# ZEBRA MUSSELS AS ECOSYSTEM ENGINEERS: THEIR CONTRIBUTION TO HABITAT STRUCTURE AND INFLUENCES ON BENTHIC GASTROPODS

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*Abstract.* In this study, the fractal properties of zebra mussel, *Dreissena polymorpha*, beds and the size and abundance of co-occurring gastropods were assessed. Data collected support the hypothesis that zebra mussels increase the roughness of intertidal bedrock. An analysis of plaster casts, made from rocks removed from Norrie Point (Hudson River, river mile 86), showed that the fractal dimension (FD) of the rocky substrates significantly decreases if mussels are removed (mussel covered rock mean FD: 1.43, bare rock mean FD:1.26). Fractal dimension values obtained from rocks with zebra mussels ranged between 1.03 and 1.52. However, variation in the size and density of snails did not correlate with the fractal dimension of these rocks. Further investigation comparing snail colonization rates in rocks with and without zebra mussels (or structural mimics) will help to elucidate whether modification of the fractal properties of the rocky substrate by ecosystem engineers affect gastropod abundance and distribution.

## INTRODUCTION

Ecosystem engineers are defined as organisms that control the availability of resources to other organisms by causing physical state changes in biotic or abiotic materials (Jones et al. 1994, 1997). Many exotic species engineer the environment by altering its three-dimensional structure and, thus, the magnitude of a variety of resource flows (Crooks 2002). Aquatic mollusks are particularly important as engineers because of their ability to produce shells that often occur at high densities and persist over for long times (Gutiérrez et al. 2003). Shell production by aquatic mollusks is an important engineering process as it can increase the availability of hard substrate, decrease the impact of predators and environmental extremes, and modulate the characteristics of water flow with concomitant consequences for the transport of particle and solutes (Gutiérrez et al. 2003). Although mollusks invasions are currently a threat to aquatic ecosystems worldwide (Carlton 1992, 1999, Gutiérrez et al. 2003) the consequences of changes in habitat structure due to increased shell production are poorly known.

Zebra mussels (*Dreissena polymorpha*) are one of the most important invasive species in North America given their rapid dispersal and large ecological impact. They were first introduced in the Great Lakes in ~1985 –1986, supposedly through ballast water of European vessels. Zebra mussels arrived in the Hudson River around 1991 via anthropological means and their filtration activities caused massive transformation of the ecosystem. Zebra mussels filter the entire volume of the Hudson River estuary every ~3-5 days. The invasion of the Hudson River by zebra mussels implied a 10- to 30-fold increase in filtration activity with concomitant decreases in phytoplankton and microzooplankton biomass and water turbidity (Strayer et al. 1999). Consequences of shell production by zebra mussels on habitat structure and benthic organisms are also documented. Clusters formed by zebra mussels increase structural complexity and provide invertebrates with a refuge from predation and physical sources of stress and mortality (Mayer et al. 2002). The introduction of zebra mussels to the Hudson River has been accompanied by dramatic changes in benthic macroinvertebrate populations (Strayer et al. 1998, Prescott 2002).

Ricciardi et al. (1997) observed that dense zebra mussel colonization enhances populations of small gastropods and small predatory invertebrates but displaces large gastropods and certain large filter-feeders. However, it is unknown whether such size-specific effects are mediated by changes in the three-dimensional structure of the

substrate. For instance, increased substrate three-dimensionality may provide shelter for small organisms but a tortuous surface for the movement or attachment of larger ones. In this study, I investigate: (1) if zebra mussel colonization contributes to the three-dimensional structure of the rocky substrate (measured here as the fractal dimension), and (2) whether natural variation in the fractal dimension of mussel-covered rocks influences the gastropod density and size distribution as well as the taxonomic structure of the gastropod assemblages occurring on individual rock boulders.

## METHODS

### *Study site and sampling dates*

I collected rocks at Norrie Point (Hudson River, ~river mile 86 [138.46 km]), New York, on June 28th (12 rocks), and July 6th, 2004 (25 rocks). These rocks were transported to the laboratory and refrigerated.
### *Recording of rock contours*

I first recorded contours of mussel-covered rocks by means of a 6-inch (15.24 cm) contour gauge and the contour outline was traced onto paper. Then, I constructed casts of the mussel-covered rocks by pouring plaster of paris mixture over the rock surface and allowing it to dry for a few hours. I applied petroleum jelly to the rocks before plaster addition to facilitate the removal of the casts after drying. Once the casts were removed from the mussel-covered rocks, the zebra mussels were scraped off with a razor and casts of the bare rock were made using the same procedure. I used a hacksaw to cut cross-sections of the hardened casts. Cross-sections of casts from both bare and mussel-covered rocks were purposely made over the same line where contour gauge measurements were recorded.

### *Comparison of the three-dimensional structure of mussel-covered and bare rocks*

I compared the three-dimensional structure of mussel-covered and bare rocks using the fractal dimension as a measure of substrate complexity. Fractals are "a shape made of parts similar to the whole in some way" (Mandelbrot 1982). The fractal dimension ($D$), in the case of a contour, relates the length of the contour and the size of the scale used to measure it. $D$ is a useful measure of the three-dimensional complexity of a contour because it incorporates the size, shape, and scale of roughness elements into a simple, numerical metric (Commito and Rusignuolo 2000). Fractal dimension measurements of mussel-covered and bare rocks were carried out on photocopies (100% magnification) of one side of the cast profiles. The boundary-grid method (Sugihara and May 1990) was used to determine the fractal dimension of each profile. Five transparent grids containing squares with a side length (n) of 1, 2, 3, 6 and 9 mm respectively were superimposed to each of the photocopied profiles. I counted the number of squares entered by each profile (N) for each grid. Fractal dimension, D, was determined from the following equation (where k represents a constant):

$$N = kn^{-D}$$

where D equals the negative of the slope from the linear regression of $\log_2 n$ against $\log_2 N$. A paired sample t-test (Zar 1984) was used to compare the $D$ values of rocks before and after zebra mussel removal.

### *Relationship between fractal dimension measures obtained from casts and contour gauge measurements*

Once traced on paper, the fractal dimension ($D$) of the outlines of rock contours obtained from contour gauge measurements (see *Recording of rock contours*) was calculated as in the case of photocopied cast profiles. I used regression analysis (Zar 1984) to evaluate the functional relationship between measures of $D$ obtained from contour gauge outlines and those obtained from plaster casts of the same rocks.

*Relationship between gastropods and the fractal dimension of zebra mussel covered rocks*

Recordings of the contour of 15 rocks were non-destructively obtained using a contour gauge. Then, I scraped off the surface of these rocks with a razor. The scraped material was collected and sieved into a combination of 1 mm and 0.5 mm screens. This allowed for the removal of excess mud and sand. I placed the contents of the 1 mm sieve in a large tray and sorted though in a well lighted room, to obtain the gastropods. The contents of the 0.5 mm sieve were also removed, but they were placed in a round glass container (~5mm diameter) and sorted under a dissecting microscope (10X magnification). Snails were removed with tweezers and then stored in small vials (without preservatives) for identification and measurement. Gastropods were determined to the family level according to Jokinen (1992) using a dissecting microscope (10X magnification). The size of the snails was measured as their length ranged from 0.6mm to 5.4mm using a 100-µm scaled ruler. Depending on the snail family, I measured the maximum dimension of the snail's shell.

After the rocks were cleared of mussels and the snails collected, I calculated their surface area to convert measures of the abundance of snails in individual rocks to density estimates. I placed aluminum foil over the portion of the rock that was protruding from the sediment at the time of collection (distinguishable from differences in color) and removed excess foil. The foil was then removed from the rock and weighed. A $64cm^2$ reference foil was measured out and weighed (0.27g) for comparison and calculation of the rock's surface area. I did this by setting up a proportion of measured weight (grams) of a rock's foil and the unknown surface area of that rock (x) and comparing it to $0.27g/64cm^2$.

I obtained fractal dimension (*D*) values of each sampled rock from outlines of contour gauge recordings using the methods explained above (see *Comparison of the three-dimensional structure of mussel-covered and bare rocks*). *D* values obtained from contour gauge outlines were corrected to those expected to be observed from plaster cast profiles using the functional relationship between measures of *D* obtained from plaster casts and measures of *D* obtained with the contour gauge calculated above (see *Relationship between fractal dimension measures obtained from casts and contour gauge measurements*). I used correlation analysis (Zar 1984) to evaluate the relationship between snail-related variables (density, mean size, maximum size and standard deviation of snail sizes) and *D*. Snail density was log (x + 1) transformed to remove heteroscedasticity residuals. I used T-tests (Zar 1984) to compare the *D* values of between rocks showing presence or absence of snail families that were non-uniformly present (or absent) among rocks.

## RESULTS

*Comparison of the three-dimensional structure of mussel-covered and bare rocks*

The mean fractal dimension of rocks significantly decreased after mussel removal (Before mussel removal: Mean = 1.43, SD =0.06; After mussel removal: Mean = 1.26, SD = 0.14; paired-sample t-test:  t = 2.36, df = 7, p = 0.02).

*Relationship between fractal dimension measures obtained from casts and contour gauge measurements*

The relationship between fractal dimension values measured from casts and those measured from contour gauge outlines was best described by the equation y= 1.36x – 0.57 ($r^2$ = 0.87, *F* = 92.97, df = 1, 14, p < 0.01). Visual analysis indicates that the contour gauge method tends to increasingly underestimate fractal dimension as fractal dimension values approximate 1 (Figure 1).

*Relationship between gastropods and the fractal dimension of zebra mussel covered rocks*

Mean snail size ($r^2 < 0.01$, $F = 0.04$, df = 1, 17, $p = 0.84$), maximum snail size ($r^2 = 0.09$, $F = 1.63$, df = 1, 17, $p = 0.22$), and the standard deviation of snail sizes ($r^2 < 0.01$, $F < 0.01$, df = 1, 17, $p = 0.99$) were not correlated with the fractal dimension of the rocks. However, snail density (natural log-transformation [base e]) was positively correlated with the fractal dimension of the mussel-covered rocks ($r^2 = 0.22$, $F = 4.80$, df = 1, 17, $p = 0.04$; Fig. 2)

Snails of six families were collected in this study (Table 1). Except for lymnaeids (which were abundant and present in most rocks) and ancylids (which were scarce and present in a few rocks), the four others families were far from being uniformly present (or absent) among different rocks. However, no differences were found in the fractal dimension between rocks showing presence or absence of each of these families (Table 2).

## DISCUSSION

*Zebra mussels and fractal dimension*

The zebra mussel invasion has led to an increase in the fractal dimension of rocky substrates in the Hudson River. A greater fractal dimension of the substrate due to zebra mussel colonization and shell production shows that zebra mussel engineering increases the physical complexity and topography of the benthic environment. This is important at the population level because mussel dislodgement, predation, recruitment, growth, and movement all are affected by bed shape and surface topography (Commito and Rusignuolo 2000). At the community level, this means a greater amount of interstitial habitat for organisms, such as gastropods, to take refuge from predation or physical forces (e.g. water flow). The roughness contributed by zebra mussels is also expected to alter boundary-layer flows (Butman *et al*. 1994; Ke *et al*. 1994; Green *et al*. 1998; Commito and Rusignuolo 2000). Such an interaction of flow and substrate heterogeneity is known to affect larval settlement (Hills *et al*. 1999; Lapointe and Bourget 1999) and subsequent population performance because it controls delivery of sediments, food, oxygen, and chemical cues (Weissburg and Zimmer-Faust 1993; Bertness *et al*. 1998; Leonard et al. 1998, 1999; Widdows et al. 1998; Lenihan 1999; Commito and Rusignuolo 2000). For instance, the interstices between mussel shells can be expected to work as traps for mussel biodeposits (Roditi et al. 1997) and other particles transported by the near-bed flows, which could enhance nutrient availability at the bottom as well as the benthic organisms that depend on these nutrients. Effects on other organisms could be, however, not necessarily positive. While zebra mussels can provide small mobile invertebrates with a refuge from predation or increased food or nutrient supply, the physical complexity of the zebra mussel beds could result in the displacement of larger organisms by preventing their attachment or movement (Mayer et al. 2002).

*Gastropods and fractal dimension*

The positive correlation between snail density and fractal dimension indicates that snails are taking advantage of a more complex habitat. Natural variation in the fractal dimension of mussel-covered rocks does indeed influence gastropod densities. A habitat with a higher fractal dimension is likely to provide more shelter space or enhance the deposition of food particles (see above) with concomitant effects on snail densities. Further, the mere increase in substrate surface due to mussel colonization is likely to provide a wider range of space for the snails to inhabit. In any of these cases, organisms other than gastropods could also increase in density in response to a larger fractal dimension. In fact, a higher fractal dimension of the habitat is often associated with higher overall organismal abundances (e.g. Jeffries 1993; Beck 1998).

The fractal dimension of mussel-covered rocks was not useful to explain the maximum size and the variability of sizes of the snails inhabiting them. This is somewhat surprising if we consider that variations in fractal dimension can be translated into variation in the size of available microhabitats, with concurrent effects on the size of organisms that can have access to these microhabitats (Caddy 1986; Mendez-Casariego et al. 2004). Moreover,

the size of the snails found in this study ranged between 0.6 and 5.4 mm, which suggests that the scale at which fractal dimension was measured in this study (9 to 1 mm) was appropriate to detect any possible effect of habitat complexity on body sizes. Therefore, a possible conclusion is that fractal dimension is not an appropriate measure of the elements of habitat complexity that are relevant to snail size.

The presence or absence of the different families of snails on individual rocks was independent of their fractal dimension. This indicates that fractal dimension is not a useful measure to explain occurrence of snail families at the scale of individual rocks. Perhaps differences could be detected at a higher level of taxonomic resolution or by considering within-rock variation in fractal dimension.

*Previous studies on fractal dimension and surface complexity*

The results of this study are quite consistent with those of Commito *et al.* (2000), who measured the fractal dimension of vertical cross-section profiles of soft-bottom blue mussel (*Mytilus edulis*) beds. Both *Mytilus edulis* beds (Commito and Rusignuolo 2000) and rocks covered by zebra mussels were observed to be fractal. The fractal dimension values of zebra mussel covered rocks (1.36 to 1.55) were larger than those of soft-bottom blue mussel beds (1.11 to 1.31). However, these differences can be an artifact of the different scales at which fractal dimension was measured in each study (Commito and Rusignuolo 2000: 1.44 to 200 mm, this study: 1 to 9 mm). Alternatively, the higher fractal dimension of zebra mussel covered rocks relative to soft bottom blue mussel beds can be, in part, due to the contribution of the roughness of the rocky substrate itself.

Other studies have shown that surface complexity measures are useful in tracking different characteristics of snails. Kostylev et al. (1997) used contour gauges with 1-mm wide pins to create profiles of the rocky shore covered with mussels (*Mytilus galloprovincialis*) and barnacles (*Chthamalus stellatus*). Abundances of different sizes and morphs of the snail *Littorina saxatilis* were related to the fractal dimensions of these profiles. Also, Erlandsson et al. (1999) used the same technique to show that the fractal dimension of the rocky shore surface was a good predictor of snail (*Cellana grata*) movement patterns and Beck (1998) found that fractal dimension was the best predictor of density of five gastropod species under study. The present study adds up further evidence on the relevance of fractal dimension to habitat use by aquatic gastropods.

*Future Studies*

For further studies, it would be useful to compare snail colonization rates on bare rocks and artificial zebra mussel beds of different fractal dimensions. This would decipher whether gastropods select zebra mussel beds because of their physical structure or some other variable. Placing bare rocks alongside rocks with artificial zebra mussels attached; and periodically recording the snail density present would serve this purpose. An investigation of this nature would allow unequivocal evaluation of the effect of zebra mussel on snail density. In addition, it would also serve to examine whether snail sizes and the different families correlate to fractal dimension values under more controlled conditions. Executing this task might result in data that support studies such as Kostylev et al. (1997), where fractal dimension was correlated to density, morph and sizes of snails. Moreover, it would help explain patterns of invertebrate abundances in zebra mussel beds and the role of zebra mussel engineering in benthic environments and communities.

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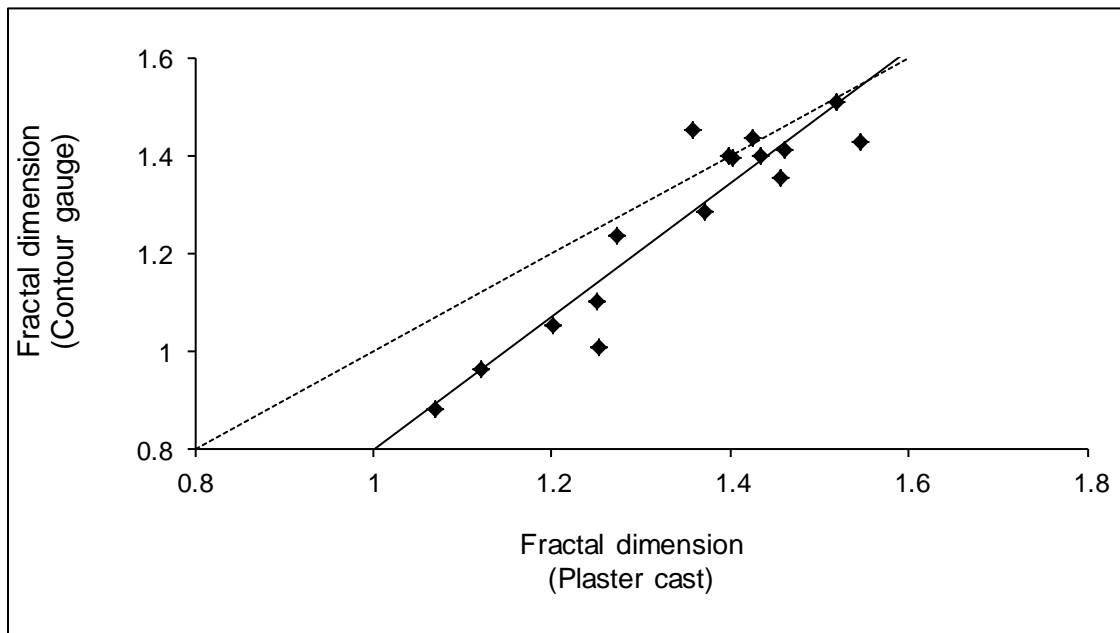
**APPENDIX**



**FIGURE 1**. Relationship of between measures of fractal dimension taken from contour gauge outlines and from plaster casts of the same rock profiles. Dotted line shows the 1:1 line.
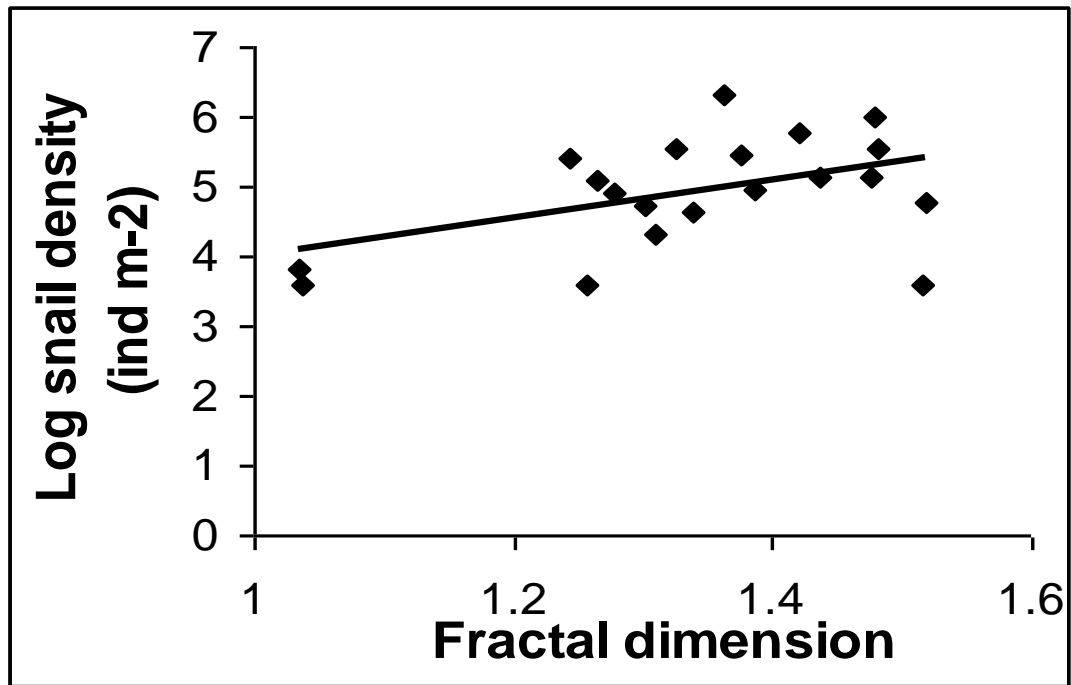
**FIGURE 2.** Relationship between snail density (log-transformed [base e] data) an the fractal dimension of mussel-covered rocks

**TABLE 1.** Mean (SD) density ($\#/m^2$) of snail families present on the twenty rocks sampled. The percentage of which each family is present on the twenty rocks is also represented.

| Family | Mean Density (SD) of Snails ($\#/m^2$) | Percentage of Snails Present on Rocks |
|---|---|---|
| Ancylidae | 0.00000469 (1.43E-05) | 15% |
| Hydrobiidae | 0.0000252 (4.27E-05) | 50% |
| Lymnaeidae | 0.000101 (8.88E-05) | 85% |
| Physidae | 0.0000218 (2.66E-05) | 50% |
| Planorbidae | 0.0000184 (3.02E-05) | 45% |
| Valvatidae | 0.00000859 (1.57E-05) | 30% |

**TABLE 2.** Mean (SD) fractal dimension of rocks showing presence and absence of particular snail families and results of the t-tests used to evaluate difference between these fractal dimension values.  * t-tests for unequal sample sizes

| Family | Fractal dimension | | t | df | p |
|---|---|---|---|---|---|
| | **Presence** | **Absence** | | | |
| Hydrobiidae* | 1.37 (0.14) | 1.30 (0.12) | 1.11 | 18 | 0.28 |
| Physidae | 1.35 (0.15) | 1.34 (0.15) | 0.15 | 18 | 0.89 |
| Planorbidae* | 1.39 (0.09) | 1.29 (0.16) | 1.54 | 17 | 0.14 |
| Valvatidae* | 1.35 (0.07) | 1.38 (0.16) | 0.36 | 18 | 0.72 |