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What happens after mussels die? Biogenic legacy effects on community structure and ecosystem processes[☆]

John A. Commito[a,b,⁎], Brittany R. Jones[a,1], Mitchell A. Jones[a], Sondra E. Winders[a], Serena Como[c]

[a] Environmental Studies Department, Gettysburg College, Gettysburg, PA 17325, USA
[b] Unità di Biologia Marina ed Ecologia, Dipartimento di Biologia, Università di Pisa, Via Derna 1, 56126 Pisa, Italy
[c] Consiglio Nazionale delle Ricerche, Istituto per l'Ambiente Marino Costiero (CNR-IAMC), Località Sa Mardini, Torregrande 09170, Oristano, Italy

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ABSTRACT

Mussels are well-known ecosystem engineers in soft-bottom systems. *Mytilus edulis* beds have myriad effects on sediment, benthic organisms, and ecosystem processes such as hydrodynamic transport of sediment and animals. When mussels die, they may leave behind massive amounts of whole (empty) and fragmented shells. The legacy effects of this long-lasting biogenic material (i.e., shell hash) on benthic systems are poorly understood. We measured percent cover values of 4 bottom cover types, i.e., live mussels, whole shells, fragmented shells, and bare sediment, at the mussel bed in Carrying Place Cove, Harrington, Maine, USA, and examined their effects on sediment characteristics, community structure of macrofauna and meiofauna, and ecosystem processes of sediment flux and dispersal of postlarval macrofauna and meiofauna. We predicted that live mussels are the cover type with the greatest effects compared to bare sediment, followed by fragmented shells and then whole shells. We discovered mostly bare sediment, substantial cover of whole and fragmented shells, and almost no live mussels in what had in past years been a robust bed. We found significant univariate and multivariate differences in sediment and animals across cover types, especially for meiofauna. Fragmented shell material in particular may be an important driver in this system. Our results are the first to quantify the 4 mussel bed cover types and demonstrate their effects. Mussel beds in the Gulf of Maine have experienced severe declines in the past two decades, attributed primarily to climate change and the invasive green crab, *Carcinus maenas*. Our results may be useful in predicting the responses of soft-bottom systems as intact mussel beds die off, leaving large areas of bare sediment and shell hash.

1. Introduction

Mussels are well-known ecosystem engineers in soft-bottom systems. Blue mussel (*Mytilus edulis*) beds have myriad effects on sediment, infauna, epifauna, and ecosystem processes like wind-generated bedload transport and animal dispersal (Bouma et al., 2009; Buschbaum et al., 2009; Commito et al., 2005, 2008; Gutiérrez et al., 2011). When soft-bodied ecosystem engineers such as polychaetes die, their impact may soon begin to wane (Gutiérrez et al., 2011; Reise, 2002). But mussels and other hard-bodied ecosystem engineers may leave behind massive amounts of whole (empty) and fragmented shells (Fig. 1A; Commito et al., 2008, 2014). The legacy effects of this long-lasting biogenic material (i.e., shell hash) on community structure and ecosystem processes are poorly understood.

Mussel beds consist of intermingled patches of live mussels, bare sediment, and whole and fragmented shells (Fig. 1B). Because beds in Maine have a hierarchical, fractal spatial structure down to the millimeter scale (Snover and Commito, 1998; Commito and Rusignuolo, 2000; Commito et al., 2016), even a small mussel bed patch may consist of smaller patches of all 4 components. Moreover, live mussels attach to each other and to whole and fragmented shells, bound together by byssal threads. Thus, ecosystem engineering effects of mussel beds cannot be attributed solely to the live mussel component. Yet to our knowledge, no study of the effects of mussel shell hash has ever been conducted at an intertidal, soft-bottom mussel bed anywhere in the world.

Mollusk shell material can have important impacts on habitat provision, water flow, recruitment, food supply, predation, and other

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⁎ Corresponding author at: Environmental Studies Department, Gettysburg College, Gettysburg, PA 17325, USA.
E-mail address: jcommito@gettysburg.edu (J.A. Commito).
[1] Present address: College of Fisheries and Ocean Sciences, University of Alaska Fairbanks, Fairbanks, AK 99775, USA.

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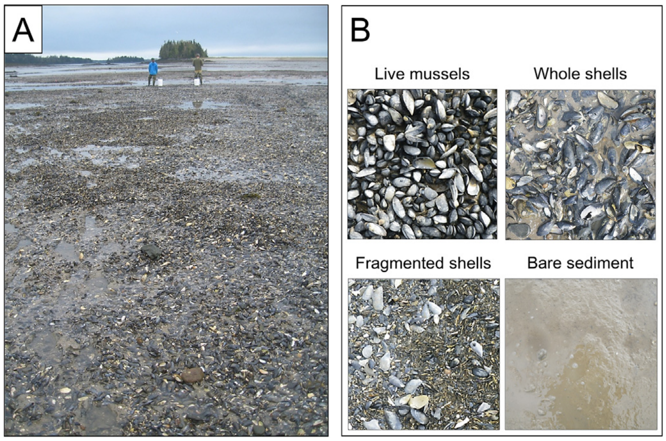

Fig. 1. Mussel bed bottom cover. (A) Shell hash at our mussel bed study site: Carrying Place Cove, Harrington, Maine, USA. (B) Types of bottom cover found in Maine mussel beds.

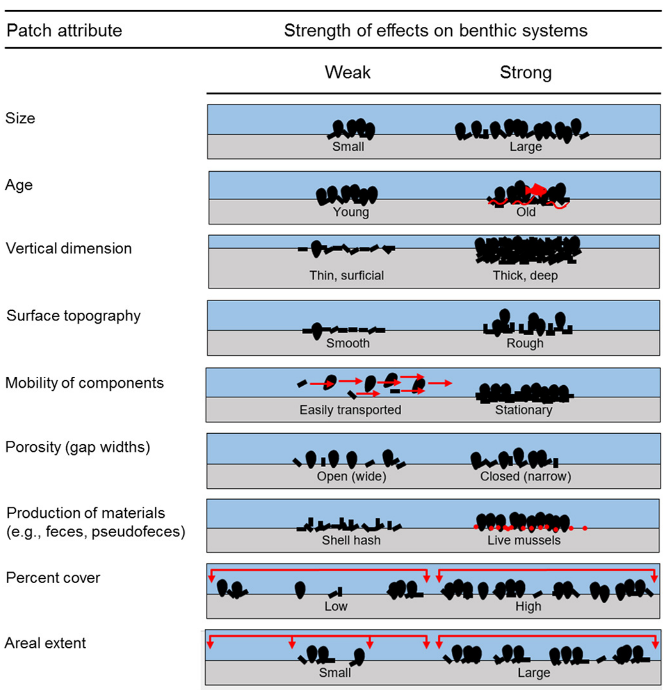

Fig. 2. Mussel bed patch characteristics. Attributes presented across the range from weak to strong effects on soft-bottom sediment, community structure, and ecosystem processes of sediment flux and animal transport in bedload.

factors (Gutiérrez et al., 2003, 2011), often causing an increase in infauna, epifauna, and species diversity in benthic systems (Guay and Himmelman, 2004; Gutiérrez et al., 2003; Hily, 1991; Hubbard, 2016; Kraeuter et al., 2003; Ribeiro et al., 2005; Rodney and Paynter, 2006; Summerhayes et al., 2009; Tomatsuri and Kon, 2017; Wilding and Nickell, 2013). However, some studies have found mixed, weak, or no significant effects (Bomkamp et al., 2004; Gutiérrez and Iribarne, 1999; Hewitt et al., 2005; Mann et al., 2016; Nicastro et al., 2009; Turner et al., 1997). The wide-ranging responses to living bivalves and non-living biogenic structure make it difficult to predict the expected magnitude and even the direction of differences among live mussels, whole shells, and fragmented shells relative to bare sediment. The impacts most likely stem from variations in bed patch attributes such as those presented in Fig. 2.

It seems plausible that effects on ambient sediment and organisms, as well as on flow-related sediment flux and animal transport, are greatest for live mussels, followed by fragmented shells and then whole shells. We make this prediction because live mussels produce copious amounts of feces and pseudofeces that increase the silt-clay fraction and create low-oxygen, high sulfide conditions that are detrimental to most species but favorable to a few others, e.g., the oligochaete *Tubificoides benedeni* and opportunistic polychaetes like *Capitella capitata* (Albrecht and Reise, 1994, Albrecht, 1998; Commito et al., 2005, 2008; Kent et al., 2017; Ragnarsson and Raffaelli, 1999). In addition, live mussels project up into the water column above the bottom, and this roughness profile has strong effects on flow dynamics that increase the capture of sediment, postlarval macrofauna, and meiofauna moving across the bottom (Commito and Rusignuolo, 2000; Commito et al., 2005).

Fragmented shells may be next in importance because they can often be observed in dense, tightly packed patches that may act as a barrier between the sediment and the water column. Packing theory demonstrates clearly that packing is tighter, with lower porosity, when the objects are of many sizes, allowing small ones to fill in the gaps between large ones (Chen et al., 2003). Thus, at our sites in Maine we observe that fragmented shell pieces, which exist in angular shapes of all sizes, are generally more tightly packed than whole shells. Fragmented shells also alter sediment structure by contributing directly to the coarse sediment fraction. Species abundances in Maine mussel beds can be positively or negatively correlated with coarse, terrestrially-derived gravel (Commito et al., 2008), so they may respond similarly to coarse, fragmented shell material as well. In particular, fragmented shells might be expected to depress animal abundance by blocking the movement of oxygen into the sediment below. Their influence on flow dynamics, hence the movement of sediment and animals, is probably less than that of live mussels because fragments do not project as high up into the water column.

Whole shells are often loosely packed. They are generally larger than fragments, and their large-radius curves leave sizable gaps between neighboring shells even when touching because they have no straight, parallel sides. This porosity due to gaps within a patch may create less of a sediment-water column barrier compared to fragmented shell cover. We also observe that whole shells tend to lie flat on the bottom, often concave-side down, presenting a relatively smooth bed surface that may not induce as much turbulent flow as does a bed with the rough topography of live mussels or fragmented shell pieces. Thus we expect whole shells to have less of an impact on sediment, animals, and hydrodynamics than do live mussels and fragmented shells.

In this study we investigated biogenic legacy effects by comparing sediment characteristics, community structure of macrofauna and meiofauna, and the ecosystem processes of sediment flux and faunal transport in isolated patches of live mussels, bare sediment, whole shells, and fragmented shells in a Maine soft-bottom mussel bed. Mussel beds in the Gulf of Maine have recently experienced severe declines, with reduced larval settlement and decimated abundances of juveniles and adults in the past two decades (Petraitis and Dudgeon, 2015; Sorte et al., 2011, 2016). The bottom cover proportions of whole shells, fragmented shells, and bare sediment may be increasing relative to that of live mussels. If so, our results could be useful in understanding how soft-bottom systems respond to the apparent mussel bed decline.

2. Methods

2.1. Study site

The research was conducted at the intertidal, soft-bottom *Mytilus edulis* bed in Carrying Place Cove, Harrington, Maine, USA (44.5451°N, −67.7844°W), a relatively protected embayment with a bottom of muddy sand (Fig. 3). As is typical in this region, the bed extends across the mouth of the cove near the low tide line. The ecology of eastern Maine soft-bottom mussel beds like this one has been well studied, including their spatial abundance patterns (Commito et al., 2006, 2014; Crawford et al., 2006), sediment and macrofauna (Commito et al.,