattern is broadly similar in the other metrics (Fig. 2b; c). The remaining two species have the lowest *b* values and broadly intermediate mVO_2, *a*, and L_m values in relation to the other species.

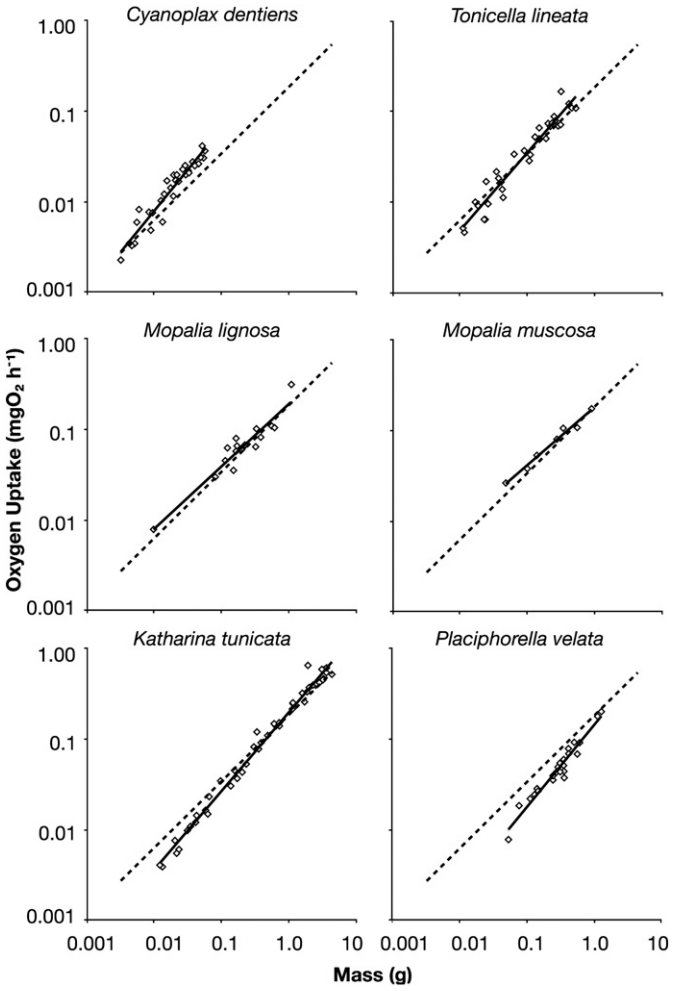

Fig. 1. Intraspecific OLS regressions. Horizontal axes indicate body mass (g), and vertical axes indicate oxygen uptake rate ($mgO_2\ h^{-1}$). Dashed line indicates the interspecific regression line for all six species (Table 1). Regression equations and R values are reported in Table 2. All plots use the same logarithmic scale.

4. Discussion

This study provides further evidence that significant natural variation in scaling exponents exists between similar species, but the same data used in an interspecific analysis can provide a result not significantly different from the archetypal 0.75 value.

The intraspecific *b* values reported for the six species here effectively fall within the boundary values of 0.667 and 1.0 as proposed by Glazier (2010) in the MLB hypothesis (the exception being *M. muscosa*, where it is within the range of error). Exponent values outside these boundaries are occasionally reported (e.g. Biggs, 1977; Dye and McGwynne, 1980; Marsden et al., 2011; Newell and Roy, 1973; Wallace, 1972). These outlying results could reflect true natural variability between species, even outside the boundaries proposed by Glazier (2010), but could equally be due to methodological shortcomings or error (Brey, 2010). Determination (or even definition) of organismal metabolic rate is notoriously difficult (Agutter and Wheatley, 2004; Savage et al., 2004a), and studies use a variety of metrics and methods that somewhat confound direct comparison. Factors that may affect small or large individuals disproportionately can significantly skew the results in such studies and greatly affect the reported *b* values. For instance, not taking proper account or controlling for the contribution of microbial action to aquatic oxygen consumption is likely to disproportionately affect calculations of uptake in smaller individuals, with the result that uptake rates are overestimated. This would cause the slope of the mass-respiration plot to be shallower, and calculated mass exponent values to be substantially lower than the true values.

Metabolic allometry can naturally demonstrate extreme scaling values over short time periods when metabolism is particularly depressed or elevated, such as during periods of hibernation (Glazier, 2010) or fast growth (Riisgård, 1998). Extrinsic factors may also affect the value of the scaling exponent *b*. Many experimental studies that reported high or low values for *b* in mollusks involve examination of specimens in different physical conditions (e.g. Kennedy and Mihursky, 1972; Newell and Roy, 1973), with various experimental

Table 2
Summary data showing variations in mass of the species examined. All masses are reported in grams (g) and represent ash-free dry tissue (AFDT) mass. Minimum and maximum masses are those of smallest and largest specimens of each species examined in this study. N indicates number of specimens examined.

	N	Mean mass	Mass range	Mass range (ratio max:min)
Cyanoplax dentiens	31	0.023	0.003–0.057	18
Tonicella lineata	33	0.152	0.011–0.531	48
Mopalia lignosa	18	0.287	0.010–1.106	112
Mopalia muscosa	7	0.340	0.048–0.911	19
Katharina tunicata	46	1.177	0.012–4.428	361
Placiphorella velata	23	0.375	0.053–1.275	24
			Interspecific mass range (ratio max:min)	1373

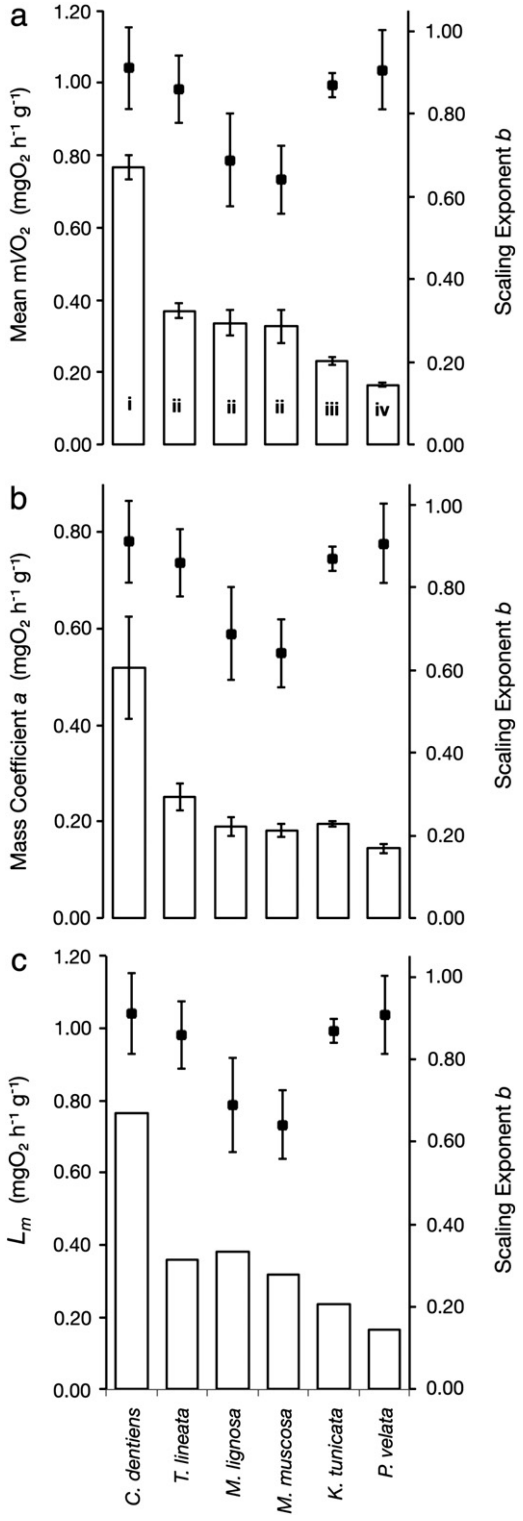

Fig. 2. Three measures of species metabolic level (left vertical axis) with exponent *b* values (right vertical axis, bars indicate 95% CI). Left axis indicates; (a) mean basal mass-specific oxygen uptakes rates (mVO_2) for each species (bars indicate standard error; labels on columns indicate significant differences; ANOVA, Post-hoc Tukey tests, $\alpha = 0.05$); (b) mass coefficient *a* (bars indicate standard error); (c) L_m, the predicted mass-specific metabolic rate at the midpoint of each species' regression line in log space.

treatments imposed. These stresses may have differential effects on smaller or larger individuals within species, skewing the allometric relationship. Some other studies examined metabolic rates during different seasons (e.g. Dye and McGwynne, 1980), when there may be confounding factors affecting metabolism such as preparation for spawning or seasonal reduction in metabolic rates. Many studies do not include representative ontogenetic series of specimens, and in fact some make efforts to limit size differences between examined specimens. A limited size range increases the potential for error in estimating *b* values, and in addition may cause other factors to have a proportionally greater effect on metabolic rates, thus reducing the observed effect of body mass. Remarkably few of the studies from which scaling exponents are commonly cited are designed exclusively to determine this parameter, and *b* values are commonly derived incidentally from data collected for other purposes, such as of the effect of different physical conditions on metabolism. Meta-analyses pooling the results of such disparate experiments, which have different goals, biases and methodological limitations are of limited value as the observed scaling exponents may not reflect natural values. However, there are a number of interacting ecological and abiotic factors which may cause *b* to vary naturally, apart from the extremes of stress or hibernation, including lifestyle, activity level, metabolic level, growth rate and phylogeny (Atanasov, 2010; Czarnołeski et al., 2008; Glazier, 2005, 2009; Hughes et al., 2011; Killen et al., 2010; Ohlberger et al., 2011; Rezende et al., 2004; Rosa et al., 2009; Seibel, 2007).

The data presented here are especially valuable in this context, as the explicit aim of the present study was to determine the value(s) of *b*, and if this value varied between species. The best way to demonstrate variation in *b* values is through comparative studies that examine full ontogenetic series of co-occurring, closely-related species in the same, close-to-natural conditions, and control for extrinsic factors that might influence metabolic rate (e.g. temperature and salinity). It is also important to standardize metabolic rates by maintaining specimens in the same, as close as is possible, physiological condition, hence a period of acclimation and starvation. This study is the first report of metabolic scaling in chitons where such variables have been properly controlled.

Prior to the present authors' recent work (Carey et al., 2012), the last study reporting empirical data on chiton metabolism dates from over twenty years ago (McMahon et al., 1991). Only one previous study has examined a group of co-occurring species under the same conditions (Murdoch and Shumway, 1980). Some of these studies report *b* values with varying degrees of error or confidence interval; 0.73 in *T. lineata* (Kincannon, 1975); 0.37 to 0.47 (0.62 to 0.82 in air) (Murdoch and Shumway, 1980); 0.69 and 0.65 (0.79 and 0.75 in air) (Horn, 1985). In addition Vladimirova et al. (2003) reported a value of 0.70 for the class Polyplacophora, but with no indication of which species were examined.

That variation in *b* is common in mollusks is supported by other comparative studies (e.g. Marsden et al., 2011; Vladimirova et al., 2003). Similar variation has been observed in many other taxa (see Glazier (2005) for numerous examples). Some studies supportive of the "3/4 power law" even point to the large observed variability in *b*, between 0.667 and 1.0, as supporting that model, because the peak of the normal distribution of observed values often falls close to 0.75 (Savage et al., 2004a). There is often an assumption that the values distributed away from 0.75 are due to methodological error alone (e.g. Savage et al., 2004a).

Comparisons of metabolic rates between species are often difficult, due to the confounding factor of differences in body size. A simple comparison of mean mass-specific metabolic rates is possible, but does not take into account the scaling of metabolic rates in species with different size ranges. Many previous studies have used the intercept of the regression line, the mass coefficient *a*, as a comparative measure with which to compare metabolic levels of different groups because it is mass independent (Brown et al., 2004; Riveros and Enquist, 2011; Seibel and Drazen, 2007). However, such comparisons are commonly made under the assumption that scaling exponents (i.e. slopes) are equal, and therefore that *a* values are independent of *b*. However, as previously discussed, there is ample evidence that

b values vary (Bokma, 2004; Brey, 2010; Duncan et al., 2007; Glazier, 2005; Suarez et al., 2004), which means that *a* is not independent; any alteration of the value of the slope *b* necessarily means that the intercept *a* will also change, and this confounds direct comparisons of metabolic level using this metric. Killen et al. (2010) attempt to solve this problem of comparison by using L_m, the predicted mass-specific metabolic rate at the midpoint of each species' regression line in log space. This is the only point in the linear regression at which changes in slope will not affect estimates of the value of the intercept. This method has the advantage of avoiding the problems associated with autocorrelation between *a* and *b*, however it has a disadvantage in that values are not standardized to the same body mass (Glazier, 2010).

We examined species-specific *b* values in relation to the three measures of metabolic level described above; mean mVO_2 per species; the mass coefficient *a*; and L_m. A similar broad pattern can be seen when *b* values are examined alongside each of these metrics (Fig. 2). *C. dentiens* apparently operates at a much higher metabolic level than the other species, while *K. tunicata* and *P. velata* operate at a relatively lower level than other species. These three species are also associated with high *b* values.

Among these chiton species, there are a number of ecological factors which, combined with differences in metabolic level, may explain the observed variations in scaling exponent, especially in the context of the MLB hypothesis (Glazier, 2010). The species examined here broadly co-occur; however, it is apparent that they inhabit distinct but overlapping microhabitats. Species-specific adaptations and behavior related to these microhabitats (e.g. the unusual feeding mode of *Placiphorella*) may explain activity patterns, metabolic rates, and hence differences in scaling exponent values. Higher metabolic rates may often be associated with higher activity levels, and these in turn may be associated with the lifestyle of species and the habitats in which they are found (Glazier, 2005, 2010; Seibel, 2007). Two species here with high *b* values may be particularly active. *C. dentiens* is commonly found on relatively bare, exposed rock where it feeds on diatoms (Piercy, 1987). The high metabolic rate of this species might be related to its need to graze relatively large areas of this resource-poor microhabitat. We have found similar patterns among the Atlantic fauna, with a species that is ecologically similar and which inhabits relatively resource-poor habitat (*Lepidochitona cinerea*) possessing a greatly higher metabolic rate than other co-occurring species (Carey et al., 2012). In addition, species occurring higher on the shore may be more active to better exploit the narrow window of submersion between tides. Another species with a high *b* value, *T. lineata*, is low-shore but feeds exclusively on coralline algae (Andrus and Legard, 1975), which is particularly nutritionally poor (Paine and Vadas, 1969). It has to process large amounts of this food resource to provide enough energy to meet metabolic requirements (Barnes, 1972). *T. lineata* is particularly active and eats almost continually, continuing to feed even when exposed to air despite other species clamping down to avoid desiccation (Barnes, 1972; Demopulos, 1975).

Of the two other species that show high *b* values, *P. velata* is an ambush predator, and has the lowest metabolic rate of the species examined. It is extremely inactive, almost sedentary (McLean, 1962). Ambush predators have been noted in previous literature to have low metabolic rates relative to closely-related species, including within cephalopod mollusks (Seibel et al., 2007). *K. tunicata* also has a low mass-specific metabolic rate and a relatively high *b* value. Movement behavior in this species has not been described in the literature, but it apparently spends long periods of time in a sedentary position as it commonly inhabits exposed rock surfaces where it crams itself into rock crevices as protection from desiccation and being washed off by wave action (Carey & Sigwart, unpub. obs.).

Within the experiments conducted here, parameters that might affect respiratory rates were controlled, except for individual behavior. Within the respirometry chambers, specimens had an internal surface area on which to move around and were otherwise unrestrained (specimens were not observed to interfere with the stir bar and tended to keep clear of it). While activity was not monitored in a systematic manner, broad patterns were apparent. Both *C. dentiens* and *T. lineata* were active, moving around within the chambers. *P. velata* behavior was similar to that described by McLean (1962) in that it was sedentary and once attached did not otherwise move around. *K. tunicata* tended to move around initially, but then attach where the walls and the ends of the cylindrical chamber meet. Patterns in the activity of the other two species, *M. lignosa* and *M. muscosa* were not readily apparent, but were intermediate between the distinctive behaviors represented by the other study species.

The pattern of high *b* values associated with highly active and highly inactive behavior is supportive of the MLB model proposed by Glazier (2010). In this model, *b* values follow a U-shaped trend depending on activity and metabolic level, tending towards the value of 1.0 with high activity (or maximal metabolic rate) and low activity (or minimal metabolic rate), with intermediate states tending towards 0.667. The MLB hypothesis is among the few models (see also Seibel, 2007) to recognize that organisms do not distribute and utilize resources in the same way at all times, or do so consistently within a taxon, and that this will affect the scaling of metabolism across different size ranges. In some cases metabolism will be limited by the surface area to volume ratio (i.e. 0.667), while at other times volume-limits on energy production are the major factor affecting the scaling exponent and these scale at values close to isometric. At times of high activity, more common in those organisms with high metabolism, the limiting factor determining metabolic rate is the production of energy, which scales isometrically with muscle mass, this in turn scaling isometrically with body mass. At times of dormancy or low activity, more common in organisms with low metabolic rates, the limiting factor is again directly proportional to tissue mass and thus scales close to isometrically, in this case being the low metabolic energy demand required to sustain the tissues. In these two boundary cases within the model, the surface area to volume ratio of 0.667 does not constrain metabolic rate because the supply of resources exceeds the metabolic demand; in the case of high activity and demand, in the form of stored energy reserves and a temporary tolerance to waste accumulation; in the case of low activity and demand, supply of resources across the organismal surface area exceeds that needed to sustain tissues. At intermediate activity states or metabolic demand between these two extremes, surface area limits on fluxes of resources, waste products and/or heat will be the major factor affecting the scaling exponent, and these will scale at values approaching 0.667.

Glazier (2006) provided evidence that *b* values may be higher in pelagic than in benthic species across a range of aquatic taxa, potentially associated with the higher activity levels and metabolic rates that some pelagic lifestyles require. Seibel and Drazen (2007) showed similar results in cephalopods. In this way the high *b* values of *C. dentiens* and *T. lineata* may be explained by activity patterns and lifestyle, as two naturally highly active chiton species. Similarly the MLB model predicts that sedentary or dormant species with low metabolic rates should also have *b* values tending towards 1.0, as is the case here for *K. tunicata* and, particularly, *P. velata* (Fig. 2). Within such seemingly inactive animals as chitons one side of the MLB 'U-shape' model, that of low activity/minimal metabolic rate, might be expected to be dominant. However, as within any taxon of animals there exists a continuum of metabolic and activity levels determined by evolutionary adaptation. The present evidence suggests that some chitons are much more active than others, both metabolically and physically, even within their constrained body plan.

The species examined here may represent a natural spectrum across the MLB model. *P. velata* and *C. dentiens* in particular represent extremes within the model, and if acting naturally should both have *b* values approaching 1.0; a near dormant organism with low metabolic rate, and an active one with a high metabolic rate. The other

species have intermediate metabolic rates, and *b* values closer to (in some cases not significantly different from) the lower boundary of 0.667 (Figs. 1, 2). As such, the observed results are highly supportive of the MLB model (Glazier, 2010) and of other studies (e.g. Rosa et al., 2009; Seibel et al., 2007), in that variation in scaling exponents can be linked to lifestyle, activity and metabolic rates. The MLB model suggests that rather than physical laws constraining scaling relationships towards a particular value, they determine the boundaries within which *b* values may naturally vary due to a range of factors. In this way the values reported in this study reflect natural behavior, lifestyle and metabolic level.

Physical laws must influence the scaling of metabolism, but to suggest there is a single physical law determining all allometric relationships is unsupported by the evidence. Rather, metabolic rates and scaling relationships represent the complex interactions of different physiological and ecological factors. Such factors and how they affect energetic demands in species must be considered alongside body size as potential determinants of metabolic rates and thus of scaling relationships.

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