

# SCALING OF ECOSYSTEM ENGINEERING: SIZE MATTERS IN CORAL BIOEROSION

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*Abstract.* Although there are many case studies of ecosystem engineers, there is a lack in ability to generally predict the magnitude of their ecosystem engineering effects. The magnitude of ecosystem engineering by a species may depend on its physical size. Coral bioeroders are ecosystem engineers that scrape, bore, or bite coral substrates, consequently modifying the reef in profound ways. This study aims to determine if the size of the bioeroding species can predict the magnitude of coral bioerosion rate by using data on per capita coral bioerosion rate and bioeroder fresh weight. It was predicted that ecosystem engineering effect scales with metabolic rate for species that erode coral during feeding ( $M^{0.66-0.75}$ ), while species that erode coral to create shelter have an ecosystem engineering effect that scales proportionally with their body size ( $M^1$ ). Overall, there was a significant relationship between per capita erosion rate and bioeroder size, where coral bioerosion rate scaled at  $M^{1.584}$ . The relationship between per capita erosion rate and bioeroders that erode coral through feeding was significant. Interestingly, the bioeroders that eroded coral during feeding resulted in a per capita erosion rate that scaled at  $M^{1.524}$ , which is different than what would be expected based on metabolic scaling. It is possible that per capita erosion rate superscales to metabolism due to factors such as feeding selectivity for high quality patches and collateral damage that increases with increasing body size. There was a significant relationship between per capita erosion rate and the size of bioeroders that feed directly on coral, where per capita erosion rate scaled at  $M^{1.406}$ . For coral bioeroders that erode coral through feeding on epilithic or crustose algae, the relationship between per capita erosion rate and bioeroder size was significant, with a scaling relationship of  $M^{1.587}$ . There were too few bioeroders that eroded coral for shelter to determine if coral bioerosion rate scaled proportionally to body size. Large-bodied bioeroders have a greater per-capita erosion rate, and the greatest ecosystem engineering effects. A scaling relationship for coral erosion rate has significant practical implications for the coral reef monitoring and management.

## INTRODUCTION

Ecosystems are disproportionately influenced by certain biota that engineer them. Ecosystem engineers are organisms that create or modify the physical structures in their environment, which alters living spaces, abiotic resources, and conditions (Jones et al. 1994). These changes in the environment, in turn, feedback to the ecosystem engineer directly or indirectly (Jones et al. 2010). Well-known examples of ecosystem engineers include forest trees, beavers, and earthworms. Trees engineer the forest with its trunks, branches, and roots, which create habitats for other organisms (Jones et al. 1997). Beavers fell trees to create dams that alter hydrology and sedimentation in profound ways (Wright et al. 2002). The construction of dams creates novel wetland habitats that support plant communities with high species richness. Earthworms modify the belowground environment by burrowing, which alters how water and gases move through the soil, and, in turn, regulates soil organic matter and plant growth (Jouquet et al. 2006). Although there are many case studies of ecosystem engineers, we do not yet have the means to generally predict the magnitude of their ecosystem engineering effects.

Scaling may be a powerful tool for creating a general model predicting the magnitude of ecosystem engineering effects. The physical size of an ecosystem engineer may greatly influence the magnitude of its engineering effect; however, the relationship between the size of the engineer and the magnitude of its

effects has yet to be investigated. Scaling has historically been used to scale intrinsic characteristics species. Notably, metabolic rate scales at  $M^{0.66-0.75}$ , where  $M$  is the organism's body mass (Brown et al. 2004). However, scaling has yet to be successfully applied to the extrinsic effects of species (LaBarbera 1989), such as ecosystem engineering.

Although they have received less attention by researchers, organisms that destroy important physical structures are also ecosystem engineers (Jones et al. 1997). Bioeroders such as echinoderms, polychaete worms, and fish engineer coral reef ecosystems by scraping, boring, or biting the coral substrate as they feed or create shelter, thereby greatly modifying the habitat for other biota (Talley and Crooks 2011). For example, farmerfish engineer coral reefs by claiming a territory on the coral, defending it from competitors such as fish and urchins, removing algae growing on the coral that they find unpalatable, and nourishing algal communities they feed on by defecating (White and O'Donnell 2010). By engineering coral, bioeroders alter coral reef communities, coral zonation, and algal diversity. Bioeroders impact the reef accretion-degradation balance more than physical erosion of waves, and are major forces shaping coral reef habitats (Reaka-Kudla et al. 1996). The effects of bioeroders on coral reefs can continue long after bioerosion has occurred. For example, bioeroders may weaken the skeleton so the reef is more susceptible to damage from natural storms (Glynn 1997). Bioeroders that produce excessive sediments in the eroding process reduce calcification of the coral reefs. Bioeroders enable the coral to access light to photosynthesize after removing algae cover from the reef.

Data on the body sizes and engineering effect of bioeroders are available and can be utilized to ascertain whether or not there is a scaling relationship. An organism's metabolic rate can be valuable in predicting the rate of resource usage and controls many ecological processes (Brown et al. 2004, Whitfield 2004). I postulated that species that erode coral by feeding should erode at a rate similar to their metabolic rates, with a 0.66-0.75 scaling exponent. I further postulated that species that are corallivores may erode at a greater rate than species that feed on coralline algae or epilithic algae, because they remove the coral substrate itself, rather than the algae attached to it. In contrast, organisms that erode coral to make shelter may erode at a rate that scales geometrically to their body size, with a scaling exponent of 1.

## METHODS

I compiled a data set on per-capita coral bioerosion rate and bioeroder fresh weight from the literature. The use of coral by each species was classified as shelter for organisms that erode coral for shelter ( $n = 2$ ) or as feeding for species that erode coral as they feed ( $n = 32$ ). Feeding bioeroders were further divided by diet: coral, coralline algae, or epilithic algae. Fresh weight of the species was often derived from different literature sources than the data for bioerosion rate. Organisms with indeterminate body sizes (e.g. sponges and fungi) were excluded from this study ( $n = 7$ ).

Data on bioeroder weight and coral erosion rate were log-transformed. Model II reduced major axis regression, an accepted method for analyzing scaling trends (LaBarbera 1989), was used to determine the relationship between bioeroder weight and coral erosion rate. In R, the output for reduced major axis regression is abbreviated as SMA (R Development Core Team 2008). A separate analysis was conducted on bioeroders that erode coral as they feed. There was insufficient data to analyze shelter-bioeroders separately. A further reduced major axis regression examined bioeroders that erode coral by eating the coral itself and compared to bioeroders that erode coral via feeding on algae.

## RESULTS

Body size explained 76.5% of the variation in *per capita* coral bioerosion rate ( $R^2 = 0.765$ ) (Figure 1a). The relationship between bioeroder body size and *per capita* coral erosion rate was significant ( $p = 0.001$ ,  $n = 34$ ). *Per capita* coral erosion rate scaled at  $M^{1.584}$ , where  $M$  is the bioeroder body mass (95% CI<sub>scaling</sub>

exponent: 1.332 – 1.885). Excluding shelter-making bioeroders ( $n = 2$ ) did not greatly change the scaling relationship. The relationship between feeding-bioeroder body size and per capita erosion rate was statistically significant ( $p = 0.001$ ,  $n = 32$ ), where feeding-bioeroder body size explained 77.3% of the variation in per capita erosion rate ( $R^2 = 0.773$ ) (Figure 1b). Per capita erosion rate for bioeroders that erode coral while feeding scaled at  $M^{1.524}$  (95% CI scaling exponent: 1.277 – 1.819). Surprisingly, the scaling exponent for this relationship markedly and significantly exceeded what was expected based on metabolic scaling (0.66 – 0.75).

The relationship between body size of bioeroders that fed directly on coral and per capita erosion rate was significant ( $p = 0.001$ ,  $n = 15$ ), where body size explained 78.1% of the variation in per capita erosion rate ( $R^2 = 0.781$ ). Per capita erosion rate for bioeroders that fed directly on coral scaled at  $M^{1.406}$  (95% CI scaling exponent: 1.066-1.854). There was a significant relationship between body sizes of feeding bioeroders that did not feed directly on the coral ( $p = 0.001$ ,  $n = 17$ ) in which body size explained 79.4% of the variation in per capita erosion rate ( $R^2 = 0.794$ ). Per capita erosion rate for these bioeroders that did not feed directly on coral scaled at  $M^{1.587}$  (95% CI scaling exponent: 1.239-2.032). Per capita erosion rate scaling did not statistically differ between bioeroders that fed directly on coral and those that did not.

## DISCUSSION

There was a statistically significant relationship between bioeroder body size and per capita erosion rate. Interestingly, the scaling relationship for bioeroders that erode coral as they feed markedly differed from expectations of  $M^{0.66 - 0.75}$ , where smaller bioeroders would exhibit disproportionately greater per gram fresh weight erosion rates. Rather, my results indicate that larger bioeroders exhibit greater per gram fresh weight erosion rates, which super-scales as  $M^{1.524}$ . It is challenging to determine why this relationship deviates so greatly from what is predicted by feeding rate and metabolism. We speculate that collateral damage from feeding may be a plausible explanation. To elaborate, coral is spatially heterogeneous in food quality (Anthony and Hoegh-Guldberg 2003). Bioeroders that erode coral by feeding on coral itself or associated algae may feed in high-food quality patches, whether it be high quality coral or high quality algae (Mantyka and Bellwood 2007). As bioeroder body size increases, it becomes more difficult to target small patches of high food quality. In attempt to access high quality food patches, larger bioeroders may cause collateral damage as they feed, with the magnitude of collateral damage increasing with increasing bioeroder size.

In addition, I predicted that bioeroders that feed directly on coral would show higher coral bioerosion rates than those that feed on coralline and epilithic algae. However, bioeroders that feed on coral eroded coral at rates that did not differ from those feeding on coralline and epilithic algae. Bioeroders that fed on algae on the coral eroded at a slightly greater rate than those that fed directly on coral. It is possible that those that are not feeding directly on coral need to consume more algae to fulfill their metabolic requirements and thus erode more coral in the process.

Coral reefs are threatened by a variety of anthropogenic influences, including climate change (Bellwood et al. 2004). Effectively managing coral reefs is therefore a pressing need. This model scaling coral bioerosion rate may have useful conservation implications. Coral reefs can be monitored and assessed quickly by determining the body size-frequency and abundances of coral bioeroders, combining this with the allometric equation. Coral reef managers may no longer have to measure erosion, species by species.

Which species have the largest ecosystem engineering effects and why, is a central question in ecosystem engineering research. Here I showed that large-bodied species have the greatest ecosystem engineering effects; that is, large bioeroders erode more grams of coral per gram of their body weight than smaller bioeroders. Why they do so is still a mystery, and so I can only speculate that this is due to collateral erosion. It is also important to ascertain the traits of species most relevant to ecosystem engineering

(Jones et al. 1997). In this study, I showed that body weight was a powerful predictor of the magnitude of ecosystem engineering. Further studies should investigate why larger bioeroders have a greater ecosystem engineering effect than smaller organisms, and whether this holds true for other kinds of ecosystem engineering.

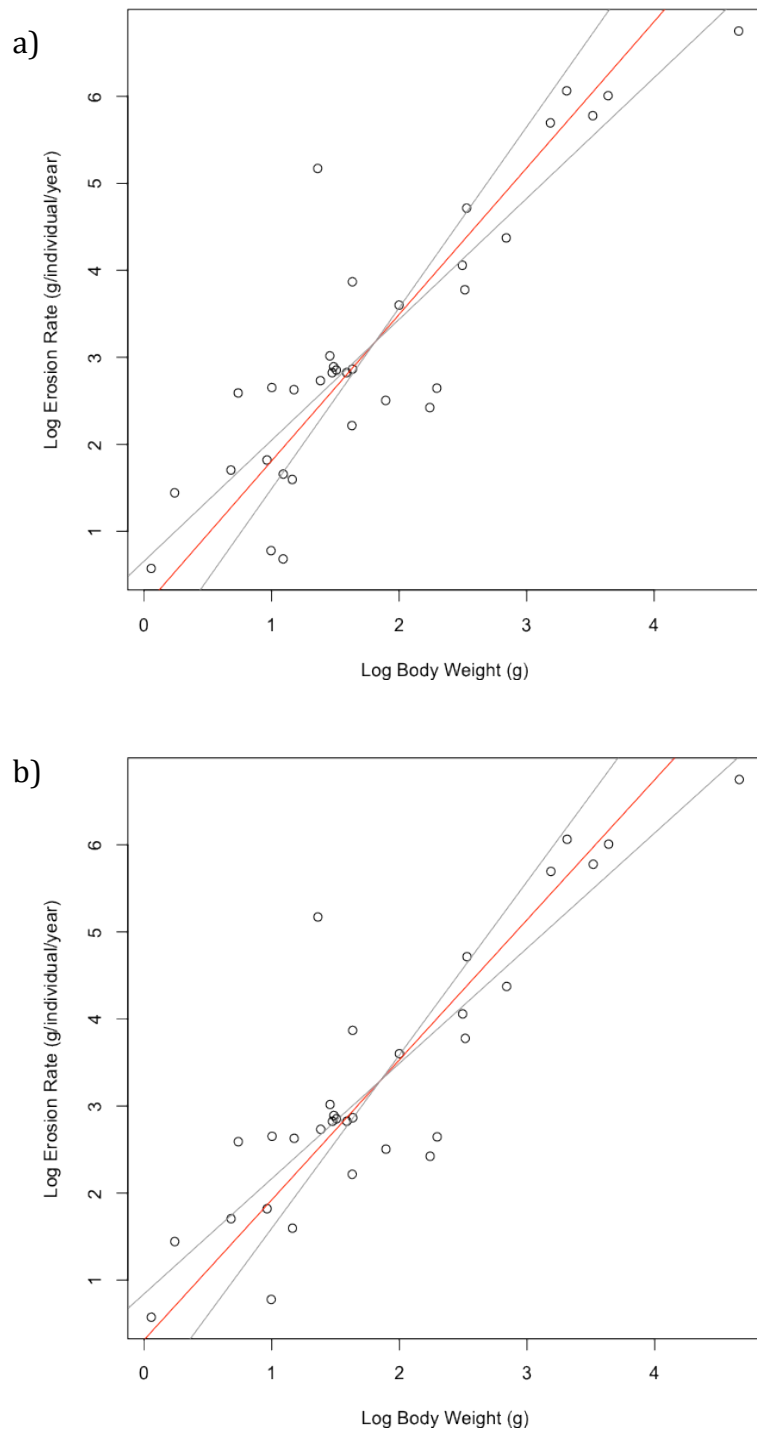
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APPENDIX



**FIGURE 1.** Scaling of coral bioerosion rate with bioeroder body weight for a) all bioeroders, b) only bioeroders that erode coral through feeding.