© 2024. Published by The Company of Biologists Ltd | Journal of Experimental Biology (2024) 227, jeb246362. doi:10.1242/jeb.246362

RESEARCH ARTICLE

The scaling of metabolic traits differs among larvae and juvenile colonies of scleractinian corals

Nina K. Bean[1,2,*] and Peter J. Edmunds[1]

ABSTRACT

Body size profoundly affects organism fitness and ecosystem dynamics through the scaling of physiological traits. This study tested for variation in metabolic scaling and its potential drivers among corals differing in life history strategies and taxonomic identity. Data were compiled from published sources and augmented with empirical measurements of corals in Moorea, French Polynesia. The data compilation revealed metabolic isometry in broadcasted larvae, but size-independent metabolism in brooded larvae; empirical measurements of *Pocillopora acuta* larvae also supported size-independent metabolism in brooded coral larvae. In contrast, for juvenile colonies (i.e. 1–4 cm diameter), metabolic scaling was isometric for *Pocillopora* spp., and negatively allometric for *Porites* spp. The scaling of biomass with surface area was isometric for *Pocillopora* spp., but positively allometric for *Porites* spp., suggesting the surface area to biomass ratio mediates metabolic scaling in these corals. The scaling of tissue biomass and metabolism were not affected by light treatment (i.e. either natural photoperiods or constant darkness) in either juvenile taxa. However, biomass was reduced by 9–15% in the juvenile corals from the light treatments and this coincided with higher metabolic scaling exponents, thus supporting the causal role of biomass in driving variation in scaling. This study shows that metabolic scaling is plastic in early life stages of corals, with intrinsic differences between life history strategy (i.e. brooded and broadcasted larvae) and taxa (i.e. *Pocillopora* spp. and *Porites* spp.), and acquired differences attributed to changes in area-normalized biomass.

KEY WORDS: Scleractinia, Respiration, Planula, *Pocillopora*, *Porites*, Metabolic scaling

INTRODUCTION

Organism size and physiological traits associated with size have profound implications for organismal performance and the dynamics of populations, communities and ecosystems (Brown et al., 2004; Norkko et al., 2013; Schmidt-Nielsen, 1984). Organism size, reproduction, and physical and chemical constraints drive metabolic scaling (Glazier, 2014; White et al., 2022), which describes the relationship between metabolic rate (R, expressed per organism) and size (M) with a power function (Glazier, 2010; Schmidt-Nielsen, 1984). In these relationships, a scaling exponent (b) of 1 indicates isometry, with other values indicating positive (b>1) or negative (b<1) allometry. Determining the drivers of metabolic scaling is important because it can lead to a better understanding of biological processes across a range of organism sizes (Brown et al., 2004).

The study of metabolic scaling has a long history in biology, with initial studies focusing on single-value models for the scaling exponent, for which departures from expectation (e.g. b=0.75) were construed as noise rather than signal (Glazier, 2005). In contrast, contemporary research has embraced the notion that metabolic scaling is plastic in response to natural selection, permeability of the organism surface, and resource transport within the organism (Glazier, 2014; White et al., 2019, 2022). Two approaches gaining support in explaining variation in metabolic scaling take either a metabolic theory (Glazier, 2014; Kearney, 2021) or a life history theory (Stearns, 1989; White et al., 2019, 2022) perspective, where the former relies on first principles, and the latter focuses on evolution as the ultimate driver of biological variation.

Douglas Glazier has been a strong proponent of metabolic theory (Glazier, 2014) that encompasses multiple theories, herein referred to as 'sub-theories', explaining how physiological traits vary with organism size, including: the surface area, resource transport, resource demand and system composition sub-theories. The surface area sub-theory suggests that metabolism is constrained by the rate of gas exchange across the surface area of organisms and, therefore, the rate at which surface area varies with organism size (Rubner, 1883). The resource transport sub-theory suggests that the scaling of metabolism is dependent on the ways by which metabolites are transported internally within the organism such as with the fractal geometry of supply networks (Glazier, 2014; Kleiber, 1932; West et al., 1997). The resource demand sub-theory suggests that the scaling of metabolism is modulated by the metabolic demands of biomass (i.e. the magnitude of metabolic rate). Finally, the system composition sub-theory suggests that the scaling of metabolism is determined by the proximal composition of organism biomass (e.g. the percentage composition of lipids, protein and carbohydrates), and assumes that tissues differing in composition modulate the size dependency of metabolic demand. Craig White and colleagues, in contrast, suggest that although physical and chemical constraints of resource usage set the absolute bounds of metabolic scaling, variation is subject to natural selection and is optimized through trade-offs between growth and reproduction (White et al., 2022).

To date, studies of metabolic scaling have focused mostly on unitary organisms, with less attention to marine organisms with colonial modular designs (but see Hartikainen et al., 2014; Lagos et al., 2017; Vollmer and Edmunds, 2000 for examples), which rely on the asexual iteration of modules (e.g. zooids or polyps) within a colony (Burgess et al., 2017; Glazier, 2010). This is unfortunate because colonial modular organisms are ubiquitous in the marine realm and they provide opportunities for intellectual advances in understanding the mechanistic basis of scaling of their unique body plan. In colonial scleractinian corals, for example, metabolic scaling

[1]Department of Biology, California State University, 18111 Nordhoff Street, Northridge, CA 91330-8303, USA. [2]Department of Biology, Florida International University, 3000 NE 151st St, North Miami, FL 33181, USA.

*Author for correspondence (nbean@fiu.edu)

N.K.B., 0000-0001-7610-201X; P.J.E., 0000-0002-9039-9347

Received 17 July 2023; Accepted 8 April 2024

Journal of Experimental Biology (2024) 227, jeb246362. doi:10.1242/jeb.246362

exponents range from ∼0.17 to 0.99 (Jokiel and Morrissey, 1986; Sebens, 1987; Vollmer and Edmunds, 2000), and in the case of *Siderastrea siderea*, strong negative allometry of aerobic respiration (b=0.17) corresponded with negative allometry of surface area as a function of dry tissue biomass (b=0.73) (Vollmer and Edmunds, 2000). To account for the unusually low scaling exponent (cf. common scaling components of ⅔, ¾ or 1; Glazier, 2014) of metabolism in *S. siderea*, Vollmer and Edmunds (2000) hypothesized that the ratio of surface area to biomass declined with colony size, thus limiting mass transfer and depressing aerobic metabolism in larger colonies as proposed by the surface area sub-theory of metabolic scaling (Ellenby, 1937; Glazier, 2014; Rubner, 1883). Similarly, change in the quantity of biomass was one of two hypotheses used by Edmunds (2006) to account for variation among years in the scaling of *in situ* growth (i.e. changes in diameter) in juvenile corals. Colder years were hypothesized to support an increase in biomass, with larger corals accumulating larger absolute reserves compared with smaller corals, leading to positive allometric growth, where biomass represents the accumulation of tissue reserves that could be used to promote skeletal growth. Together, the aforementioned studies indicate that variation in the quantity of coral tissues could be a leading cause of variation in metabolic scaling in this taxon, but to our knowledge, explicit tests of this hypothesis are lacking.

The present study first evaluated the extent to which metabolic scaling is a plastic trait in tropical reef corals (i.e. whether it departs from a single value; reviewed in Glazier, 2014). Second, we evaluated the extent to which our results were mediated by changes in biomass and conform to expectations of variation in metabolic scaling as proposed by the surface area sub-theory of Glazier (2014). *A priori*, we hypothesized that biomass and the ratio of surface area to biomass would primarily drive metabolic scaling because of the reliance on gas exchange by diffusion through the body wall in cnidarians (Shapiro et al., 2014). We used a natural gradient of variation in biomass within the Scleractinia to test the surface area sub-theory (Glazier, 2014). This was done by contrasting metabolic scaling between coral larvae originating from brooding and broadcasting parents and between taxa (i.e. *Pocillopora* spp. and *Porites* spp.) for which there was an *a priori* expectation of differing biomass for both contrasts. Brooded coral larvae develop within polyps, are subject to strong maternal investment and are typically larger than broadcasted larvae, which develop in the water column (Edmunds et al., 2011; Gaither and Rowan, 2010; Nozawa and Okubo, 2011; Richmond, 1987). Brooded coral larvae vary in size (i.e. volume) from ∼0.31 to 0.61 mm^3, whereas broadcasted larvae are ∼0.02 to 0.12 mm^3 in size (Gleason and Hofmann, 2011; Nozawa and Okubo, 2011). *Porites* spp. generally have greater area normalized biomass (18.6 mg cm^{-2}; Edmunds and Davies, 1986) than *Pocillopora* spp. (1.5–2.15 mg cm^{-2}; Davies, 1984; Hoegh Guldberg and Salvat, 1995).

We contrasted metabolic scaling exponents between broadcasted and brooded larvae to provide a contrast of larval size (i.e. biomass) to test whether differences in surface area:biomass ratios mediate variation in scaling. We also contrasted metabolic scaling exponents between juvenile colonies (i.e. ≤4 cm diameter; see Bak and Engel, 1979; Edmunds, 2000) of *Pocillopora* spp. and *Porites* spp. Assuming metabolic scaling would differ between *Pocillopora* spp. and *Porites* spp. juveniles owing to the differences in area normalized biomass (Davies, 1984; Edmunds and Davies, 1986; Hoegh Guldberg and Salvat, 1995), we sought a mechanistic explanation of variation in scaling based on the surface area sub-theory (reviewed in Glazier, 2014). We achieved this outcome by testing for differences in the scaling relationships of biomass on surface area between juvenile colonies of *Pocillopora* spp. and *Porites* spp. To test for cause-and-effect relationships coupling biomass to variation in metabolic scaling in juvenile corals, we sought to indirectly manipulate biomass through starvation, and then quantify the scaling of metabolism between starved and not starved corals. Starvation was elicited by incubating corals in darkness, which affects their capacity to benefit nutritionally from photosynthetically fixed carbon that is surplus to the needs of the algal symbiont (Rodrigues and Grottoli, 2007). The density of symbiodineacean algae (hereafter 'symbiont density') in the starved corals was measured to evaluate their role in mediating changes in holobiont biomass and metabolism.

MATERIALS AND METHODS

Metabolic scaling of larvae

Data compilation

To investigate metabolic scaling of brooded and broadcasted larvae, data were compiled from peer-reviewed and grey literature identified using Web of Science, Google Scholar and the published proceedings of the International Coral Reef Symposia, which were available from 1972 to 2012 (accessed 11 May 2020). The key words '(scleractinia*) and (larva* or planula*) and (respirat* or metabolism or "metabolic rate" or metabolic)' were utilized, with the asterisks indicating different suffixes. The citation lists in the papers included in the data compilation were also searched for additional relevant sources. We searched for studies that reported oxygen consumption and dry biomass that were either standardized to or could be converted to a per larva scale. Studies that reported proximal tissue composition (i.e. lipid or protein content) from which dry biomass could be calculated based on conversion factors (Table S1, see details in the Supplementary Materials and Methods) were also included.

Because the objective of the analysis was to assess the effect of size on respiration of coral larvae, only data from studies in which larvae were kept under ambient seawater conditions (relative to the time and location of the study) with respect to temperature and P_{CO_2} were retained. Data were extracted from the other studies using values reported in the main text or supplementary materials, or by digitizing plots presented therein using the online tool WebPlot Digitizer (https://automeris.io/WebPlotDigitizer.html). Some data points from one study were not retrievable because of the resolution of the graphics and were omitted from the analysis.

Empirical data

The empirical research was conducted under permits issued by the Government of French Polynesia (Délégation à la Recherche) and the Haut-commissariat de la République en Polynésie Francaise (DTRT) (Protocole d'Accueil 2020–2022).

To quantify the scaling of metabolism in brooded larvae, respiration was measured for larvae freshly released from *Pocillopora acuta* Lamark 1816 in Moorea, French Polynesia. To obtain larvae from *P. acuta*, six adult colonies were collected from a site on the north shore (17°28′59.67″S, 149°48′49.91″W) at ∼1 m depth. Colonies were collected on 15 May 2021 (lunar day 4) to sample peak release of larvae that occurs around lunar days 8–12 (Cumbo et al., 2013; Jiang et al., 2021). The colonies were taken to the Richard B. Gump South Pacific Research Station, where each was placed in a separate aquarium under shaded natural sunlight (∼9 µmol photons m^{-2} s^{-1}), where they were supplied with sand-filtered seawater pumped directly from Cook's Bay at 8 m depth. Larvae were collected by overflowing seawater from these aquaria

into a container fitted with a 110 µm mesh window. Following the overnight release of larvae, they were collected the next morning from a single parent colony that had released the greatest number of larvae. Preliminary trials revealed that typically only one of the six colonies would release substantial numbers of larvae on any one night, and in most cases, no larvae were released by the other colonies.

Larval respiration was measured for groups of similarly sized larvae placed in 2 ml glass Autosampler vials (Biomed Scientific, part number MGV2-9-CS-100Z), with the results expressed per larva. To determine the number of larvae required in each vial to accurately measure respiration, a preliminary analysis was conducted in which the respiration rate of larvae was measured in separate groups of larvae, starting with 1 larva vial^{-1} and ending with 9 larvae vial^{-1}. The respiration rate as a function of the number of larvae in the vials became linear with 3 larvae (r^2=0.94) and, thereafter, respiration trials were conducted with 6 larvae vial^{-1}, with each trial considered a statistical replicate. The efficacy of this experimental design to evaluate scaling effects required the larvae in each vial to be of similar sizes, with mean larval size differing among vials intended to support a test of larval size effects.

To obtain larvae of similar sizes, freshly released larvae were coarsely sorted into three size classes (i.e. small, medium and large) by visual inspection using a dissecting microscope (40× magnification). Approximately 40 each of the largest, smallest and medium-sized larvae (relative to the larval sizes on each day of release) were grouped and dark acclimated for 100 min to reduce autotrophically stimulated specific dynamic action within the holobiont (Edmunds and Davies, 1988). Following dark acclimation, batches of six similarly sized larvae were randomly selected from the three size groups and allocated to autosampler vials filled with filtered seawater (0.45 µm) with a known oxygen saturation and covered with parafilm. At the conclusion of the respiration trial, larval size was measured by quantifying their protein content as described below. Throughout dark acclimation and respiration trials, larvae were maintained in filtered seawater (0.45 µm) at ambient seawater temperature (27.9°C) and salinity (34.7 ppt) relative to the time of collection of the maternal colonies. Temperature was regulated (±0.1°C) using a water bath (Lauda Ecoline, model RE 104, Lauda-Königshofen, Germany), and measured with a certified thermometer (Fisher Scientific, model 15-077-8, Waltham, MA, USA, accuracy ±0.1°C), and salinity was measured with a benchtop conductivity meter (ThermoFisher Scientific Orion Star A212).

Oxygen saturation was measured using a NEOFOX-GT optical oxygen sensing system fitted with a 1.6-mm diameter FOSPOR-R probe (Ocean Insight, Orlando, FL, USA). The probe was two-point calibrated at 0% (sodium sulfite and 0.01 mol l^{-1} sodium tetraborate) and 100% oxygen saturation [air-saturated 0.45 µm filtered seawater (FSW)]. The respiration of the larvae in the vials was measured in darkness for ∼0.5–1.5 h, over which oxygen saturation remained >80% to prevent oxygen-dependent respiration (Edmunds and Davies, 1988; Shick, 1990). Parafilm is slightly oxygen permeable, but the effects are negligible when measuring larval respiration using vials of a similar dimension to those used herein (Edmunds et al., 2011). After the incubation period, the vials were carefully inverted to mix the seawater, and the oxygen probe was inserted through the parafilm to record the oxygen saturation. Oxygen saturation was converted to concentration using Unisense conversion tables (https://unisense.com/wp-content/uploads/2021/10/Seawater-Gases-table.pdf) and corrected with controls consisting of filtered seawater (0.45 µm). Following the respiration trials, larvae were frozen in seawater (−18°C) for determination of protein biomass.

Although it was assumed that there was net energy loss during the respiration trials of the non-feeding *P. acuta* larvae, the protein content, which was measured as a proxy for larval biomass, likely did not appreciably diminish during the short experimental trials (≤3 h), in which larvae were handled carefully and kept in ambient conditions. Additionally, several studies, including some used for the present data compilation, also obtained size estimates after respiration trials, thus enhancing the comparability of the present results with previous studies (Edmunds et al., 2001; Gaither and Rowan, 2010; Graham et al., 2013). Protein content of the larvae was measured using the Bio-Rad Protein Assay (Bio-Rad Laboratories, CA, USA). Larvae were thawed, sonicated (Sonic Dismembrator 500, Fisher Scientific), heated in alkaline conditions using 1 mol l^{-1} NaOH, and neutralized with 1.65 mol l^{-1} HCl. Protein content (µg) was calculated using bovine serum albumin standards and converted to dry biomass (µg) assuming the larvae contain 17% protein (Richmond, 1987).

Metabolic scaling of juvenile corals

To test for differences in metabolic scaling between juvenile colonies of different coral taxa, 11 juvenile colonies of *Pocillopora* spp. (excluding *P. acuta*) and 10 of massive *Porites* spp. (i.e. not including branching *Porites* spp.) were collected from the back reef of Moorea (17°28′25.65″S, 149°48′46.53″W) at ∼2 m depth on 8 November 2020. The unbalanced statistical design resulted from the loss of one *Porites* spp. colony. Juvenile colonies were collected to vary in size from 1 to 4 cm diameter so that the scaling exponent for respiration could be measured. Corals were not morphologically distinguishable by species at this early life stage and were identified to genus. Colonies were chipped from the reef using a small chisel and attached to a plastic base using underwater epoxy (Z-Spar Splash Zone A-788). The portions of the colony bases that were not covered in live coral tissue were cleaned of organisms and covered with the same underwater epoxy. The colonies were left for 21 h in flowing seawater under a shaded roof to let the epoxy harden before respiration was measured.

The respiration rates of the juvenile corals were measured within 4 days of collection to minimize photo-acclimation to laboratory conditions (Elahi and Edmunds, 2007), and following 14–54 h of darkness in flowing, sand-filtered water pumped from Cook's Bay and maintained at an ambient temperature of ∼27°C. There was no relationship between biomass-normalized respiration and duration of dark acclimation for *Porites* spp. (d.f.=8, P=0.60) or *Pocillopora* spp. (d.f.=9, P=0.23). Respiration trials were run over 2 days and were conducted by coral colony, alternating between taxa, with two seawater controls run daily. For each trial, a juvenile coral was placed inside a sealed 240 ml cylindrical chamber filled with 0.45 µm FSW and surrounded by a water jacket to regulate the temperature. All trials began at ∼100% oxygen saturation, and were conducted at ∼27.3°C and ∼34.3 ppt, which were the ambient conditions at the collection site when the analyses were completed (November 2020). A stir bar below the juveniles mixed the seawater during the trials, and juvenile corals were acclimated to chamber conditions for 10 min prior to sealing the chamber and measuring respiration through oxygen consumption recorded using a FOSPOR-R optical oxygen probe (Ocean Insight). The probe was calibrated in the same manner as described above for larval respiration, and incubations lasted 20–60 min until a steady decline of oxygen saturation was recorded while ensuring that saturation remained >80% (Edmunds and Davies, 1988; Shick, 1990).

Journal of Experimental Biology (2024) 227, jeb246362. doi:10.1242/jeb.246362

Following respiration trials, the surface area and the dry biomass of the corals were measured. Surface area of the juveniles was estimated geometrically by measuring two perpendicular diameters (i.e. length and width) and height, and assuming the colonies were vertical cylinders (see details in the Supplementary Materials and Methods). Biomass was quantified by fixing the juvenile corals in 10% formalin in seawater for 48 h, then decalcifying in 5% HCl in distilled water over 1–7 days. The tissue was rinsed of formalin residue with deionized (DI) water before being placed in HCl to avoid the formation of bis-chloromethyl ether, a carcinogen. The tissue tunic was rinsed in DI water before being dried to a constant mass at 60°C.

Metabolic scaling between taxa in light and dark

To evaluate the role of biomass in mediating scaling relationships, biomass of corals was indirectly manipulated by exposing corals to darkness (i.e. starvation) or natural photoperiods (i.e. 12 h:12 h light:dark) of ambient light relative to the collection site as a control. Two tanks were maintained in darkness and two at a maximum of 967±9 µmol photons m^{-2} s^{-1} (±s.e.m.; measured with a Li-Cor 4π sensor fitted to a Li-Cor meter, LI-1400, Lincoln, NE, USA) on a 12 h:12 h light:dark photoperiod supplied through LED lights (75 W, Sol LED Module, Aqua-illumination, Ames, IA, USA). Thirty-two juvenile colonies of both *Pocillopora* spp. and massive *Porites* spp. were collected on 20 May 2021 from the back reef of Moorea at ∼2 m depth (17°28′25.65″S, 149°48′46.53″W). Colonies were acclimated to laboratory conditions for 4 days before experimental trials took place. Tanks (150 liters) were held at 28.5°C and 34.7 ppt and supplied with sand-filtered seawater from Cook's Bay at ∼400 ml min^{-1}, and each contained eight colonies of *Pocillopora* spp. and eight colonies of *Porites* spp. Colonies were held at treatment conditions for 9–12 days, depending on when they were used for respiration trials, and arranged daily in each tank to minimize position effects. Respiration was measured starting at 9 days because the colonies in the dark tanks showed signs of physiological stress (i.e. paling). Two juveniles were measured concurrently for respiration in separate chambers, with one control completed in each chamber daily. Colony selection for respiration trials alternated between tanks within each treatment and between taxa, and with 14–18 corals processed each day, all corals were processed in 4 days. The respiration rate of each colony was measured using the methods described above for juvenile corals.

Following respiration trials, corals were frozen (−20°C) and crushed with 2500 µl of 0.45 µm FSW to produce a slurry of skeleton and tissue. To maintain consistency of sampling, ∼13 cm^2 of each coral colony was crushed with the area chosen as the size of the smallest colony in the experiment. The homogenate was used for the analysis of ash free dry mass (AFDM) using a muffle furnace (5 h at 450°C) (Fisher Scientific, model 650–126) and symbiont density using a hemocytometer (8 replicate counts per sample).

Statistics

All statistics were completed using R software (https://www.r-project.org/, v1.4.1103) using the stats package (R v4.0.3), with the car package (Fox and Weisberg, 2019, v3.0-10) used to test for the statistical assumptions of the procedures employed. Metabolic scaling relationships (slopes and elevation) were calculated using ordinary least squares (OLS) on double logarithmic plots of larvae respiration (pmol O_2 $larva^{-1}$ min^{-1}) or juvenile respiration (µmol O_2 $individual^{-1}$ h^{-1}) versus dry tissue biomass (larvae: µg $larva^{-1}$; juveniles: mg $individual^{-1}$). The relationships of dry tissue biomass as a function of surface area (mg cm^{-2}) and symbiont cell counts as a function of size (AFDM, mg) were also calculated using the OLS estimates on double logarithmic plots. The slopes were compared between species and treatment using analysis of covariance (ANCOVA). The scaling relationships from OLS for respiration were qualitatively compared with the scaling of select physiological traits (i.e. biomass and symbiont density) to assess whether the results conform to expectations based on the surface area sub-theory (sensu Glazier, 2014). The sample sizes for the present experiments were chosen based on results of previous experiments (e.g. Edmunds et al., 2011; White et al., 2011).

RESULTS

Metabolic scaling of larvae

Data compilation

The literature search identified seven studies with 12 independent experiments (n=7 for brooding species and n=5 for broadcasting species) published between 2001 and 2014 (Table S1) and conforming to the search criteria. These studies reported metabolic rates for *Acropora nasuta*, *A. spathulata*, *A. tenuis*, *Goniastrea aspera*, *Montipora digitata*, *Pocillopora damicornis*, *Porites astreoides* and *Seriatopora caliendrum*, and the sizes of individual larvae (i.e. biomass) ranged from 0.65 to 26.08 µg for broadcasted larvae, and from 20.88 to 422.31 µg for brooded larvae (Table S1).

Respiration rates for brooded larvae varied from 29.01 to 169.63 pmol O_2 $larva^{-1}$ min^{-1}, and they were unrelated to size ($F_{1,34}$=0.17, P=0.69; Fig. 1; Table S2). Because respiration rates were unrelated to size in brooded larvae, a formal ANCOVA comparing the slopes between brooded and broadcasted larvae was not completed. Most of the data came from *P. damicornis* (i.e. 86%) and only five results came from other species (Table S1); removal of

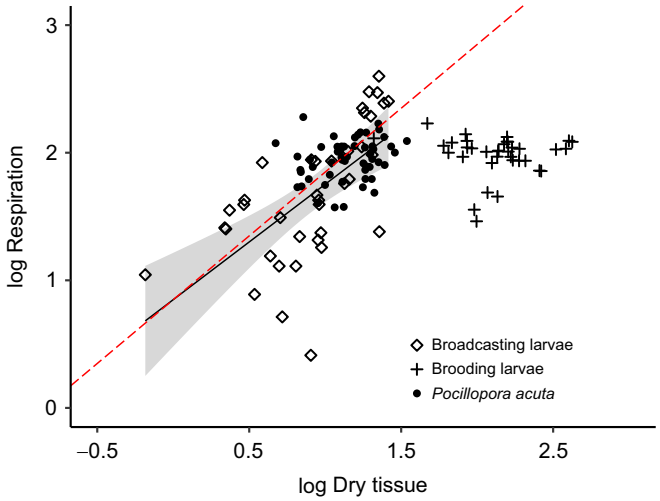

Fig. 1. Logarithmic plot of larval-specific respiration (pmol O_2 min^{-1}) against biomass (µg $larvae^{-1}$) of brooded (n=36) and broadcasted (n=38) larvae, as well as larvae freshly released from *Pocillopora acuta* (n=54, 6 larvae in each biological replicate). Each datum for *P. acuta* larvae in Moorea represents the respiration rate of a single larva derived from a single determination of the respiration rate of six larvae combined divided by the number of larvae to represent one larva, whereas values for brooded and broadcasted larvae from the data compilation were average rates reported by the studies. Regression lines were fit using ordinary least squares, and grey shaded regions show 95% confidence bands on data where the regression was significant (P<0.05). The dashed red line represents a slope of 1. The experiment shown was replicated once and each datum represents a biological replicate.

Journal of Experimental Biology (2024) 227, jeb246362. doi:10.1242/jeb.246362

the values from *P. damicornis* confirmed that respiration rates were unrelated to size in brooded larvae.

Respiration rates for broadcasted larvae varied from 2.58 to 397.48 pmol O_2 $larva^{-1}$ min^{-1}, and they were related to size with an isometric relationship [b=0.90±0.18 (±95% CI, unless otherwise noted), $F_{1,36}$=24.28, r^2=0.40, P<0.01; Fig. 1; Table S2]. Most of the results (35 of 38 data points) for broadcasted larvae came from Graham et al. (2013), with the remaining three from Harii et al. (2010), which were from a species not included in Graham et al. (2013) (i.e. *M. digitata*) (Table S1). Although collectively, respiration increased with larval size, *M. digitata* larvae in Harii et al. (2010) had a negative relationship between respiration and larval size. The species analyzed in Graham et al. (2013) (i.e. *A. nasuta*, *A. spathulata*, *A. tenuis* and *G. aspera*) all independently showed positive scaling relationships.

Empirical data

Larvae freshly released from *P. acuta* over 17–20 May (lunar days 6–9) ranged in length from 0.48 to 1.54 mm, and in protein content from 0.80 to 9.01 µg $larva^{-1}$. Larvae were collected from the same parent colony on lunar days 6 and 7, and from a different parent colony on lunar days 8 and 9, encompassing two parental genotypes. Fifty-four larval trials (31 from one parental genotype and 23 from the other) and 36 seawater controls were run over 4 days, with larvae freshly released each day. Respiration rates varied from 37.30 to 190.24 pmol $larvae^{-1}$ min^{-1}, and were not related to biomass on a double logarithmic plot when all data points were pooled ($F_{1,52}$=3.19, P=0.08; Fig. 1; Table S2), or when the data were analyzed separately by genotype ($F_{1,50}$=1.24, P=0.27).

Metabolic scaling of juvenile corals

Juvenile colonies of *Pocillopora* spp. (n=11) ranged from 1.65 to 3.58 cm in diameter, from 12.64 to 87.72 cm^2 in area, and had a biomass of 5.80–49.60 mg. Their respiration rates ranged from 0.14 to 0.36 µmol O_2 cm^{-2} h^{-1}, which increased with a significant isometric relationship on biomass (b=1.0±0.10, $F_{1,9}$=110, r^2=0.92, P<0.01; Fig. 2A; Table S2). The juvenile colonies of massive *Porites* spp. (n=10) ranged in size from 1.00 to 4.04 cm in diameter and 7.42 to 31.90 cm^2 in size, and had a biomass of 2.10–64.50 mg. Respiration rates ranged from 0.06 to 0.36 µmol O_2 cm^{-2} h^{-1} and increased significantly and positively with biomass ($F_{1,8}$=46.21, r^2=0.85, P<0.01; Fig. 2A; Table S2). On log–log axes, the slope of this relationship was 0.67±0.10 and was significantly different from the metabolic scaling slope of *Pocillopora* spp. ($F_{1,17}$=4.94, P=0.04; Table 1, Fig. 2A; Table S2). Area normalized biomass ranged from 0.46 to 0.94 mg cm^{-2} in *Pocillopora* spp. and dry tissue mass (mg) on surface area (cm^2) scaled with a slope of 0.98 ±0.12 ($F_{1,9}$=68.35, r^2=0.88, P<0.01; Fig. 2B; Table S2). Area-normalized biomass for *Porites* spp. ranged from 0.28 to 2.80 mg cm^{-2} and the dry tissue mass (mg) on surface area (cm^2) scaled with a slope that significantly deviated from that of *Pocillopora* spp. ($F_{1,17}$=10.69, P<0.01; Table 1, Fig. 2B; Table S2) with a value of 2.07±0.36 ($F_{1,8}$=33.71, r^2=0.81, P<0.01; Fig. 2B; Table S2).

Metabolic scaling between taxa in light and dark

Juvenile *Pocillopora* spp. in the light manipulation experiment ranged from 1.50 to 4.20 cm diameter and from 11.78 to 140.01 cm^2 in area, with *Porites* spp. ranging from 1.20 to 4.05 cm diameter and from 9.08 to 51.89 cm^2 in area. One *Pocillopora* spp. colony and four *Porites* spp. colonies were omitted from analyses because of mortality (n=2) or sample loss (n=3), and one *Porites* spp. colony

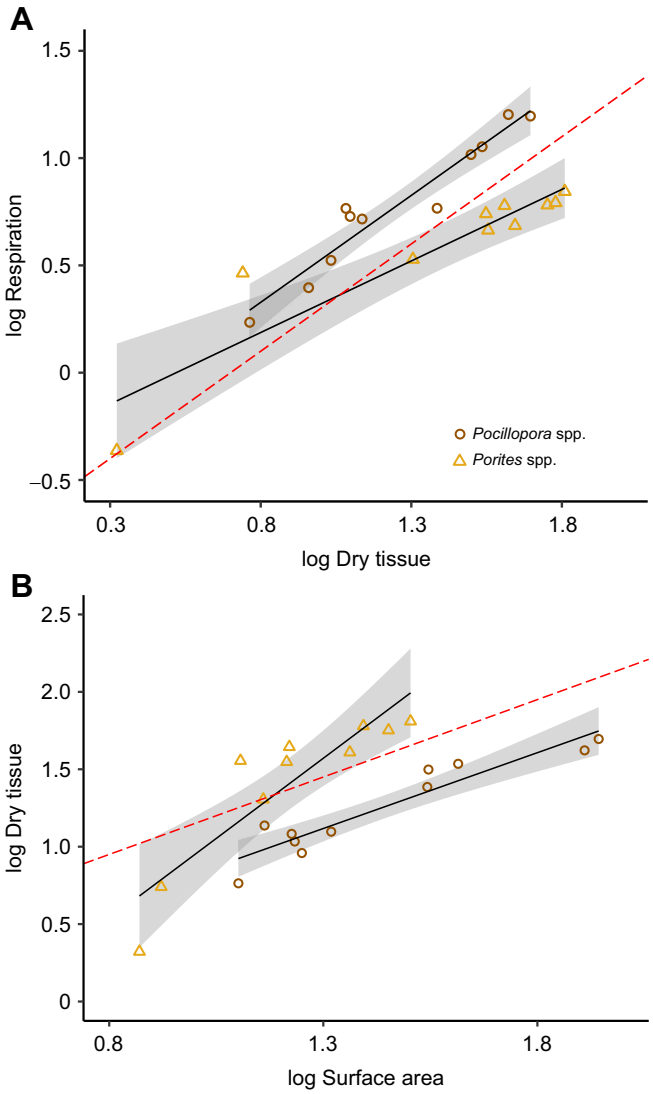

Fig. 2. Logarithmic plots of relationships between respiration, biomass and surface area in juvenile *Pocillopora* spp. (n=11) and *Porites* spp. (n=10). (A) Respiration (µmol O_2 $individual^{-1}$ h^{-1}) against biomass (mg) and (B) biomass (mg) against surface area (cm^2). Regression lines were fit using ordinary least squares, and grey shaded regions show 95% confidence bands on data where the regression was significant (P<0.05). The dashed red line represents a slope of 1. The slopes were compared between juvenile *Pocillopora* spp. and *Porites* spp. using ANCOVA. The experiment shown was replicated once and each datum represents a biological replicate.

was omitted from the symbiont analysis owing to sample loss. The metabolic scaling exponents and intercept of *Pocillopora* spp. and *Porites* spp. between tanks within the same treatment did not significantly differ, which allowed for the pooling of individuals within treatments (Tukey multiple comparisons; P>0.05).

On a log–log scale, tissue biomass was reduced by ∼9% in the dark treatment for *Pocillopora* spp. and by ∼15% in the dark treatment for *Porites* spp. ($F_{1,51}$=13.25, P<0.01; Fig. 3B, Table 2). Similarly, the average symbiont density was significantly reduced by ∼83% for both *Pocillopora* spp. ($F_{1,27}$=44.14, P<0.01; Fig. 3C, Table 2) and *Porites* spp. (Wilcoxon rank sum exact test; P<0.01; Fig. 3C) held in the darkness. *Porites* spp. ($F_{1,24}$=27.89, P<0.01) and *Pocillopora* spp. ($F_{1,27}$=108.31, P<0.01) in the dark respired, on average, 2.03 µmol mg^{-2} h^{-1} (∼63% reduction) and

Journal of Experimental Biology (2024) 227, jeb246362. doi:10.1242/jeb.246362

Table 1. ANCOVA tests for variation in respiration and tissue biomass between taxa (*Pocillopora* spp. versus *Porites* spp.) using biomass and surface area as covariates, respectively

Dependent variable	Source	SS	d.f.	MS	*F*	*P*
Respiration	Biomass	1.545	1	1.545	107.535	<0.001
	Species	0.471	1	0.471	32.795	<0.001
	Biomass×Species	0.071	1	0.071	4.936	0.040
	Residual	0.244	17	0.014		
Biomass	Surface area	1.515	1	1.515	48.758	<0.001
	Species	0.864	1	0.864	27.815	<0.001
	Surface area×Species	0.332	1	0.332	10.686	0.005
	Residual	0.528	17	0.031		

5.86 µmol mg^{-2} h^{-1} (~65% reduction) slower than colonies in the light, respectively (Fig. 3A).

The scaling of AFDM as a function of surface area ($F_{1,51}$=0.14, P=0.71; Fig. 3B, Table 2), and symbiont counts as a function of AFDM (*Pocillopora* spp.: $F_{1,27}$=2.21, P=0.15; *Porites* spp.: OLS, P=0.07–0.38; Fig. 3C, Table 2), did not differ between treatments. The metabolic scaling exponent for *Porites* spp. in the light was 0.89±0.19 and 0.96±0.29 in the dark (Table S2), and the two values did not significantly differ ($F_{1,24}$=0.04, P=0.84; Fig. 3A). For *Pocillopora* spp., the metabolic scaling exponent was 1.17±0.10 in the light and 1.63±0.26 in the dark (Table S2), and these also did not differ significantly ($F_{1,27}$=2.89, P=0.10; Fig. 3A). However, the scaling exponents between taxa significantly differed ($F_{1,51}$=4.74, P=0.03; Fig. 3A, Table 2).

DISCUSSION

Metabolic scaling is a widely studied biological phenomenon that relates metabolic rate to body size and encompasses multiple interrelated concepts to explain the causes of metabolic scaling. Understanding the drivers of metabolic scaling improves our capacity to understand and predict biological processes that may relate to organism efficiency and productivity across body sizes (Brown et al., 2004). Further, recognizing emergent properties of size provides guidelines determining the accuracy with which predictions can be made about organisms outside of the size class studied. To date, studies of metabolic scaling have focused mostly on organisms with unitary designs and less on organisms with colonial modular designs such as scleractinians. The present study focused on metabolic scaling in tropical scleractinians and made comparisons between two life stages (i.e. larvae and juveniles) and taxa (i.e. *Pocillopora* spp. and *Porites* spp.) that vary in biomass to evaluate the roles of variation in biomass and life history in driving plasticity of metabolic scaling.

Metabolic scaling of larvae

There is a limited number of studies that report respiration as a function of size in coral larvae, and these have been conducted with only eight species. The paucity of empirical data highlights a knowledge gap to which our study appeals by measuring metabolic scaling of larvae freshly released from *P. acuta* collected from the back reef of Moorea. We predicted that metabolic scaling exponents would differ between broadcasting and brooding species because of the *a priori* expectations for biomass and the ratio of surface area to biomass to differ between life histories, eliciting differing mass transfer rates of gases at the tissue surface (Shapiro et al., 2014). Corresponding with our predictions, the data compiled from the literature revealed that broadcasted larvae ranged in size from 0.65 to 26.08 µg, and were generally smaller than brooded larvae (brooders=20.88–422.31 µg). Based on the compiled data, the respiration of broadcasted larvae scaled isometrically with size, but that of brooded larvae was independent of size. The empirical analysis of metabolic scaling in brooded *P. acuta* larvae also revealed an independence of metabolic rate with size, thus corroborating the result obtained from the compiled data and supporting the generality of a metabolic scaling slope of 0 in brooded larvae. Although it is possible that limited genetic diversity can influence estimates for metabolic scaling exponents, this possibility is unlikely with the empirical analysis in the present study because the scaling slopes were indistinguishable between the two parental genotypes.

A higher metabolic scaling exponent in broadcasted larvae compared with brooded larvae is consistent with the predictions of the surface area sub-theory (Glazier, 2014), in which metabolism is hypothesized to be constrained by the rate of gas exchange across the outer surface area of organisms (Rubner, 1883). Broadcasted larvae in the literature survey were typically smaller with higher surface area to biomass ratios compared with brooded larvae, and it is likely that they had fewer limitations on mass transfer, explaining the isometric relationship of metabolism and body size. Brooded larvae, in contrast, may have experienced mass transfer limitations, thereby affecting the rates of gas exchange and depressing the metabolic scaling exponent (Graham, 1988).

Alternatively, life history theory, as proposed by White et al. (2022), provides an alternative explanation to classic metabolic theory (sensu Glazier, 2014) to account for the variation in metabolic scaling exponents between brooded and broadcasted larvae. White et al. (2022) predicted that for a given magnitude of aerobic respiration, species with metabolic scaling exponents closer to zero have life history attributes corresponding to lower fecundity, a greater allocation of their energy to achieving early sexual maturity, and rapid growth. In addition, White et al. (2022) predicted the species with metabolic scaling exponents between 0.6 and 0.9 with a mean of ~0.75 correspond with life history strategies that maximize lifetime reproduction. In the present study, metabolism was independent of larval size (i.e. b=~0) in brooded coral larvae, whereas broadcasting larvae had a higher scaling exponent (i.e. ~1). Brooding corals typically have earlier maturation than broadcasting corals (Knowlton, 2001; Rapuano et al., 2023; Soong, 1993), and broadcasting species generally have higher fecundity than brooding corals (Hall and Hughes, 1996; Waller et al., 2023), and this may extend to higher lifetime fecundity, especially if broadcasting species live longer than brooding species (Knowlton, 2001; Soong, 1993). The coupling of scaling exponents and life history characteristics of brooded and broadcasted larvae are in agreement with the predictions of White et al. (2022). However, this should be interpreted with caution because the predictions of White et al. (2022) refer to adults of each species whereas the present results refer to larvae. Additionally, the magnitude of

Journal of Experimental Biology (2024) 227, jeb246362. doi:10.1242/jeb.246362

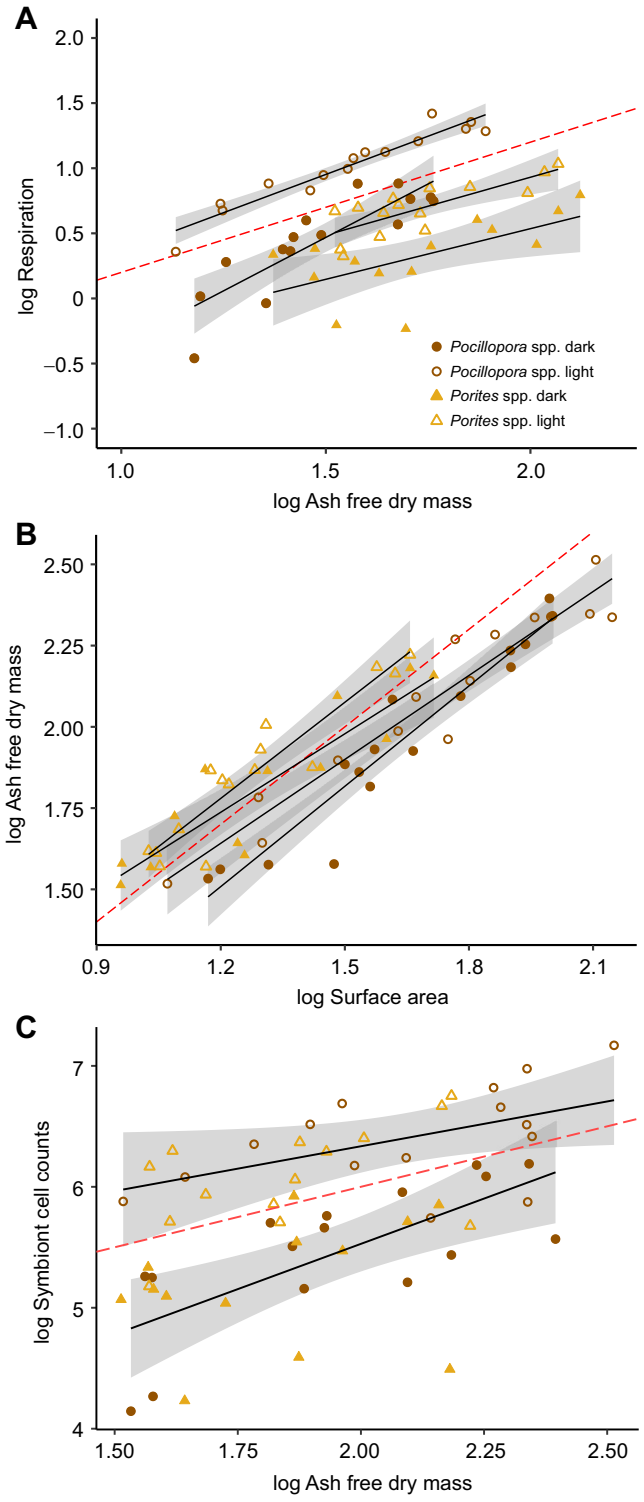

Fig. 3. Logarithmic plots describing the metabolism, biomass and symbiont density of juvenile *Pocillopora* spp. (light *n*=15, dark *n*=16) and *Porites* spp. [light *n*=15 (14 for symbionts), dark *n*=13] in light (ambient light conditions, 12 h:12 h light:dark) and dark (constant darkness) treatments. (A) Respiration (μmol O_2 individual^{-1} h^{-1}) against ashe free dry mass (AFDM; mg), (B) AFDM (mg) against surface area (cm^2) and (C) symbiont cell counts against AFDM (mg). Regression lines were fit using ordinary least squares and the grey shaded regions show 95% confidence bands on data where the regression was significant (P<0.05). The slopes were compared between treatment and species using ANCOVA. The dashed red line represents a slope of 1. The experiment shown was replicated once and each datum represents a biological replicate.

aerobic respiration was not the same between brooded and broadcasted larvae, which was an assumption associated with the aforementioned predications of White et al. (2022).

Metabolic scaling of juvenile corals

We contrasted metabolic scaling between juvenile colonies (e.g. 1–4 cm diameter) of *Pocillopora* spp. and *Porites* spp. and explored the role of biomass as a driver of variation in metabolic scaling. Our results for *Porites* spp. are similar to those reported for juvenile colonies of *Siderastrea siderea* (Vollmer and Edmunds, 2000), which also were characterized by negative allometry for metabolism and positive allometry for biomass. To reconcile the difference in scaling exponents for metabolism and biomass, Vollmer and Edmunds (2000) hypothesized that mass-specific respiration decreased with coral size because of increases in tissue thickness. Such an effect could lead to reduction in metabolic rates in bigger corals by lengthening diffusion pathways of metabolites from the seawater to the bottom of the tissue layer (Kühl et al., 1995; Putnam et al., 2017). Although Vollmer and Edmunds (2000) did not measure tissue thickness, they assumed that larger corals had thicker tissue compared with smaller corals because larger corals had greater area-normalized biomass than smaller corals, and because biomass and tissue thickness are positively correlated in reef corals (Edmunds, 2008). The rationale of Vollmer and Edmunds (2000) may also apply to the juvenile corals in the present study, and could also explain why both metabolism and biomass scaled isometrically in juvenile *Pocillopora* spp. Together, these results suggest that metabolic scaling in juvenile corals is driven by changes in biomass, and the way in which it varies with surface area both within and between taxa. We recognize that relying on two genera to make broad conclusions for juvenile corals has limitations (Garland and Adolph, 1994), but these concerns are reduced by the consistency of our results with those of Vollmer and Edmunds (2000).

Metabolic scaling between taxa in light and dark

To further investigate the role of biomass in mediating metabolic scaling in juvenile scleractinians, juvenile colonies of *Porites* spp. and *Pocillopora* spp. were maintained in darkness to manipulate the quantity of biomass through starvation of metabolites derived from the symbionts (Edmunds and Davies, 1986; Muscatine and Hand, 1958; Muscatine et al., 1981, 1984; Yellowlees et al., 2008). Starvation was expected to necessitate the use of food reserves (i.e. lipid) as a respiratory substrate (Davies, 1991; Grottoli et al., 2004; Stimson, 1987), thereby supporting a test for a cause-and-effect relationship between changes in area-normalized biomass to changes in metabolic scaling.

Exposing *Pocillopora* spp. and *Porites* spp. juveniles to starvation did not affect the scaling of metabolism, tissue biomass (AFDM) or symbiont cell counts as a function of size, but it did affect the scaling intercepts (i.e. the measure of magnitude) of these traits. Based on the observations of the unmanipulated *Pocillopora* spp. and *Porites* spp. in this study, and hypothesizing that corals can experience mass transfer limitations when area-normalized biomass is high, it was expected that a reduction in area-normalized biomass would liberate tissues from mass-transfer limitations and result in higher metabolic scaling exponents. Matching the aforementioned prediction, starvation in darkness resulted in a reduction in biomass by 9% and 15% for *Pocillopora* spp. and *Porites* spp., respectively. This effect was coupled with a reduction in metabolism and a trend for higher metabolic scaling exponents for starved corals versus those kept in the light.

Table 2. ANCOVA tests for variation in respiration, ash free dry mass and symbiont counts among species and treatments as appropriate

Dependent variable	Source	SS	d.f.	MS	*F*	*P*
Respiration	Biomass	1.877	1	1.877	67.730	<0.001
	Treatment	2.831	1	2.831	102.149	<0.001
	Species	2.717	1	2.717	98.056	<0.001
	Treatment×Species	0.030	1	0.030	1.094	0.300
	Biomass×Treatment	0.027	1	0.027	0.971	0.329
	Biomass×Species	0.131	1	0.131	4.736	0.034
	Biomass×Treatment×Species	0.021	1	0.021	0.756	0.389
	Residuals	1.413	51	0.028		
AFDM	Surface area	3.670	1	3.670	476.291	<0.001
	Treatment	0.070	1	0.070	9.066	0.004
	Species	0.272	1	0.272	35.240	<0.001
	Surface area×Treatment	0.001	1	0.001	0.142	0.708
	Surface area×Species	0.003	1	0.003	0.359	0.552
	Treatment×Species	0.003e-1	1	0.003e-1	0.044	0.835
	Surface area×Treatment×Species	0.027	1	0.027	3.551	0.065
	Residuals	0.393	51	0.008		
Symbionts	Treatment	6.963	1	6.963	44.145	<0.001
	Dry mass	3.111	1	3.111	19.725	<0.001
	Treatment×Dry mass	0.349	1	0.349	2.211	0.149
	Residual	4.259	27	0.158		

Two-factor ANCOVA comparing respiration between taxa (*Pocillopora* spp. versus *Porites* spp.) and treatment (light versus dark) using biomass as a covariate; two-factor ANCOVA comparing ash free dry mass (AFDM) between taxa (*Pocillopora* spp. versus *Porites* spp.) and treatment (light versus dark) using surface area as a covariate; and ANCOVA comparing symbiont counts between treatments for *Pocillopora* spp. using biomass as a covariate.

In both taxa, there was a reduction in symbiont density in starved corals, which likely influenced the decrease in holobiont biomass and respiration. Symbionts can contribute ∼5 to 15% of holobiont biomass in reef corals (Kemp et al., 2020) and ∼3–24% (in *Fungia scutaria* and *Pocillopora eydouxi*) of the aerobic respiration of the holobiont (Davies, 1984; Edmunds and Davies, 1986; Muscatine et al., 1981). In the present study, symbiont density decreased by ∼84% in both taxa, which means that at maximum, ∼20% of the decrease in holobiont respiration and ∼13% of the decrease in holobiont biomass could be attributed to symbiont loss. Disentangling the changes in biomass and metabolism from effects attributed to coral tissue or symbionts was beyond the scope of this study and therefore our analysis does not rule out the possibility that symbiont density could modulate metabolic scaling in these corals.

Summary

The present study detected differences in metabolic scaling in broadcasted and brooded coral larvae, and these findings were consistent with two concepts accounting for variation in metabolic scaling – life history theory (White et al., 2022) and the surface area sub-theory of metabolic scaling (Ellenby, 1937; Glazier, 2014; Rubner, 1883) – thus suggesting there could be benefits to combining the theories in order to acquire a holistic understanding of metabolic scaling in coral larvae. For juvenile corals, our results support the hypothesis that metabolic scaling is likely driven by the surface area to biomass ratio. In juvenile corals, isometric scaling of biomass on area coincided with metabolic isometry, but positive allometric scaling of biomass on area coincided with negative metabolic allometry. Although the scaling of biomass and metabolism in our corals was not altered by starvation, biomass declined in *Pocillopora* spp. and *Porites* spp. Because this effect was coupled with higher metabolic scaling exponents, it is reasonable to infer that variation in biomass underpins variation in metabolic scaling in these corals.

Acknowledgements

We are thankful to California State University, Northridge, and the Richard B. Gump South Pacific Research Station for providing facilities that allowed us to carry out this research. We are grateful to N. J. Silbiger and S. C. Burgess for their valuable comments on earlier drafts of the manuscript, K. W. Johnson for field assistance, and N. Davies and the staff of the Gump Station for making our trips to Moorea productive and enjoyable. We also thank the editor and two anonymous reviewers for their edits and comments, which have contributed significantly to improving the article. This research was submitted in partial fulfillment of the MSc degree to N.K.B.

Competing interests

The authors declare no competing or financial interests.

Author contributions

Conceptualization: N.K.B., P.J.E.; Methodology: N.K.B., P.J.E.; Software: N.K.B.; Validation: N.K.B., P.J.E.; Formal analysis: N.K.B.; Investigation: N.K.B.; Resources: N.K.B., P.J.E.; Data curation: N.K.B.; Writing - original draft: N.K.B., P.J.E.; Writing - review & editing: N.K.B., P.J.E.; Visualization: N.K.B.; Supervision: P.J.E.; Project administration: N.K.B., P.J.E.; Funding acquisition: N.K.B., P.J.E.

Funding

This work was supported by the United States National Science Foundation through the Moorea Coral Reef Long-Term Ecological Research [OCE 16-37396], COVID supplementary funds [to OCE 17-56678] and the California State University, Northridge Graduate Studies Thesis Support Program, and it benefitted from gifts from the Gordon and Betty Moore Foundation.

Data availability

Data are available from the Dryad digital repository (Bean, 2024): doi:10.5061/dryad.pk0p2ngx0.

ECR Spotlight

This article has an associated ECR Spotlight interview with Nina Bean.

References

Bak, R. P. M. and Engel, M. S. (1979). Distribution, abundance and survival of juvenile hermatypic corals (Scleractinia) and the importance of life history strategies in the parent coral community. *Mar. Biol.* **54**, 341-352. doi:10.1007/BF00395440

Bean, N. (2024). The scaling of metabolic traits differs among larvae and juvenile colonies of scleractinian corals [Dataset]. Dryad. doi:10.5061/dryad.pk0p2ngx0

Brown, J. H., Gillooly, J. F., Allen, A. P., Savage, V. M. and West, G. B. (2004). Toward a metabolic theory of ecology. *Ecology* **85**, 1771-1789. doi:10.1890/03-9000

Burgess, S. C., Ryan, W. H., Blackstone, N. W., Edmunds, P. J., Hoogenboom, M. O., Levitan, D. R. and Wulff, J. L. (2017). Metabolic scaling in modular animals. *Invertebr. Biol.* **136**, 456-472. doi:10.1111/ivb.12199

Cumbo, V. R., Edmunds, P. J., Wall, C. B. and Fan, T.-Y. (2013). Brooded coral larvae differ in their response to high temperature and elevated pCO_2 depending on the day of release. *Mar. Biol.* **160**, 2903-2917. doi:10.1007/s00227-013-2280-y

Davies, P. S. (1984). The role of zooxanthellae in the nutritional energy requirements of *Pocillopora eydouxi*. *Coral Reefs* **2**, 181-186. doi:10.1007/BF00263571
Davies, P. S. (1991). Effect of daylight variations on the energy budgets of shallow-water corals. *Mar. Biol.* **108**, 137-144. doi:10.1007/BF01313481
Edmunds, P. J. (2000). Patterns in the distribution of juvenile corals and coral reef community structure in St. John, US Virgin Islands. *Mar. Ecol. Prog. Ser.* **202**, 113-124. doi:10.3354/meps202113
Edmunds, P. J. (2006). Temperature-mediated transitions between isometry and allometry in a colonial, modular invertebrate. *Proc. R. Soc. B Biol. Sci.* **273**, 2275-2281. doi:10.1098/rspb.2006.3589
Edmunds, P. J. (2008). The effects of temperature on the growth of juvenile scleractinian corals. *Mar. Biol.* **154**, 153-162. doi:10.1007/s00227-008-0910-6
Edmunds, P. J. and Davies, P. S. (1986). An energy budget for *Porites porites* (Scleractinia). *Mar. Biol.* **92**, 339-347. doi:10.1007/BF00392674
Edmunds, P. J. and Davies, P. S. (1988). Post-illumination stimulation of respiration rate in the coral *Porites porites*. *Coral Reefs* **7**, 7-9. doi:10.1007/BF00301975
Edmunds, P. J., Gates, R. D. and Gleason, D. F. (2001). The biology of larvae from the reef coral *Porites astreoides*, and their response to temperature disturbances. *Mar. Biol.* **139**, 981-989. doi:10.1007/s002270100634
Edmunds, P. J., Cumbo, V. and Fan, T.-Y. (2011). Effects of temperature on the respiration of brooded larvae from tropical reef corals. *J. Exp. Biol.* **214**, 2783-2790. doi:10.1242/jeb.055343
Elahi, R. and Edmunds, P. J. (2007). Determinate growth and the scaling of photosynthetic energy intake in the solitary coral *Fungia concinna* (Verrill). *J. Exp. Mar. Bio. Ecol.* **349**, 183-193. doi:10.1016/j.jembe.2007.05.007
Ellenby, C. (1937). Relation between body size and metabolism. *Nature* **140**, 853.
Fox, J. and Weisberg, S. (2019). *An R Companion to Applied Regression*, 3rd edn Thousand Oaks, CA: Sage.
Gaither, M. R. and Rowan, R. (2010). Zooxanthellar symbiosis in planula larvae of the coral *Pocillopora damicornis*. *J. Exp. Mar. Bio. Ecol.* **386**, 45-53. doi:10.1016/j.jembe.2010.02.003
Garland, T., , Jr and Adolph, S. C. (1994). Why not to do two-species comparative studies: limitations on inferring adaptation. *Physiol. Zool.* **67**, 797-828. doi:10.1086/physzool.67.4.30163866
Glazier, D. S. (2005). Beyond the '3/4-power law': variation in the intra- and interspecific scaling of metabolic rate in animals. *Biol. Rev.* **80**, 611-662. doi:10.1017/S1464793105006834
Glazier, D. S. (2010). A unifying explanation for diverse metabolic scaling in animals and plants. *Biol. Rev.* **85**, 111-138. doi:10.1111/j.1469-185X.2009.00095.x
Glazier, D. S. (2014). Metabolic scaling in complex living systems. *Systems* **2**, 451-540. doi:10.3390/systems2040451
Gleason, D. F. and Hofmann, D. K. (2011). Coral larvae: from gametes to recruits. *J. Exp. Mar. Bio. Ecol.* **408**, 42-57. doi:10.1016/j.jembe.2011.07.025
Graham, J. B. (1988). Ecological and evolutionary aspects of integumentary respiration: body size, diffusion, and the invertebrata. *Am. Zool.* **28**, 1031-1045. doi:10.1093/icb/28.3.1031
Graham, E. M., Baird, A. H., Connolly, S. R., Sewell, M. A. and Willis, B. L. (2013). Rapid declines in metabolism explain extended coral larval longevity. *Coral Reefs* **32**, 539-549. doi:10.1007/s00338-012-0999-4
Grottoli, A. G., Rodrigues, L. J. and Juarez, C. (2004). Lipids and stable carbon isotopes in two species of Hawaiian corals, *Porites compressa* and *Montipora verrucosa*, following a bleaching event. *Mar. Biol.* **145**, 621-631. doi:10.1007/s00227-004-1337-3
Hall, V. R. and Hughes, T. P. (1996). Reproductive strategies of modular organisms: comparative studies of reef-building corals. *Ecology* **77**, 950-963. doi:10.2307/2265514
Harii, S., Yamamoto, M. and Hoegh-Guldberg, O. (2010). The relative contribution of dinoflagellate photosynthesis and stored lipids to the survivorship of symbiotic larvae of the reef-building corals. *Mar. Biol.* **157**, 1215-1224. doi:10.1007/s00227-010-1401-0
Hartikainen, H., Humphries, S. and Okamura, B. (2014). Form and metabolic scaling in colonial animals. *J. Exp. Biol.* **217**, 779-786. doi:10.1242/jeb.093484
Hoegh Guldberg, O. and Salvat, B. (1995). Periodic mass-bleaching and elevated sea temperatures: bleaching of outer reef slope communities in Moorea, French Polynesia. *Mar. Ecol. Prog. Ser.* **121**, 181-190. doi:10.3354/meps121181
Jiang, L., Sun, Y.-F., Zhang, Y.-Y., Tian, Y., Lei, X.-M., Zhou, G.-W., Yuan, T., Yuan, X.-C., Liu, S. and Huang, H. (2021). Ocean acidification alters the thermal performance curves of brooded larvae from the reef coral *Pocillopora damicornis*. *Coral Reefs* **40**, 1437-1449. doi:10.1007/s00338-021-02161-3
Jokiel, P. L. and Morrissey, J. I. (1986). Influence of size on primary production in the reef coral *Pocillopora damicornis* and the macroalga *Acanthophora spicifera*. *Mar. Biol.* **91**, 15-26. doi:10.1007/BF00397566
Kearney, M. R. (2021). What is the status of metabolic theory one century after Pütter invented the von Bertalanffy growth curve? *Biol. Rev.* **96**, 557-575. doi:10.1111/brv.12668
Kemp, D. W., Kempf, S. C. and Fitt, W. K. (2020). The weight of it all: symbiotic dinoflagellates in Caribbean reef-building corals. *Mar. Biol.* **167**, 121. doi:10.1007/s00227-020-03737-3
Kleiber, M. (1932). Body size and metabolism. *Hilgardia* **6**, 315-353. doi:10.3733/hilg.v06n11p315
Knowlton, N. (2001). The future of coral reefs. *Proc. Natl. Acad. Sci. USA* **98**, 5419-5425. doi:10.1073/pnas.091092998
Kühl, M., Cohen, Y., Dalsgaard, T., Jørgensen, B. B. and Revsbech, N. P. (1995). Microenvironment and photosynthesis of zooxanthellae in scleractinian corals studied with microsensors for O_2, pH and light. *Mar. Ecol. Prog. Ser.* **117**, 159-177. doi:10.3354/meps117159
Lagos, M. E., White, C. R. and Marshall, D. J. (2017). Do invasive species live faster? Mass-specific metabolic rate depends on growth form and invasion status. *Funct. Ecol.* **31**, 2080-2086. doi:10.1111/1365-2435.12913
Muscatine, L. and Hand, C. (1958). Direct evidence for the transfer of materials from symbiotic algae to the tissues of a coelenterate. *Zoology* **44**, 1259-1263.
Muscatine, L., McCloskey, L. R. and Marian, R. E. (1981). Estimating the daily contribution of carbon from zooxanthellae to coral animal respiration. *Limnol. Oceanogr* **26**, 601-611. doi:10.4319/lo.1981.26.4.0601
Muscatine, L., Falkowski, P. G., Porter, J. W. and Dubinsky, Z. (1984). Fate of photosynthetic fixed carbon in light- and shade-adapted colonies of the symbiotic coral *Stylophora pistillata*. *Proc. R. Soc. Lond. Ser. B Biol. Sci.* **222**, 181-202.
Norkko, A., Villnäs, A., Norkko, J., Valanko, S. and Pilditch, C. (2013). Size matters: implications of the loss of large individuals for ecosystem function. *Sci. Rep.* **3**, 2646. doi:10.1038/srep02646
Nozawa, Y. and Okubo, N. (2011). Survival dynamics of reef coral larvae with special consideration of larval size and the genus *Acropora*. *Biol. Bull.* **220**, 15-22. doi:10.1086/BBLv220n1p15
Putnam, H. M., Barott, K. L., Ainsworth, T. D. and Gates, R. D. (2017). The vulnerability and resilience of reef-building corals. *Curr. Biol.* **27**, R528-R540. doi:10.1016/j.cub.2017.04.047
Rapuano, H., Shlesinger, T., Roth, L., Bronstein, O. and Loya, Y. (2023). Coming of age: onset of coral reproduction is determined by age rather than size. *iScience* **26**, 106533. doi:10.1016/j.isci.2023.106533
Richmond, R. H. (1987). Energetics, competency, and long-distance dispersal of planula larvae of the coral *Pocillopora damicornis*. *Mar. Biol.* **93**, 527-533. doi:10.1007/BF00392790
Rodrigues, L. J. and Grottoli, A. G. (2007). Energy reserves and metabolism as indicators of coral recovery from bleaching. *Limnol. Oceanogr.* **52**, 1874-1882. doi:10.4319/lo.2007.52.5.1874
Rubner, M. (1883). Ueber den Einfluss der Körpergrösse auf Stoff- und Kraftwechsel. *Z. Biol.* **19**, 536-562.
Schmidt-Nielsen, K. (1984). *Scaling: Why is Animal Size so Important?* 1st edn. Cambridge: Cambridge University Press.
Sebens, K. P. (1987). The ecology of indeterminate growth in animals. *Annu. Rev. Ecol. Syst* **18**, 371-407. doi:10.1146/annurev.es.18.110187.002103
Shapiro, O. H., Fernandez, V. I., Garren, M., Guasto, J. S., Debaillon-Vesque, F. P., Kramarsky-Winter, E., Vardi, A. and Stocker, R. (2014). Vortical ciliary flows actively enhance mass transport in reef corals. *Proc. Natl. Acad. Sci. USA* **111**, 13391-13396. doi:10.1073/pnas.1323094111
Shick, J. M. (1990). Diffusion limitation and hyperoxic enhancement of oxygen consumption in zooxanthellate sea anemones, zoanthids, and corals. *Biol. Bull.* **179**, 148-158. doi:10.2307/1541749
Soong, K. (1993). Colony size as a species character in massive reef corals. *Coral Reefs* **12**, 77-83. doi:10.1007/BF00302106
Stearns, S. C. (1989). Trade-offs in life-history evolution. *Funct. Ecol.* **3**, 259-268. doi:10.2307/2389364
Stimson, J. S. (1987). Location, quantity and rate of change in quantity of lipids in tissue of Hawaiian hermatypic corals. *Bull. Mar. Sci.* **41**, 889-904.
Vollmer, S. V. and Edmunds, P. J. (2000). Allometric scaling in small colonies of the scleractinian coral *Siderastrea siderea* (Ellis and Solander). *Biol. Bull.* **199**, 21-28. doi:10.2307/1542703
Waller, R. G., Goode, S., Tracey, D., Johnstone, J. and Mercier, A. (2023). A review of current knowledge on reproductive and larval processes of deep-sea corals. *Mar. Biol.* **170**, 1-27. doi:10.1007/s00227-023-04182-8
West, G. B., Brown, J. H. and Enquist, B. J. (1997). A general model for the origin of allometric scaling laws in biology. *Science* **276**, 122-126. doi:10.1126/science.276.5309.122
White, C. R., Kearney, M. R., Matthews, P. G. D., Kooijman, S. A. L. M. and Marshall, D. J. (2011). A manipulative test of competing theories for metabolic scaling. *Am. Nat.* **178**, 746-754. doi:10.1086/662666
White, C. R., Marshall, D. J., Alton, L. A., Arnold, P. A., Beaman, J. E., Bywater, C. L., Condon, C., Crispin, T. S., Janetzki, A., Pirtle, E. et al. (2019). The origin and maintenance of metabolic allometry in animals. *Nat. Ecol. Evol.* **3**, 598-603. doi:10.1038/s41559-019-0839-9
White, C. R., Alton, L. A., Bywater, C. L., Lombardi, E. J. and Marshall, D. J. (2022). Metabolic scaling is the product of life-history optimization. *Science* **377**, 834-839. doi:10.1126/science.abm7649
Yellowlees, D., Rees, T. A. V. and Leggat, W. (2008). Metabolic interactions between algal symbionts and invertebrate hosts. *Plant Cell Environ.* **31**, 679-694. doi:10.1111/j.1365-3040.2008.01802.x