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Abstract: Animals are heterotrophic by definition, but species from many taxonomic groups are hosts to epibiota that may alter their net metabolism. We tested the degree to which snail-shell epibiota can generate net ecosystem productivity for snails and their epibiota (snail–epibiota ecosystems; SEEs) after accounting for snail respiration. We focused on 3 species from the *Lavigeria* snail assemblage in Africa's Lake Tanganyika and quantified the scaling of SEE metabolism with shell size under light and dark conditions. The metabolism of snails and their epibiota shifted significantly across the size gradient. SEEs of large snails (>20 mm) were consistently autotrophic during the daytime, reflecting increases in shell algae as snails move into well-lit microhabitats after reaching a size refuge from predation by crabs. We extrapolated daytime individual SEE metabolism patterns to snail assemblages at 11 sites and found that SEEs range from heterotrophic to autotrophic in aggregate, reflecting spatial differences in size distributions. Our integration of organismal traits, species interactions, and assemblage structure reveals the important role of epibiota in organismal metabolism. Large epibiotic contributions to organismal metabolism could be widespread among animals that live in well-lit environments and fertilize their epibiota, but depend on the scaling of epibiotic and host metabolism with body size.
Key words: *Lavigeria*, Lake Tanganyika, primary production, respiration, co-evolution, microhabitat, assemblage, community

Animals are heterotrophic by definition, but species from many taxonomic groups host epibiota that may alter their net metabolism. For example, some caddisflies (Mooney et al. 2014), sloths (Suutari et al. 2010), and turtles (Neil 1954) have substantial epibiotic communities that include both primary producers (e.g., epiphytic algae) and heterotrophs (e.g., heterotrophic bacteria). The biomass of epibiota rarely exceeds that of the host, but small organisms (e.g., algae) have much higher mass-specific metabolic rates than larger organisms (Makarieva et al. 2008). Thus, primary production of epibiota could partially offset or even exceed the respiration of their animal host (Allen 1971, Pollard and Kogure 1993), potentially creating autotrophy of the host–epibiota ecosystem.

The relative role of epibiota in the net metabolism of host–epibiota ecosystems depends on the host's traits and its environment. For instance, sedentary animals generally have lower basal metabolic rates than more active animals, independent of size (Nagy and Montgomery 1980). In addition, a high ratio of host surface area to mass might enable epibiota to contribute substantially to metabolism, even achieving net autotrophy if sufficient area were available to epibiotic primary producers to offset respiration by their host. Hairy or spinous animals might be especially attractive hosts because their surface texture increases the surface area available to epibiota. Moreover, host excreta may fertilize epibiota on various time scales, as in cases of urine washing by primates (Milton 2010) or local enrichment of the water by aquatic organisms (Mooney et al. 2014). Environmental context also might mediate the metabolic balance between a host animal and its epibiota. Primary production per unit area generally increases with solar irradiance. Therefore, hosts that dwell in well-lit environments are likely to support substantial epibiotic primary producers. The relative contribution of epibiotic metabolism to net host–epibiota metabolism may be highest when the host is

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sedentary, textured, and fertilizes the environment available to epibiota.

We evaluated the metabolic balance between snails and their epibiota in Lake Tanganyika, the oldest and deepest lake in Africa. Lake Tanganyika is exceptionally clear and nutrient poor. Its nearshore zone is highly productive with species-rich animal communities including a radiation of freshwater snails (West and Michel 2000), many of which are hosts for epibiota including algae, bryozoans, sponges, rotifers, and insects. Several abundant *Lavigeria* species achieve relatively large shell sizes by the standards of freshwater snails (>20-mm length), offering opportunities to quantify metabolic scaling with size. The benthic algae in the nearshore zone of Lake Tanganyika have exceptionally high productivity per unit biomass (O'Reilly 2006), in part because abundant and diverse grazers prevent periphyton accumulation (McIntyre et al. 2006). Our observations also suggest that snail shells frequently have more algal biomass per area than littoral rocks at the same depth. Thus, Lake Tanganyika's snails are an ideal model system for comparing epibiotic primary production to snail respiration to assess the degree to which snail–epibiota ecosystems (SEEs) can be autotrophic.

We measured the respiration and primary production of SEEs across a broad range of snail shell lengths (L) for 3 species of *Lavigeria* snails in the nearshore zone of Lake Tanganyika. We expected that SEE respiration (R) would scale with $L^{2.54}$ based on the scaling of R with snail soft tissue mass (M) ($R \propto M^{0.75}$; Gillooly et al. 2001) and the scaling of snail tissue mass with length ($M \propto L^{3.38}$). Furthermore, assuming that SEE gross primary production (GPP) scales linearly with snail shell area, we would expect SEE GPP to scale with L^2 based on the surface area of a conical shell. Thus, we predicted that differential scaling of R and GPP with snail length would lead to changes in net metabolism with snail size. Last, we applied our size-based model of SEE metabolism to snail density and size distribution data from 11 nearshore sites to assess spatial variability in potential SEE metabolism in aggregate across snail assemblages. Merging survey data and metabolic measurements allowed us to use snail traits to estimate their collective role in littoral ecosystem metabolism.

METHODS

Study system

Lake Tanganyika is the 2nd-oldest and most voluminous lake in the world. The lake never fully mixes and has a permanently anoxic zone below 100- to 200-m depth. The lake ecosystem is under threat from a number of sources including climate change (O'Reilly et al. 2003, Tierney et al. 2010, Kraemer et al. 2015) and anthropogenic sedimentation, which reduces habitat availability for snails living on rocky substrates (Cohen et al. 1993, McIntyre et al. 2005).

Tanganyika is among the most species-rich lakes in the world, and most animal taxa in the lake are endemic (Vadeboncoeur et al. 2011) and part of species flocks (i.e., in situ evolutionary radiations of closely related species; Salzburger et al. 2014). The high endemicity of its fauna reflects the lake's size, age, and diversity of nearshore habitats. Lake Tanganyika has at least 81 species of gastropods (West et al. 2003), nearly all of which are endemic. The actual number of gastropod species in the lake may be double that described. Over 40 additional *Lavigeria* and 20 *Paramelania* species have been recognized from recent collections (Burgon et al. 2014). We focused on the 3 largest snail species that are sympatric and locally common on rock surfaces in <10-m water depth at shallow rocky nearshore habitats near Kigoma, Tanzania (*Lavigeria nassa*, *Lavigeria grandis*, and *Lavigeria coronata*; Fig. 1) (McIntyre et al. 2005). Pop-

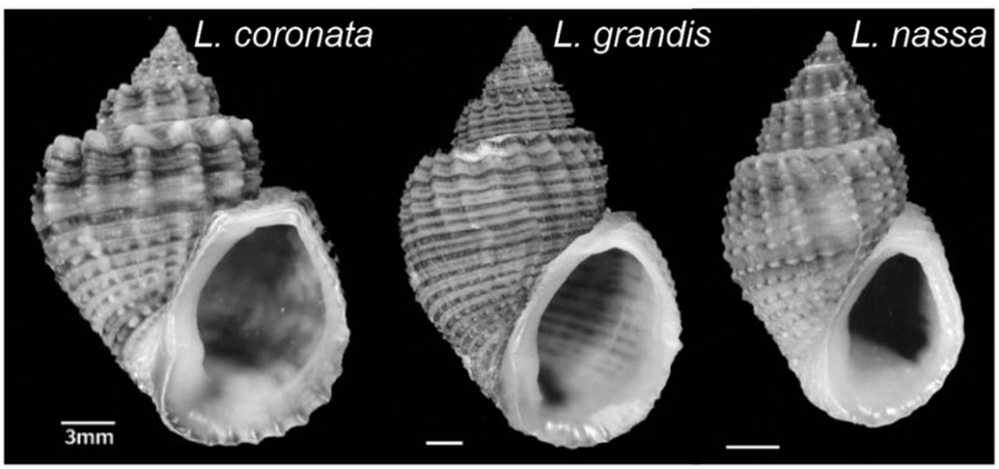

Figure 1. Empty shells cleaned of epibiota of *Lavigeria coronata*, *Lavigeria grandis*, and *Lavigeria nassa* (left to right). Scale bars = 3 mm. *Lavigeria nassa* shows scar in center of final whorl from a crab attack.

ulation densities and size distributions of these and other species vary enormously among sites (McIntyre et al. 2005).

Metabolism measurements

We measured daytime metabolism of SEEs from ~5 m depth at 2 rocky nearshore sites (3 and 6 in Fig. 2A) near Kigoma between 14 July and 10 August 2012. Snails used for the incubations were *L. coronata* (Bourguignat, 1888) (n = 8, all from site 3), *L. nassa* (Woodward, 1859) (n = 13, all from site 3), and *L. grandis* (Smith, 1881) (n = 22 from site 3, n = 8 from site 6). Immediately upon collection between 1000 and 1500 h, we transferred each snail into its own clear plastic incubation chamber of lake water (114 mL) suspended 1 m below the surface from a moored boat. We measured initial dissolved O_2 levels after the snail re-emerged from its shell (1–5 min). Light measurements (Hobo Pendant; Onset Corporation, Bourne, Massachusetts) indicated that shading from the boat and the dissolved O_2 probe produced light levels inside the chamber that matched those typical at 5 m depth during the daytime when SEE metabolism incubations took place. We suspended a control chamber containing only lake water adjacent to the incubation chamber. To distinguish net SEE metabolism from snail and epibiota respiration, we randomly selected 28 snails for incubation in opaque chambers to eliminate epibiotic primary productivity while we incubated 23 snails in transparent chambers to measure net SEE daytime metabolism. We logged dissolved O_2 and temperature every 30 s with an YSI ProODO meter (Yellow Springs Instruments, Yellow Springs, Ohio) with the sensor head sealed inside the chamber.

Incubations lasted 30 min, unless the dissolved O_2 fell below 4 mg/L (thereby stressing snails) or rose above 10 mg/L (enabling loss of O_2 by outgassing). We calculated the daytime SEE O_2 flux as the difference in change in dissolved O_2 between the SEE and control incubations, standardized for incubation time and water volume. We used the differ-

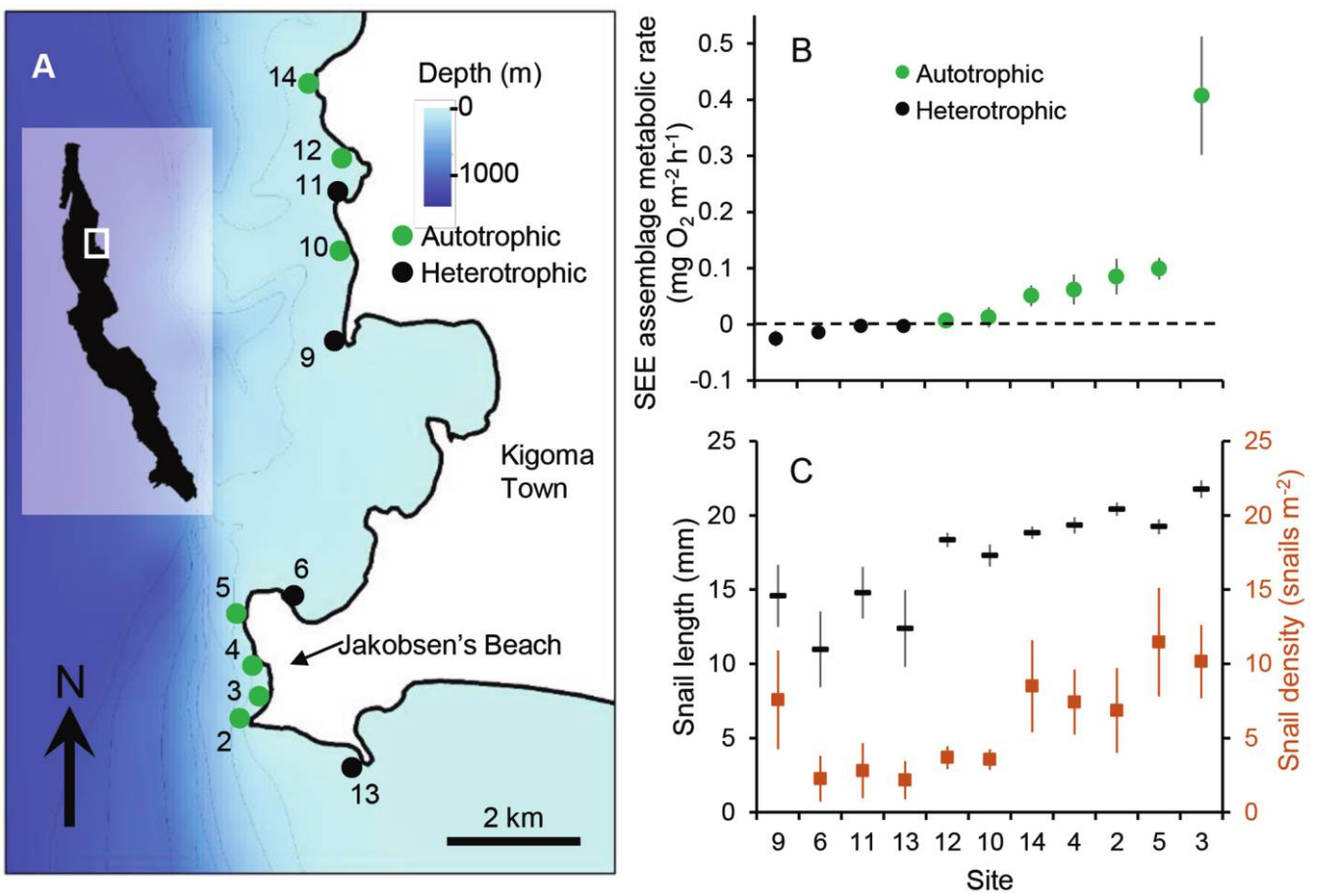

Figure 2. Survey sites in Lake Tanganyika at 5 m depth (A), mean (±95% CI) snail epibiota ecosystem (SEE) net metabolic rate (B), and snail shell length and density (C). Sites 3 and 6 were the focal sites where snails were taken for metabolism incubations. SEE net productivity estimates were extrapolated from the size-based models of SEE gross primary production and respiration. Sites in panels B and C are ordered by their net metabolic rate, but site numbers correspond to numbers in panel A. Sites 1 to 12 are the same as in work by Corman et al. (2010) with the addition of 2 sites (13 and 14). Sites 1, 7, and 8 were excluded from this analysis because of their proximity to human settlements.

ence between the SEE and control incubations to remove the effect of background GPP and ER in the water in which snails were incubated. After each incubation, we measured the shell length (L) along the coiling axis from the apex to the anterior-most edge of the aperture. We corrected the chamber volume for an approximation of the volume displaced by the snail ($^4/_3\pi L^3$). These estimates of net metabolism were not integrated over a full day because we do not have nighttime measurements of SEE metabolism, which could differ from daytime rates.

The conditions of the SEE incubations reflected the underwater environmental conditions and snail populations found at 5-m depth. The average water temperature inside snail incubation chambers was 26.56°C (range: 25.51–27.45°C), which was within the range of observed seasonal temperature variation in Lake Tanganyika. The range of lengths of incubated snails was 13 to 35 mm, representing the full size range observed in our field surveys of these species from juveniles to adults. The median snail lengths for incubated *L. grandis*, *L. nassa*, and *L. coronata* were 21.8, 20.3, and 27.6 mm, respectively.

Snail metabolism modeling

For all analyses, we standardized daytime metabolic rates to 26.5°C using general, empirically derived relationships between temperature and benthic metabolism (Yvon-Durocher et al. 2010) and snail metabolism (Gillooly et al. 2001). This technique enabled us to compare rates directly without the influence of small differences in water temperature. Corrections were always minor. First, we used R data from the dark incubations to quantify the scaling of SEE R with L. We used analysis of covariance (ANCOVA) to test whether the scaling of $\log_{10}$(SEE R) with $\log_{10}$(L) varied by snail species (for all 3 species) or by site (for *L. grandis* only). If we found no species or site effects, we pooled the data across species and site and used Theil–Sen's nonparametric regression (Theil 1950, Sen 1968, Peng et al. 2008) to estimate the relationship between $\log_{10}$(SEE R) and $\log_{10}$(L). We selected Theil–Sen's nonparametric regression because it is less sensitive than least squares regression to outliers. The slope coefficient for $\log_{10}$(L) in the Theil–Sen regression is the scaling exponent between R and L for SEEs. We used the 95% confidence interval (CI) to test our expectation that R scales with $L^{2.54}$ based on metabolic scaling and shell geometry.

Second, we used SEE GPP data (standardized to 26.5°C) to test the hypothesis that GPP scales with L^2. We calculated SEE GPP by subtracting estimated SEE R (predicted from shell size; described above) from the net change in dissolved O_2 during light incubations. This approach is analogous to using dark and light incubations to estimate GPP and R in the water column (Staehr et al. 2012). We used an analysis of covariance (ANCOVA) to test whether the scaling of SEE GPP with L differed across snail species (for all 3 species) or sites (for *L. grandis* only). If we found no effect of species or site, we used Theil–Sen's nonparametric regression to estimate the relationship between $\log_{10}$(GPP) and $\log_{10}$(L). We used the 95% CI for the slope coefficient to test our expectation that GPP scales with L^2 based on shell surface area. All statistics were run with *mblm* and *base* packages in the software R (version 3.1.3; R Project for Statistical Computing, Vienna, Austria).

To assess whether changes in SEE GPP with shell size were attributable to epibiota, we quantified epibiotic biomass on a separate set of 14 *L. grandis* from site 3 in October 2015. We used a brass brush to gently scrub all epibiota from a shell, then filtered the resulting slurry onto a preweighed glass-fiber filter. We measured epibiotic dry mass after oven-drying filters (60°C, 48 h). This measurement was based on the assumption that erosion of the mineral parts of the shell was minimal. We used Theil–Sen's nonparametric regression to estimate the relationship between $\log_{10}$(epibiotic dry mass) and $\log_{10}$(L). We used the 95% CI for the slope coefficient to test our expectation that epibiotic dry mass scales with L^2 based on shell surface area.

Snail densities and assemblage metabolism

We used the size-scaling of individual SEE metabolism to estimate aggregate SEE metabolism of snail assemblages at 11 rocky littoral sites (~1 km between sites; see Corman et al. 2010). These sites are our long-term monitoring sites that receive little or no sediment loading. We avoided sites where sedimentation has shifted the size structure and species composition of the snail assemblage (McIntyre et al. 2005) and potentially has affected SEE metabolism. We quantified snail densities, species composition, and size distributions by collecting snails from 8 replicate quadrats (1- × 1-m square, ~5-m spacing) at 5-m depth in July–August 2012. We scrubbed each snail of its epibiota for identification, measured it, and checked for scars from crab predation attempts. We applied the fitted size-scaling model of SEE GPP and R to each *L. grandis*, *L. nassa*, and *L. coronata* observed in our quadrats to estimate aggregate metabolism associated with the snail assemblage. For each individual snail in the assemblage, we randomly selected a coefficient from the distribution of pairwise coefficients from the Theil–Sen method to account for uncertainty in scaling coefficients for GPP and R of SEEs. For these calculations, we assumed that water temperatures were uniform across sites (26.5°C), in keeping with observations (Corman et al. 2010). We estimated the site means and 95% CIs for site snail density, average snail length, and SEE metabolism by resampling 200 times with replacement from the 8 quadrat-level estimates of these variables.

RESULTS

SEEs were heterotrophic in dark and tended to be autotrophic in light conditions (all data from our study can be

found in Appendix S1). Dissolved O_2 concentrations declined relative to the control in all dark incubations (mean ± SD: –0.21 ± 0.18 mg O_2/h) but increased in 67% of light incubations (0.07 ± 0.20 mg O_2/h).

The size-scaling of SEE metabolism was only partially explained by simple size-scaling rules. Theil–Sen slopes indicated that R increased with $L^{2.23}$ (Figs. 2B, C, 3), and the 95% CI for the scaling coefficient of R (1.71–2.83) included the hypothesized value of 2.54. Thus, we did not find evidence to reject the null hypothesis that SEE R can be explained by simple allometric scaling rules. SEE GPP increased with $L^{3.06}$ (Fig. 3), and the 95% CI (2.63–4.10) did not include the hypothesized value of 2. Snail epibiotic dry mass increased with $L^{3.76}$, and the 95% CI (3.23–4.00) for the scaling coefficient also did not include the hypothesized value of 2. Size-scaling of R and GPP of SEEs did not differ among snail species (ANCOVA, $p = 0.16$ and $p = 0.93$, respectively) or between sites (ANCOVA, $p = 0.11$ and $p = 0.88$, respectively).

SEEs in the light incubations—which included both R and GPP processes—shifted gradually from heterotrophic to autotrophic with increasing snail length (Fig. 4A). The point at which SEEs switched from heterotrophic to autotrophic occurred at L ≈ 20 mm (Fig. 4A), which is also the size at which we observed increases in epibiotic biomass on shells (Fig. 4B) and frequencies of shell scars from failed predation attempts by crabs from snail surveys (Fig. 4C). Predation scars occurred on 178 of 546 snails measured in the snail-assemblage surveys. Small snails (L < 15 mm) rarely had scars, whereas snails >20 mm were frequently scarred (Fig. 4C).

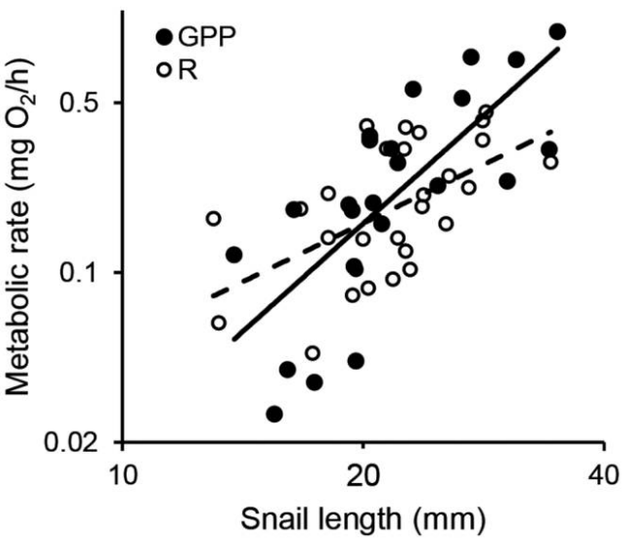

Figure 3. Respiration (R) and gross primary production (GPP) of *Lavigeria* snails and their epibiota on a gradient of snail size. Axes are on a log scale. Lines are median-based best-fit lines for GPP (scaling coefficient = 3.06) and R (scaling coefficient = 2.23).

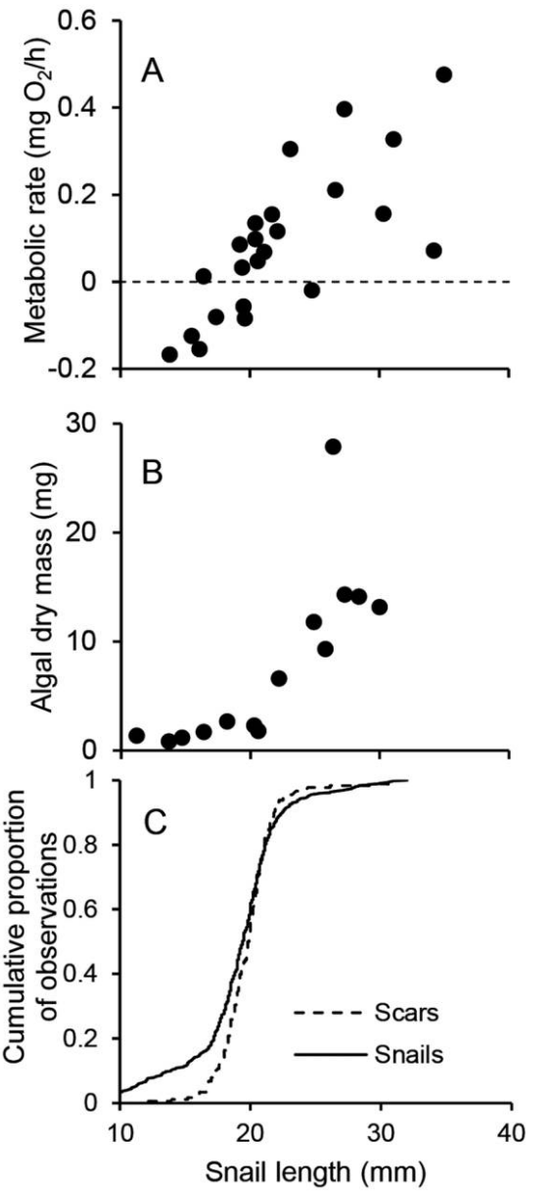

Figure 4. Net metabolic rate (A), epibiotic dry mass (on *Lavigeria grandis* shells only) (B), and presence of scars from crab attacks on snail shells (C) as a function of snail length. Metabolic rate is the difference between *Lavigeria* snail–epibiota ecosystem gross primary production and respiration. The solid black line in panel C represents the cumulative size frequency distribution for 547 snails collected during the site survey. The dashed black line represents the cumulative proportion of scars from crab attacks across the same snail size distribution (178 of 547 snails had ≥1 scar).

Results obtained by applying the size-scaling equations for SEE GPP and R to the size frequency distributions for *L. nassa*, *L. grandis*, and *L. coronata* from each site suggest that snail assemblages at 7 of 11 sites are autotrophic at 5 m during the daytime (Fig. 2B). Across sites, assemblage-level

daytime net metabolism of SEEs ranged from –0.04 mg O_2 h^{-1} m^{-2} to 0.47 mg O_2 h^{-1} m^{-2} (mean: 0.06 mg O_2 h^{-1} m^{-2}; Fig. 2B). Densities of the 3 focal species ranged from 2.2 to 11.5 snails/m^2, and average L ranged from 11.0 to 21.8 mm across the 11 survey sites (Fig. 2C). Sites with higher density tended to have larger snails. *Lavigeria nassa* and *L. grandis* were found at all sites, but *L. coronata* was found at only 3 sites (sites 2, 3, and 11; Fig. 2A). *Lavigeria coronata* tended to be larger on average than the other species. Median snail lengths for *L. grandis*, *L. nassa*, and *L. coronata* in the site survey were 19.0, 19.4, and 27.8 mm, respectively.

DISCUSSION

The relationship between SEE R and L matches general predictions of metabolic scaling with soft tissue mass for large *Lavigeria* snails in Lake Tanganyika, suggesting that epibiotic R plays a minimal role in SEE metabolism. However, epibiotic GPP plays a large role in SEE metabolism and drives autotrophy at large snail size. GPP also scales more steeply with L than what would be expected from simple scaling assumptions and gives rise to a shift from daytime heterotrophy to daytime autotrophy as snails grow. The point at which SEEs change from heterotrophy to autotrophy occurs at L ≈ 20 mm, which is approximately the size at which snails begin accumulating epibiota and appear to reach a size refuge from predatory crabs (Fig. 4C).

We speculate that the shift from heterotrophy to autotrophy of SEEs as snails grow reflects ontogenetic shifts in microhabitat use by snails that is driven by the risk of crab predation (West and Cohen 1994, 1996). Several species of endemic crabs have robust molariform dentition on their chelae that enable them to crush snail shells (Marijnissen et al. 2008). Strong selective pressure from crabs is thought to be responsible for thickness, crossed-lamellar layer microstructure, and diverse shell sculpturing that differ between many Tanganyikan snails and freshwater snails elsewhere (West and Cohen 1996). Predation trials suggest that *Lavigeria* >20 mm generally withstand attacks from crabs, but smaller snails usually are killed (West et al. 1991). The risk of predation by crustaceans leads to microhabitat shifts in many snail species (Hadlock 1983, Alexander and Covich 1991, DeWitt et al. 1999, Trussell et al. 2003) and apparently in Tanganyikan snails as well. Juvenile *Lavigeria* often are found under rocks or in cracks where they can avoid crabs, whereas larger conspecifics are found almost exclusively in the open where they are exposed to crabs (West et al. 1991). Thus, the shells of juvenile snails may provide poor habitat for epiphytic algae because they occupy poorly lit microhabitats. Only when snails are large enough to withstand most crab attacks (Fig. 4C) do epibiota accrue on their shells (Fig. 4B). Our metabolic data suggest that increasing epibiotic biomass in turn gives rise to a shift from heterotrophy to autotrophy of SEEs as snails shift microhabitats (Fig. 4B). This series of correlations leads us to surmise that a causal chain links the coevolutionary arms race between crabs and snails in Lake Tanganyika (West et al. 1991) to the role of epibiota in snail metabolism, mediated by adaptive microhabitat shifts that limit algal growth on snail shells.

Nutrients excreted and egested by snails are likely to enhance epibiotic GPP on their shells. Epibiota growing on other slow-moving animals benefit from the nutrients that their hosts excrete (Ings et al. 2012, Mooney et al. 2014). Because of their proximity, epibiota may have ready access to the nutrients that snails release as waste, especially below the wave surge zone (typically the upper 3–4 m of the water column) where water mass movements are less likely to sweep away excreted and egested nutrients. Nutrient recycling in the form of feces and liquid excretion may create miniature biogeochemical hotspots in freshwater ecosystems (McIntyre et al. 2008), which could be critical for fueling primary production in a nutrient-scarce environment like Lake Tanganyika (McIntyre et al. 2006). Some snails secrete mucus to deter predators, and mucus also could be a nutrient source for epibiota (Coffroth 1990). The combination of light limitation of primary production on juvenile snails and nutrient-enrichment of algal growth on adult snails may be responsible for the high size-scaling exponent for SEE GPP (3.06) and epibiota dry mass (3.76).

The 3 species that we studied differ in their degree of shell sculpturing (Fig. 1) and, thus, potentially the surface area available to epibiota. Despite interspecific differences in shell sculpturing, species identity did not significantly affect the size scaling of SEE GPP. Snails with spines or highly raised shell sculpturing could provide additional substrate for algal colonization and growth and a structural refuge for epibiota from grazing (Feifarek 1987, Abbott and Bergey 2007). Stronger tests of the effect of shell sculpturing on epibiotic GPP could include larger sample sizes or individuals with more disparate shell types. Snail species from Lake Tanganyika span a wide range in the degree of shell sculpturing. Thus, Tanganyika's sympatric snail species could provide an ideal system for future work to disentangle the effects of shell sculpture from other influences on SEE metabolism.

We were unable to estimate daily metabolism of SEEs because our light–dark incubations were conducted only during daylight hours. Snail R is likely to vary with diel cycles in activity and feeding, so our data may not be applicable throughout a 24-h period. Future tests of whether SEEs are heterotrophic or autotrophic when integrated over the full daily cycle will depend on the diel variability in SEE GPP and R. Our calculations suggest that snails with L > 20 mm were autotrophic during the day, but integrating over the full daily light cycle (assuming 12 h of GPP and 24 h of R per day) would create heterotrophy of SEEs at the individual level. However, if daytime SEE R exceeds nighttime SEE R because snails decrease their activity to avoid

nocturnal predators (Sih and McCarthy 2002), or if SEE R depends partially on contemporaneously produced organic C (Sandeen et al. 1954, Reddy et al. 1978, Tobias and Böhlke 2007, Staehr et al. 2010), then extrapolating to the full daily light cycle based on daytime SEE R would overestimate daily SEE R. If nighttime SEE R were <60% of daytime SEE R, some large individual SEEs (L > 25 mm) might still be autotrophic even over the full daily cycle.

Extrapolating individual daytime SEE metabolism to populations of our 3 focal species at 11 sites suggests 10× differences in daytime aggregate SEE metabolism. The shift from daytime heterotrophy to daytime autotrophy along the gradient of individual snail sizes was echoed by a similar shift at the assemblage level. Sites where *Lavigeria* had small average sizes were estimated to have strongly heterotrophic SEEs even during the daytime, whereas those at sites with larger snails tended to be balanced or marginally autotrophic when summing across SEEs. This pattern was most pronounced at site 3, where the snail assemblage is relatively lacking small snails (whose SEE is heterotrophic even during the day) and comprises the largest species (*L. coronata*) and large individuals of the other species.

Our extrapolations to the assemblage level have several limitations. We assumed no differences in the metabolism of SEEs among sites because we observed comparable size scaling at the 2 sites where measurements were taken. However, algal biomass on rock surfaces varies considerably among the 11 sites used for extrapolation (Meyer et al. 2011, Vadeboncoeur et al. 2014), so epibiotic biomass on snail shells also might differ. In addition, algal biomass, GPP, and R and ambient light levels shift strongly with depth at any given site (Vadeboncoeur et al. 2014). We might expect stronger autotrophy of SEEs at depths <5 m because of higher light availability, unless epibiotic primary producers become photoinhibited. Density, assemblage composition, and size distribution of snails also shift with depth (McIntyre et al. 2005), which would affect aggregate SEE metabolism of the snail assemblage. Last, our calculations focus only on 3 large-bodied *Lavigeria* species that make up most of snail biomass at most sites, but at least 3 to 4 additional species usually are present. We suspect that other species would show either higher (*Lavigeria* species J; West et al. 2003) or lower (*Reymondia hori*, *Spekia zonata*, *Vinundui guillemi*) GPP of SEEs than our focal species based on visible differences in epibiotic biomass. Thus, further work will be necessary to fully assess net metabolism of SEEs for the entire snail community across depths or sites.

Placing our extrapolations of the net metabolism of SEEs in a broader context, snails clearly play a minor role in littoral ecosystem metabolism. Over the period from June 2012–August 2013, we estimated average ecosystem-level R and GPP at 1 of our nearshore study sites (site 3) to be 103 and 104 mg O_2 h^{-1} m^{-2}, respectively. Thus, daytime SEE GPP and R make up <1% of total ecosystem metabolism at that site. Given the small proportion of rocky habitat covered by snails at all of our survey sites, their minimal role in whole-ecosystem metabolism is not surprising despite the evidence for metabolic rates of SEEs that are disproportionately high for their area. Our study supports the general conclusion that microbes and algae that are not attached to snails are responsible for most littoral ecosystem C fluxes.

Snails in Lake Tanganyika face several anthropogenic stressors that could modify the net metabolism of SEEs (Glaeser and Overmann 2003). At individual sites, anthropogenic sedimentation causes mortality (Donohue and Irvine 2003), alters species interactions (McIntyre et al. 2005), and shifts the size distribution of snails (McIntyre et al. 2005), any of which could affect SEE metabolism. The surface of Lake Tanganyika has warmed by ~1.4°C over the last century (Kraemer et al. 2015), which may have increased SEE metabolic rates because of the temperature dependence of metabolism (Gillooly et al. 2001). The variability of temperature over our incubations was not sufficient to test its effect on SEE metabolism, but the possibility of differential effects of warming on SEE GPP vs R is worth exploring (Kraemer et al. 2016).

Our study provides insight into the role that epibiotic primary producers can play in offsetting the metabolic demands of animals at the organismal and ecosystem levels. Large snails are autotrophic when their epibiota are included in measurements of daytime metabolic rates under high light availability. The switch in SEE metabolic balance at ~20-mm L appears to arise from greater epibiotic biomass as snails shift from concealed, aphotic microhabitats to fully illuminated rock surfaces as they reach a size refuge from predatory crabs. Whether our finding of daytime autotrophy of SEEs applies to other metazoans and their epibiota will depend on the characteristics of the host and the environment in which it lives. Slow-moving hosts with large surface-area-to-mass ratios that provide recycled nutrients for epibiota and live in well-lit environments are the most promising candidates for epibiotic GPP to offset host R. A variety of invertebrates with shells or cases, aquatic turtles, and crocodilians may fulfill these conditions. Thus, autotrophy of organismal ecosystems is unlikely to be limited to snails in Lake Tanganyika but, rather, is plausible for a variety of other taxa and ecosystem contexts.

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