

# DO BENTHIC ORGANIC MATTER AND PERIPHYTON BIOMASS DIFFER BETWEEN RUSTY CRAYFISH AND AMERICAN EEL HABITATS?

SARA GABRIELSON

*Vassar College, Poughkeepsie, NY 12604, USA*

MENTOR SCIENTISTS: DRs. DAVID STRAYER & EMMA ROSI-MARSHALL

*Cary Institute of Ecosystem Studies, Millbrook, NY 12545, USA*

*Abstract.* The American eel (*Anguilla rostrata*), a fish native to the Hudson Valley, and the rusty crayfish (*Orconectes rusticus*), a highly aggressive invasive species, both live in streams in southeastern New York, are nocturnal, and use similar resources for food and shelter. Little research has been done relating these two species, but the information could be used to help conserve the American eel by limiting competition and prevent further rusty crayfish invasion through biocontrol. Though they have many similarities, the American eel and rusty crayfish have never been found in the same stream, which may be due to competition, predator-prey relationship, or a difference in habitat. To understand the habitats of these two species, this study examined the amount of benthic organic matter and algae in streams with high densities of American eels, streams with high densities of rusty crayfish, and streams with neither high densities of American eels nor rusty crayfish. I measured the amount of benthic organic matter on rocks and to a depth of 5cm in the substrate. The biomass of algae was measured by chlorophyll *a* concentration using a methanol extraction. The results showed that variation within stream types was high and there were no significant differences in ash-free dry mass or chlorophyll *a* concentrations among any of the stream types.

## INTRODUCTION

All over the world invasive species are altering the ecology of freshwater systems (Ricciardi and Rasmussen 1998; Strayer 2010). Aquatic invasive species are often accidentally introduced through human activities such as ballast water taken on by ships in one area and released in another, bait release from anglers, and sometimes intentionally introduced without knowledge of their ecological impacts through fish stocking. Freshwater invasive species often outcompete native species for resources, decrease biodiversity, and can alter the way a stream ecosystem functions.

One of the most aggressive aquatic invasive species is the rusty crayfish (*Orconectes rusticus*). In 1969 the first rusty crayfish was reported in New York State where it had spread from its native range in the Ohio River basin (Gunderson 2008; Johnson and Nack 2010). Introduced primarily through bait release, this highly aggressive species outcompetes native crayfish and probably alters native communities of plants and macroinvertebrates (Kershner and Lodge 1995; Mount 2009; Strayer 2010). The aggressive behavior of the rusty crayfish and its ability to live at very high densities decreases diversity and abundance of native species of crayfish as well as other native fish (Kershner and Lodge 1995; Olden et al. 2006; Gunderson 2008). This change in species diversity and elimination of native species may have negative effects on streams in southeastern New York.

One native species that the rusty crayfish may be affecting is the American eel (*Anguilla rostrata*). The rusty crayfish seems to occupy the same niche as the American eel. Both rusty crayfish and American eels are predators of macroinvertebrates, are nocturnally active, and use similar substrate types (cobble-boulders) for shelter and feeding (Lodge et al. 1994; Kershner and Lodge 1995; Hammers 1996). The American eel is native to the entire eastern seaboard of North America and is common in the Hudson

River and its tributaries (Mount 2009; Velez-Espino and Koops 2010). In recent decades American eel populations have been declining due to obstruction by dams, overfishing, and pollution (Schmidt et al. 2009). The American eel is therefore the target of current conservation efforts, as it is an important predator as well as a commercial fish (Hammers 1996; Machut 2006; Velez-Espino and Koops; 2010).

The relationship between the American eel and the rusty crayfish is of interest because they live in similar habitats and may impact each other's populations and behavior. If the rusty crayfish is outcompeting the American eel for shelter or food resources, it could have a major impact on the health of the American eel populations as the rusty crayfish invasion continues. If the American eels are predators of juvenile rusty crayfish, they may help prevent the further spread of the rusty crayfish. A better understanding of the relationship between rusty crayfish and American eels and their habitats may support conservation efforts for the American eels and prevention of the further invasion of the rusty crayfish. However, rusty crayfish have not been observed in the same streams as American eels. The possible reasons for this lack of overlap include outcompeting each other for shelter, potential predator-prey relationships, or a difference in habitat that might exclude one or the other (Mount 2009).

Due to the lack of in-depth research about American eels and rusty crayfish, very little is known about their habitats and the effects they may have on their habitats. Both species prey upon macroinvertebrates, many of which are consumers of algae and leaf detritus or benthic organic matter (BOM). BOM is the basis of the food webs within these stream ecosystems. In this study I compared streams with high densities of American eels, streams with high densities of rusty crayfish and streams which lacked eels and crayfish (containing instead minnows, native/nonnative fish, native crayfish, etc.). In streams where they are present, both rusty crayfish and American eels occur at such high densities (often  $>1$  per  $m^2$ ) that they are essentially the sole species at the top trophic level (Schmidt et al. 2009). In streams with neither rusty crayfish nor American eels, there may be a lower density of predators but a greater diversity of species at the top trophic level. I examined BOM mass and chlorophyll *a* concentration (a measure of algal biomass) in these streams and explored differences in these basal resources among these stream types.

The objective of the study was to determine if there are differences in the amount of BOM and chlorophyll *a* concentrations of algae in streams with high populations of American eels, streams with high populations of rusty crayfish, and streams without either. Due to the differences in behavior, and the occurrence of the two species in separate streams, I hypothesized that the BOM would differ significantly in all three stream types. If the habitats are different with respect to BOM there is reason to continue research to see if these two species are choosing different habitats or if their behavior has created those habitats. If the habitats are the same, understanding why these two species do not co-exist must be attributed to something other than BOM.

### *Study Area*

This study examined four streams with high American eel populations: Crum Elbow Creek, Saw Kill Creek, South Lattintown Creek, and Landsmans Kill. The four streams with high rusty crayfish populations were Webatuck Creek, East Branch Croton River, Swamp River, and Lattintown Creek. The four streams with neither high populations of American eels or rusty crayfish were Upper Crum Elbow Creek (the upper sections of the streams are separated from the lower sections with dams which prevent the eels from traveling upstream), Little Wappinger Creek, Upper Saw Kill, and Upper Landsmans Kill. All of these streams are located in the Mid-Hudson Valley and surrounding areas. They all have similar climate, salinity, and calcium concentrations. All streams were shallow, generally around 30 cm deep, mostly clear with rocky bottoms covered in algae and silt. They all had trees along their banks and were mostly shaded. The surrounding land use was a mix of mostly wooded neighborhoods, forest, and some fields, but there was no heavy agriculture in close proximity to the areas I was sampling.

At each stream a reach was defined that was 20 m long and had an average width of 5-8m. I chose reaches where the dominant substrate was cobble (the majority of the substrate composed of rocks between golf ball and basketball size). Presence of rusty crayfish and American eels were determined using a timed search and previous data collected by Sarah Mount, Catherine O'Reilly, and Bob Schmidt (Mount 2009).

## MATERIALS AND METHODS

At five arbitrary points spaced out along the reach I used the bottomless bucket method to measure benthic organic matter on surface areas of rocks as well as up to a 5-cm depth in the substrate. This method entailed inserting the bottomless bucket 10 cm into the substrate and creating a seal so that there was no water transfer between the inside of the bucket and outside stream. I measured the volume of water within each bucket sample. I used this volume and the area of the bottom of the bucket to calculate the dilution of each benthic organic matter sample. The substrate within the bucket was agitated to a depth of 5 cm to suspend organic matter in the substrate. If there were any rocks within the bucket they were scrubbed clean and washed into the bucket to capture the organic matter on their surface. When I had completely agitated the sample, I collected a subsample (~ 100 mL) of this water for analysis in the laboratory.

I gathered ten arbitrarily selected rocks from the reach to measure BOM on rocks. Each rock was scrubbed clean and all matter was washed into a 150 mL bottle and taken back to the lab. I wrapped each rock in aluminum foil to measure its surface area.

I homogenized all samples in a blender and filtered 10 mL of sample onto preweighed glass-fiber filters. After drying them in a drying oven at 60° ° C for 24 hours, they were weighed and then combusted at 450° C and re-weighed to determine the ash-free dry mass of benthic organic matter per m<sup>2</sup> (modified from Entekin et al. 2007).

To determine chlorophyll *a*, I filtered 5mL of each sample onto glass fiber-filters and froze them for 24 hours. Each sample was then immersed in 8mL of methanol in the dark for 24 hours at room temperature. Chlorophyll *a* concentrations were determined using a Turner Designs Model TD-700 fluorometer (Turner Designs, Sunnyvale, CA) (Holm-Hansen and Riemann 1978).

Differences between BOM mass and chlorophyll *a* concentrations among stream categories were evaluated using ANOVA. All statistical analyses were completed using JMP software.

## RESULTS

The BOM ash-free dry mass was high in all stream types within the substrate (Table 1, Fig. 1). The chlorophyll *a* concentrations were low in all stream types. Variation was extremely high in all stream types for BOM and chlorophyll *a*. There were no statistically significant differences in BOM or chlorophyll *a* among the stream types and no patterns in the means across substrate or rocks (Figs. 1, 2).

## DISCUSSION

There was no significant difference in benthic organic matter and algal biomass among streams with rusty crayfish, streams with American eels, or streams with neither. Therefore there is no significant difference in habitat that the rusty crayfish or American eels are thriving within with respect to BOM. At the same time, neither the rusty crayfish nor the American eels have a detectable top-down trophic effect on BOM in their respective streams.

Other abiotic and biotic factors could produce these results. The abiotic factors include water level in the

streams, nutrient loads, and seasonal changes. The biotic factors include primarily the trophic interactions between primary producers and BOM, the primary consumers, mostly macroinvertebrates, and secondary consumers, the rusty crayfish, American eels, and other predators.

The water level in streams in southeastern New York depends on snowmelt, groundwater stores, and during our research season, June-July, primarily rain input from runoff (Lamberti et al. 2010; Boulton et al. 2010). All of the streams in this study were within 80 km of one another and no major rains occurred in the area that would have catastrophically changed the BOM. Due to the close proximity and similar water inputs, the water level most likely had similar effects on all of the streams studied.

Nutrients impact production, growth, biomass, and decomposition rates of primary producers in aquatic systems (Mulholland and Webster 2010). Inputs of nutrients most often come from land use in the form of runoff and erosion, as well as from sewage (Lackey 1956; Omernik et al. 1981; Lowrance et al. 1984, Smith 2003; Lamberti et al. 2010). Some streams in close proximity to agriculture have spikes in production after fertilizer is washed into the streams (Omernik et al. 1981; Lowrance et al. 1984). More research would be needed to prove that the nutrient levels of each stream were not different, but the similar calcium and salinity concentrations, and observations of similar land use around all of the streams, support the conclusion that these twelve streams are comparable in terms of nutrient inputs.

The time of year also affects stream conditions. There are seasonal fluctuations in the consumer populations, allochthonous input, and temperature, and because sampling was done over a short period of time, six weeks in June-July, these fluctuations were not studied (Hynes 1970; Hawkins 1981; Mollá et al. 2006; Velez-Espino and Koops 2010). However these seasonal shifts are continually having an effect on the whole region, and due to their close proximity, none of the streams individually should be different from one another. Although more research would be needed to know for certain, these abiotic factors most likely affect all streams in a similar manner.

The biotic interactions that affect stream BOM are more complex. There is no difference in BOM across categories of streams, but this is not necessarily because the same processes are occurring in all of the streams. We know that at least one of the top predators (the rusty crayfish or the American eel) is different between streams and that their interactions with lower trophic level organisms may also differ. To discuss this system simply, three levels of trophic interactions will be addressed, first the primary producers—algae and/or BOM, second the primary consumers—the macroinvertebrates that eat the BOM, third the secondary consumers or top predators—the rusty crayfish, American eels, and other large fish that eat the macroinvertebrates. If the interactions between these levels do differ significantly in terms of the amount or kind of organisms the consumers feed on, but still the results show no difference in the amount of BOM among stream types, this may be due to high primary production of algae and large input of leaf matter.

If the primary production is low in an ecosystem even top predators can significantly impact the food web all the way down to the primary producers (Schmitz 2010; Forrester et al. 1999). In streams with high densities of predators- either rusty crayfish or American eels- more macroinvertebrates would be consumed, potentially allowing the amount of BOM to be greater. On the other hand, in streams with low densities of predators, there would be more macroinvertebrates due to lower predation. These higher populations of macroinvertebrates would consume more BOM decreasing the total amount. This would be compared to a stream, with neither rusty crayfish nor American eels, that has a lower density of predators and perhaps more macroinvertebrates that could decrease BOM. However, in my study the amount of BOM did not differ among stream types, even though the densities of predators varied. One explanation for these results could be that the amount of BOM was so great that even high densities of macroinvertebrates, due to low predation, did not significantly diminish the amount of BOM. If this was the case, then the density of predators did not have a measurable top-down effect on the amount of BOM

in these streams.

Another explanation for the similar amounts of BOM and chlorophyll *a* among streams is that eels, crayfish and other consumers are functionally redundant. Although rusty crayfish and American eels occur at higher densities than top predators in the streams with neither, they may be functionally similar. Many ecosystems have multiple species that affect the ecosystem in similar ways and are functionally redundant (Naeem et al. 1994; Tilman et al. 1997; Rosenfeld 2002; Scheffer and Carpenter 2003). When one macroinvertebrate species that usually consumes BOM is not present some other species that can use the increase in BOM then replaces it functionally. Therefore, even though the composition of macroinvertebrate grazers has changed, there is no effect on BOM. The result is that there is no change in the ecosystem function due to this redundancy. This was shown by Schofield et al. (2008) in streams in North Carolina which had different predator assemblages, but showed no top-down effect on the BOM. In this study, predators in the “neither” streams may still serve the same function as rusty crayfish and American eels, therefore, creating no difference in BOM among stream types. Although possible, this seems unlikely because of the high densities of American eels and rusty crayfish compared to the predators in “neither” streams. At times rusty crayfish and American eels can occur at densities much higher than other predators. The densities are so high that if these species are functionally redundant with the predators in “neither” streams, you would expect to see significant differences in amount of BOM due to their predation on macroinvertebrates. I cannot eliminate the possibility of functional redundancy because no one has studied it in these streams, but I would be hesitant to support this hypothesis explaining the similar habitats seen in my study.

The other major possible explanation for the results is that the heterogeneous nature of BOM in streams is such that any subtle difference is canceled out by the variation within streams. BOM varies within a stream reach due to light patches, sediment loads, consumption by other organisms, and random distribution (Lamberti et al. 1989; Schofield et al. 2004; Lutscher et al. 2007). In the streams I sampled, the BOM mass from different substrate samples within in the same stream reach varied from 95-334 g/m<sup>2</sup>. Different substrate samples from the same stream reach produced chlorophyll *a* concentrations that varied from 9.5 - 57 µg/m<sup>2</sup>. The average of the coefficient of variation was 58% (excluding the outliers) (Table 1). This wide range of BOM mass and chlorophyll *a* within one 20-meter stretch of a single stream shows that the variability can be huge within even small areas. This natural variation within streams may be obscuring any patterns that might actually be due to the predators, resulting in no significant differences between streams.

High production of BOM, functional redundancy of predators, or heterogeneous BOM within a stream may be affecting the BOM, but all of these explanations still conclude that the benthic organic matter is not different among stream types. More research could be done to solidify this conclusion by increasing the amount of control within the research. As opposed to doing an observational field study an enclosure/exclosure experiment or paired sections of one stream could be studied. By creating exclosures in streams with high populations of American eels or rusty crayfish to keep them out of certain areas, the BOM within the exclosures could be examined and compared with the BOM outside of the exclosures to see if it was significantly different after a certain amount of time. Similar experimental designs have been used in streams to exclude crayfish and fish when looking at top-down effects on BOM (Schofield et al. 2008) The BOM of one stream could also be looked at if a stream was found to have American eels at the mouth of the stream and rusty crayfish farther up stream separated by a few dams or other barriers. This would keep the stream variation constant and allow for isolation of the different species within the two sections of stream. Both of these ideas would allow for higher levels of control while still asking similar questions about the BOM within rusty crayfish-dominated or American eel-dominated habitats.

On the other hand, because this study points to there being no difference between BOM in American eel habitats and rusty crayfish habitats then it may be more beneficial to focus further research on the other

causes for the separation between American eels and rusty crayfish. This research could look at predator-prey relationships or competition for shelter and food resources. The information gained from research in these areas would help us understand how to better conserve the American eel or limit the spread of the rusty crayfish.

#### LITERATURE CITED

- Charlebois, P., Lamberti, G. 1996. Invading crayfish in a Michigan stream: Direct and indirect effects on periphyton and macroinvertebrates. *Journal of the North American Benthological Society* **14**:551-563.
- Entrekin, S. A., Rosi-Marshall, E. J., Tank, J. L., Hoellein, T. J., Lamberti, G. A. 2007. Macroinvertebrate secondary production in 3 forested streams of the upper Midwest, USA. *Journal of the North American Benthological Society* **26**:472-490.
- Forrester, G., Dudley, T., Grimm, N. 1999. Trophic interactions in open systems: Effects of predators and nutrients on stream food chains. *Limnology and Oceanography* **44**:1187-1197.
- Gunderson, J. 2008. Rusty crayfish: A nasty invader. Minnesota Sea Grant. Web. 12 May 2011. <[http://www.seagrant.umn.edu/ais/rustycrayfish\\_invader](http://www.seagrant.umn.edu/ais/rustycrayfish_invader)>.
- Hammers, B. 1996. North Carolina wild: Wildlife profiles: American eel. Informational docket produced by the Division of Conservation Education of the N.C. Wildlife Resources Commission.
- Hawkins, C., Sedell, J. 1981. Longitudinal and seasonal changes in functional organization of macroinvertebrate communities in four Oregon streams. *Ecology* **62**:387-397.
- Helms, B., Schoonover, J., Feminella, J. 2009. Seasonal variability of landuse impacts on macroinvertebrate assemblages in streams of western Georgia, USA. *Journal of the North American Benthological Society* **28**:991-1006.
- Johnson, J. H., Nack, C. 2010. Ontogenetic variation in food consumption of rusty crayfish (*Orconectes rusticus*) in a central New York stream. *Journal of Freshwater Ecology* **25**:59-64.
- Kaushal S., Lewis, W., Jr., McCutchan, J., Jr. 2006. Land use change and nitrogen enrichment of a Rocky Mountain watershed. *Ecological Applications* **16**:299-312.
- Kershner, M., Lodge, D. 1995. Effects of littoral habitat and fish predation on the distribution of an exotic crayfish, *Orconectes rusticus*. *Journal of the North American Benthological Society* **14**:414-422.
- Lackey, J. 1956. Stream enrichment and microbiota. *Public Health Reports* **71**:708-718.
- Lamberti, G., Chaloner, D., Hershey, A. 2010. Linkages among aquatic ecosystems. *Journal of the North American Benthological Society* **29**:245-263.
- Lamberti, G., Gregory, S., Ashkenas, L. R., Steinman, A. D., McIntire, C. 1989. Productive capacity of periphyton as a determinant of plant-herbivore interactions in streams. *Ecology* **70**:1840-1856.
- Lodge, D., Kershner, M., Aloï, J., Covich, A. 1994. Effects of an omnivorous crayfish (*Orconectes rusticus*) on a freshwater littoral food-web. *Ecology* **75**:1265-1281.
- Lowrance R., Todd, R., Fail, J., Jr., Hendrickson, O., Jr., Leonard, R., Asmussen, L. 1984. Riparian forests as nutrient filters in agricultural watershed. *BioScience* **34**:374-377.
- Lutscher, F., McCauley, E., Lewis, M. A. 2007. Spatial patterns and coexistence mechanisms in systems with unidirectional flow. *Theoretical Population Biology* **71**:267-277.
- Machut, L. 2006. Population dynamics, *Anguillicola crassus* infection, and feeding selectivity of American Eel (*Anguilla rostrata*) in tributaries of the Hudson River, New York. Master of Science Thesis, State University of New York College of Environmental Science and Forestry Syracuse, New York 91-150.
- Mollá, S., Robles, S., Casado, C. 2006. Seasonal variability of particulate organic matter in a mountain stream in Central Spain. *International Review of Hydrobiology* **91**:406-422.
- Mount, S. 2011. Habitat competition between the American eel (*Anguilla rostrata*) and crayfish (native *Orconectes limosus*, and invasive *O. rusticus*). Reports of the Tibor T. Polgar Fellowship Program, Hudson River Foundation, New York. In press.

- Mulholland, P., Webster, J. 2010. Nutrient dynamics in streams and the role of *J-NABS*. *Journal of the North American Benthological Society* **29**:100-117.
- Naeem, S., Thompson, L., Lawler, S., Lawton, J., Woodfin, R. 1994. Declining biodiversity can alter the performance of ecosystems. *Nature* **368**:734-737.
- Olden, J., McCarthy, J., Maxted, J., Fetzer, W., Vander Zanden, M. J. 2006. The rapid spread of rusty crayfish (*Orconectes rusticus*) with observations on native crayfish declines in Wisconsin (USA) over the past 130 years. *Biological Invasions* **8**:1621-1628.
- Omernik, J., Abernathy, A., Male, L. 1981. Stream nutrient levels and proximity of agricultural and forest land to streams: Some relationships. *Journal of Soil and Water Conservation* **36**:227-231.
- Ricciardi, A., Rasmussen, J. B. 1998. Predicting the identity and impact of future biological invaders: A priority for aquatic resource management. *Canadian Journal of Fisheries and Aquatic Sciences* **55**:1759-1765.
- Riskin, M. L., Deacon, J., Liebman, M. L., Robinson, K. 2001. Nutrient and chlorophyll relations in selected streams of the New England coastal basins in Massachusetts and New Hampshire, June-September 2001. U.S. Geological Survey Water Resources Investigation 03-4191.
- Rosenfeld, J. 2002. Functional redundancy in ecology and conservation. *Oikos* **98**:156-162.
- Scheffer, M., Carpenter, S. 2003. Catastrophic regime shifts in ecosystems: Linking theory to observation. *Trends in Ecology and Evolution* **18**:648-646.
- Schmidt, R. E. 2010. Bard College at Simon's Rock. Personal communication, June 3.
- Schmidt, R. E., O'Reilly, C., Miller, D. 2009. Observations of American eels using an upland passage facility and effects of passage on the population structure. *North American Journal of Fisheries Management* **29**:715-720.
- Schmitz, O. 2010. Resolving ecosystem complexity. Princeton University Press, Princeton, NJ, USA.
- Schofield, K. A., Pringle, C. M., Meyer, J. L. 2004. Effects of increased bedload on algal- and detrital-based stream food webs: experimental manipulation of sediment and macroconsumers. *Limnology and Oceanography* **49**:900-909.
- Schofield, K. A., Pringle, C. M., Meyer, J. L., Rosi-Marshall, E. J. 2008. Functional redundancy of stream macroconsumers despite differences in catchment land use. *Freshwater Biology* **53**:2587-2599.
- Smith, V. 2003. Eutrophication of freshwater and coastal marine ecosystems: A global problem. *Environmental Science and Pollution Research International* **10**:126-139
- Strayer, D. L. 2010. Alien species in fresh waters: Ecological effects, interactions with other stressors, and prospects for the future. *Freshwater Biology* **55**:152-174.
- Tilman, D., Knops, J., Wedin, D., Reich, P., Ritchie, M., Siemann, E. 1997. The influence of functional diversity and composition on ecosystem processes. *Science* **277**:1300-1302.
- Velez-Espino, L., Koops, M. 2010. A synthesis of the ecological processes influencing variation in life history and movement patterns of American eel: Towards a global assessment. *Reviews in Fish Biology and Fisheries* **20**:163-186.

## APPENDIX

**TABLE 1.** Mean, standard deviation, and coefficient of variation for benthic organic matter and chlorophyll *a*. \*due to coarse substrate and the inability to insert a bucket up to a depth of 10 cm

Stream Type	Sample Size	Mean	Standard Deviation	Coefficient of Variation (%)
<b>g AFDM / m<sup>2</sup> from substrate</b>				
Eels	2 *	244.47	33.78	13.82
Crayfish	4	173.45	87.20	50.28
Neither	4	244.94	84.88	34.65
<b>g AFDM / m<sup>2</sup> from rocks</b>				
Eels	4	9.18	5.75	62.64
Crayfish	4	6.59	3.09	46.95
Neither	4	5.56	2.40	43.13
<b>µg Chlorophyll <i>a</i> / cm<sup>2</sup> from substrate</b>				
Eels	2 *	4.89	0.06	1.32
Crayfish	4	7.83	3.17	40.49
Neither	4	11.26	10.76	95.62
<b>µg Chlorophyll <i>a</i> / cm<sup>2</sup> from rocks</b>				
Eels	4	2.03	1.40	68.86
Crayfish	4	2.38	1.46	61.56
Neither	4	1.53	1.15	74.89

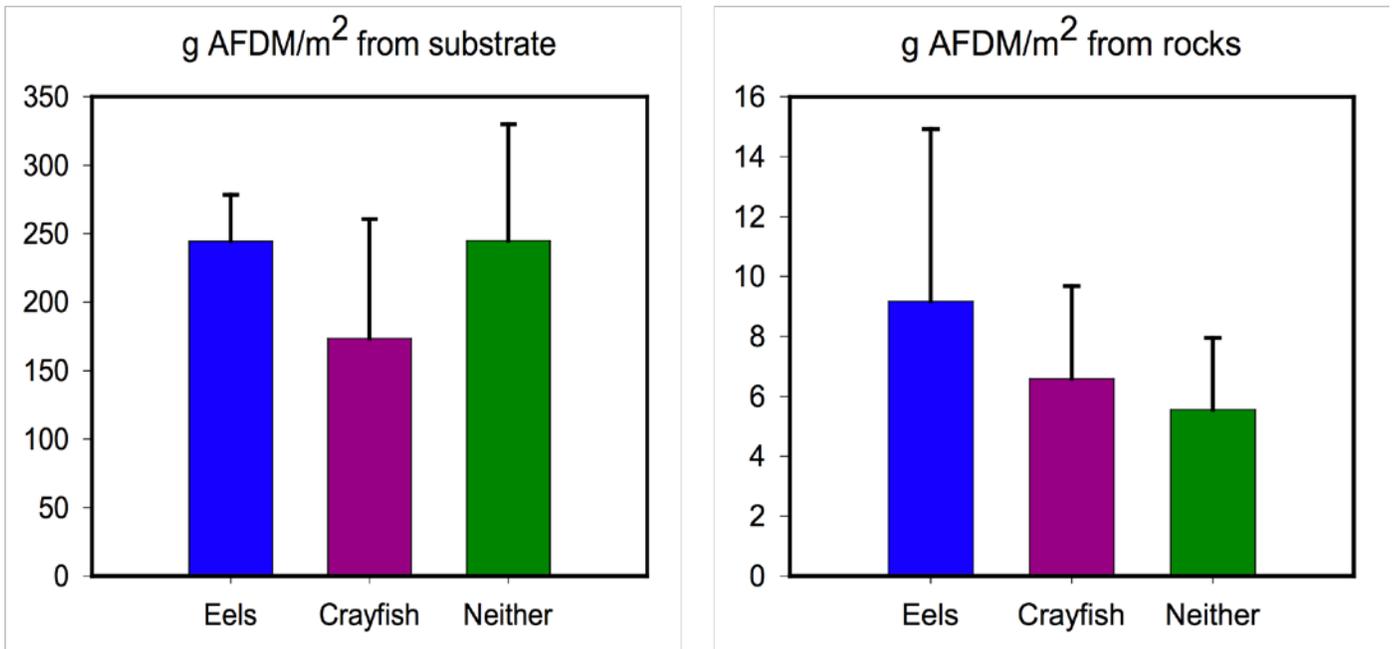


FIGURE 1. BOM biomass measured in ash-free dry mass from substrate and rock surfaces.

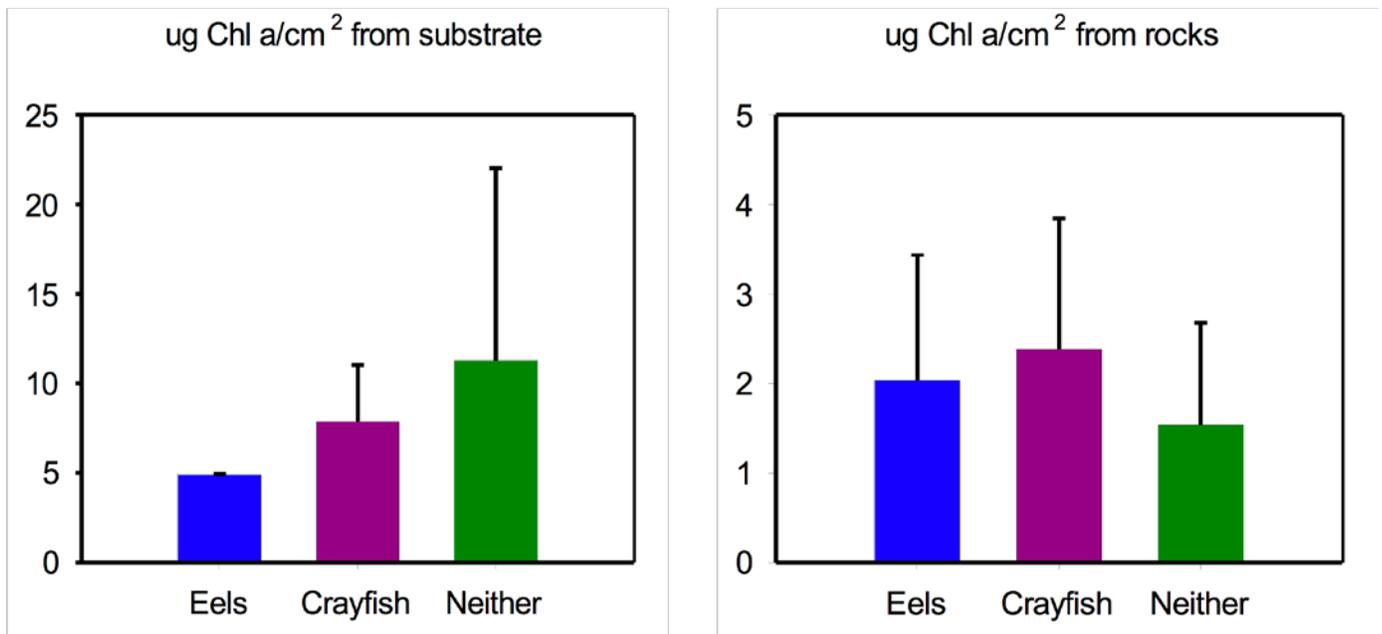


FIGURE 2. BOM chlorophyll *a* concentrations from substrate and rock surfaces.