

RESEARCH ARTICLE

Accounting for Multiple Foundation Species in Oyster Reef Restoration Benefits

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Abstract

Many coastal habitat restoration projects are focused on restoring the population of a single foundation species to recover an entire ecological community. Estimates of the ecosystem services provided by the restoration project are used to justify, prioritize, and evaluate such projects. However, estimates of ecosystem services provided by a single species may vastly under-represent true provisioning, as we demonstrate here with an example of oyster reefs, often restored to improve estuarine water quality. In the brackish Chesapeake Bay, the hooked mussel *Ischadium recurvum* can have greater abundance and biomass than the focal restoration species, the eastern oyster *Crassostrea virginica*. We measured the temperature-dependent phytoplankton clearance rates of both bivalves and their filtration efficiency on three size classes of phytoplankton to parameterize an annual model of oyster reef filtration, with and

without hooked mussels, for monitored oyster reefs and restoration scenarios in the eastern Chesapeake Bay. The inclusion of filtration by hooked mussels increased the filtration capacity of the habitat greater than 2-fold. Hooked mussels were also twice as effective as oysters at filtering picoplankton (1.5–3 μm), indicating that they fill a distinct ecological niche by controlling phytoplankton in this size class, which makes up a significant proportion of the phytoplankton load in summer. When mussel and oyster filtration are accounted for in this, albeit simplistic, model, restoration of oyster reefs in a tributary scale restoration is predicted to control 100% of phytoplankton during the summer months.

Key words: clearance rate, *Crassostrea virginica*, ecosystem services, *Ischadium recurvum*, phytoplankton, top-down control, water quality.

Introduction

The concept of foundation species, which dominate an ecological community in biomass and autogenic ecosystem engineering effects (Dayton 1972), has advanced ecological theory (Bruno et al. 2003; Crain & Bertness 2006; Hastings et al. 2007) and restoration practice (Byers et al. 2006). In coastal marine ecosystems, the planting of a single foundation species has become a common approach to spur the formation of a larger ecological community (e.g. *mangroves* Field 1999, *mussel beds* Norling & Kautsky 2007, *seagrasses* van Katwijk et al. 2009). Although foundation species have been treated on a single species basis in theory and practice, recent work demonstrates that one foundation species often facilitates the presence of others in hierarchical fashion leading to a habitat facilitation cascade (Thomsen et al. 2010; Angelini et al. 2011).

Despite being a dominant feature of many ecosystems, multiple foundation species and their interactions are often omitted

from marine restoration planning. If multiple foundation species increase ecosystem services and/or biodiversity, accounting for their effects could alter the projected approach and benefits of restoration. Of particular interest are foundation species that differ in their ecosystem engineering effects and expand the range of ecosystem services a habitat provides. More diverse assemblages can exhibit higher rates of ecosystem functioning and ecosystem service provision (van Wesenbeeck et al. 2013) for a variety of reasons including niche complementarity between species (Loreau et al. 2001; Hooper et al. 2005; Balvanera et al. 2006; Cardinale 2011) and differences in the physical structures created by different species of autogenic ecosystem engineers (Odling-Smee et al. 2003; Boogert et al. 2006). For example, Cardinale (2011) found that more diverse algal biofilms more effectively remove nutrients from experimental streams and produce a greater effect on water quality due to niche complementarity between species.

We focus here on the potential of multiple foundation species to affect the projected ecosystem services provided by oyster reef restoration. Following their widespread overexploitation and destruction (Beck et al. 2011), recognition of the wide variety of coastal ecosystem services provided by oyster reefs has made them a major target for restoration (Coen et al. 2007; Grabowski & Peterson 2007). Evaluation metrics of some of the ecosystem services enhanced by oyster reef restoration,

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such as fishery production (Peterson et al. 2003) and biodiversity benefits (Coen et al. 2007), account for species beyond the restored foundation species, whereas other measures of ecosystem services, such as carbon sequestration, erosion control, nutrient processing, and water quality regulation, are often single species focused (Coen & Luckenbach 2000). Coen and Luckenbach (2000) point out the particular importance of accounting for the effect of mussels, which can be abundant on oyster reefs, in oyster reef restoration water quality benefits.

The potential of oyster reefs to enhance water quality has been the subject of extensive research and a motivating force for large-scale oyster restorations (Grizzle et al. 2008; Zu Ermgassen et al. 2013). This is particularly true in the eutrophic Chesapeake Bay, where the oyster population is estimated at 0.3% of its historic abundance (Wilberg et al. 2011) and the levels of phytoplankton chlorophyll *a* in surface waters have more than doubled in the past 60 years (Kemp et al. 2005). Modeling studies suggest that resurrecting oyster habitat could increase water clarity and reduce hypoxia in shallow tributaries (Cercu & Noel 2007; Fulford et al. 2007). However, these studies have modeled the effects of oysters in isolation.

Secondary autogenic ecosystem engineers can be abundant on oyster reefs. In mesohaline sites, the hooked mussel, *Ischadium recurvum*, is common on natural reefs (Wells 1961; Bahr & Lanier 1981; Bergquist et al. 2006) and can be as or more abundant than oysters on restored reefs (Lipcius & Burke 2006; Rodney & Paynter 2006; Gregalis et al. 2008; Kellogg et al. 2013). In this paper, we investigate the potential for niche overlap in the ecosystem service of water quality regulation by two co-occurring foundation species, the eastern oyster *Crassostrea virginica* and the hooked mussel *I. recurvum*. In laboratory experiments, we investigate the rates of water clearance by the two species over a temperature gradient and their efficiency at clearing algae of different sizes. Using lab-derived estimates of filtration, we model annual phytoplankton control by oysters alone and by oysters and mussels together at sites where the two species co-occur and that are current and prospective restoration locales in the eastern Chesapeake Bay.

Methods

Study Species

The two study species, *Crassostrea virginica* and *Ischadium recurvum*, were chosen based on their abundance and relevance to restoration. A 1-year-old *C. virginica* was purchased in July 2011 (Marinetics, Cambridge, MD, U.S.A.). In July and September 2011, *I. recurvum* were collected from 1 to 2 m depth at two sites, a small, planted oyster reef at the Smithsonian Environmental Research Center (SERC) in Edgewater, MD, U.S.A. and a reef-dome restoration project at the Chesapeake Bay Environmental Center in Grasonville, MD, U.S.A. All animals were kept in flowing Rhode River water at SERC until December 2011, when they were transferred into experimental tanks containing 20°C Rhode River water adjusted to 10 ppt salinity (Instant Ocean Aquarium Sea Salt, United Pet Group, Blacksburg, VA, U.S.A.) and were fed a diet of cultured

Nannochloropsis oculata and *Phaeodactylum tricorutum* (DT's Live Phytoplankton Premium Reef Blend, Innovative Marine Aquaculture, Palmetto, FL, U.S.A.) and *Tetraselmis chuyi* (from the University of Maryland's Institute of Marine and Environmental Technology's plankton culture facility).

Clearance Rates and Filtration Efficiency

We characterized the filtering behavior of *I. recurvum* relative to *C. virginica* in laboratory experiments. First, we measured clearance rates in closed, well-mixed mesocosms during timed feeding trials. Secondly, we examined the clearance efficiency of the two species on three phytoplankton species that differ in cell size.

To measure clearance rates, mesocosms ($n = 12$) were filled with 2 L of 0.2 μm string-filtered Rhode River seawater adjusted to 10 ppt salinity. Thirteen trials were conducted across a range of water temperatures (8–34°C) to simulate feeding behavior during different times of year in the Chesapeake Bay region, where water temperatures range from freezing to 32°C. Mesocosms were placed in a recirculating water bath, where an Aqua Logic aquarium heating/cooling unit maintained the temperature setting to $\pm 0.1^\circ\text{C}$. Water in mesocosms was well-mixed by bubbled air. Five individual mussels or oysters were introduced into each mesocosm ($n = 5$ per species) prior to the feeding trial for 16 hours of pre-trial starvation and temperature acclimation. Two mesocosms were left empty as ungrazed controls. At the start of the experiments, mesocosms were inoculated with 0.6 mL of DT's *N. oculata* [157.5×10^6 cells/mL] and *P. tricorutum* [41.24×10^6 cells/mL] and 10 mL of *T. chuyi* culture [1.36×10^6 cells/mL]. Seawater samples (10 mL) were drawn upon inoculation and after an hour of feeding and analyzed on a Multisizer 4 Coulter particle counter (Beckman-Coulter Inc., Indianapolis, IN, U.S.A.). At the end of the feeding trial, all animals were removed from their shells and dried at 60°C prior to measuring tissue dry weight. Clearance rates (CR, $\text{L}\cdot\text{hour}^{-1}\cdot\text{gDW}^{-1}$) were calculated with the equation (Coughlan 1969):

$$\text{CR} = (V/n \times t) \times (\ln(C_0/C_t) - a) \quad (1)$$

where V is the suspension volume in liters, n is the dry tissue weight in grams, t is the time in hours, C_0 and C_t are the concentrations of particles at time = 0 and time = t , respectively, and a is the $\ln(C_0/C_t)$ correction for the change in concentration of particles in ungrazed controls due to settling, etc. Clearance rates were calculated independently for removal of 4–5 μm cells (*P. tricorutum*) and 7–10 μm cells (*T. chuyi*).

Removal of 1.5–3 μm cells (*N. oculata*) was not used to calculate a third clearance rate because oysters cannot fully capture particles less than 4 μm in size (Langdon & Newell 1990). Additionally, an unknown small particle (<2 μm) contaminant partially obscured the discrete peak of *N. oculata*. Therefore, we did six additional feeding trials to measure the efficiency of the two species in filtering particles in the 1.5–3 μm size class. Feeding trials were as above, except that mesocosms were filled with 2 L of 10 ppt deionized water instead of river water; all trials were conducted at 25°C; one oyster or mussel, rather than five

individuals, was placed in each mesocosm ($n = 4$ per species or ungrazed control); and mesocosms were inoculated with 0.6 mL of DT's phytoplankton blend alone, without *T. chuyi*. Clearance efficiency of the smaller 1.5–3 μm size class was defined as the clearance rate within the mesocosm of the 1.5–3 μm *N. oculata* cells in proportion to that of the larger 4–5 μm *P. tricorruptum* cells, which oysters can fully exploit (Langdon & Newell 1990). Non-feeding individuals ($\text{CR} \leq 0$) were excluded from analysis.

To characterize the effect of temperature on CR, we used least squares nonlinear regression to fit an existing model of oyster clearance rates (Cerco & Noel 2007) to the data:

$$\text{CR} = \text{Fr}_{\text{max}} \times e^{-\text{Ktg}} \times (T - T_{\text{opt}})^2 \quad (2)$$

where Fr_{max} is the maximum filtration rate ($\text{L}\cdot\text{hour}^{-1}\cdot\text{gDW}^{-1}$), Ktg is the temperature effect on clearance ($^{\circ}\text{C}^{-2}$), T is temperature ($^{\circ}\text{C}$), and T_{opt} is the optimum temperature for filtration ($^{\circ}\text{C}$). Non-feeding mesocosms ($\text{CR} \leq 0$) and the first two trials which had very low CR overall were excluded in model estimation. We used F -tests to investigate the effect of species identity on each parameter, testing if a model that treats a parameter as a species-specific factor fit the data better than a model that grouped the two species together for that parameter (Ritz & Streibig 2008). To analyze the effects of trial, species identity, and their interaction on clearance efficiency of 1.5–3 μm particles, we used a factorial analysis of variance (ANOVA). Statistical analyses were conducted in R (CRAN).

Phytoplankton Control Model

We modeled the proportion of phytoplankton control using a flexible approach similar to Fulford et al. (2007). Phytoplankton control by oysters was modeled monthly for 17 sites for which data were available on both oyster and mussel biomass in the Eastern Bay, Chester River, and Choptank River regions (Fig. 1) as:

$$\text{Control of phytoplankton}_x = \frac{B_o \times \text{FR}_o \times \sum (P_i \times E_{oi})}{V} \quad (3)$$

where control of phytoplankton in month x is expressed as a function of oyster biomass B_o (g), oyster filtration rate FR_o ($\text{L}\cdot\text{hour}^{-1}\cdot\text{gDW}^{-1}$), the proportion of phytoplankton biovolume P in size class i , the clearance efficiency of oysters E_o for phytoplankton of size class i , and the volume V (L) of water in the tributary segment. See Appendix S1, Supporting Information for greater detail on data sources and the model.

To incorporate top-down control by mussels, we added their phytoplankton control to that of the oysters, using the same model modified for mussel-specific filtration rates and filtration efficiencies as measured in the laboratory. Mussel biomass was estimated based on their abundance in either dredge samples from the 2011 Maryland Department of Natural Resources Fall Oyster Survey or patent tong surveys in the Choptank River and Harris Creek (see Methods in Appendix S1). We multiplied the segment level oyster biomass by the ratio of

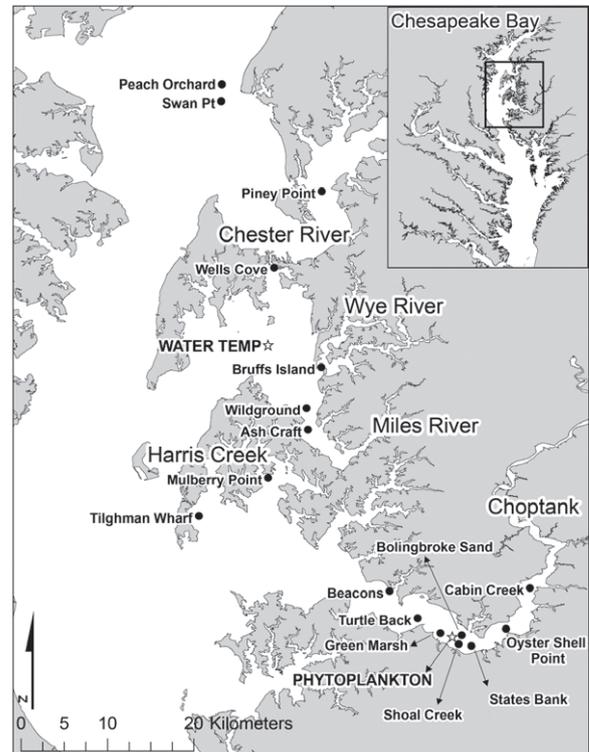


Figure 1. Map of sites in the Eastern Bay, relative to the location of MD DNR long-term water temperature data collection ("WATER TEMP," Station EE1.1) and Chesapeake Bay Program phytoplankton monitoring data collection ("PHYTOPLANKTON," Station CB3.3C).

mussel biomass:oyster biomass at each site to estimate segment level mussel biomass for use in the model. Of the 17 sites, 7 had restoration activities since 2006 of planting spat on shell (Fig. 2), according to the NOAA Restoration Atlas (NOAA 2012).

Using this model, we investigated the capacity of bivalve reefs to control phytoplankton in two ways. First, we compared estimates of top-down control of phytoplankton by oysters alone to that by oysters and mussels to quantify the contribution of mussel filtration to overall phytoplankton control. Second, we modeled the potential for future phytoplankton control in Harris Creek, MD, U.S.A., the site of one the largest oyster reef restorations ever undertaken on the U.S. Atlantic coast. Plans include restoring a minimum of 121 ha of oyster habitat by 2017, representing a 15-fold increase in oyster reef habitat (Oyster Metrics Workgroup 2011; Maryland Interagency Oyster Restoration Workgroup 2013). The three restoration scenarios that we compared to modeled present day phytoplankton control are shown in Table 1.

Results

Clearance Rates

Oyster clearance rates equaled or exceeded mussel clearance rates at all temperatures (Fig. 3). Models describing clearance rates for the two species were significantly different,

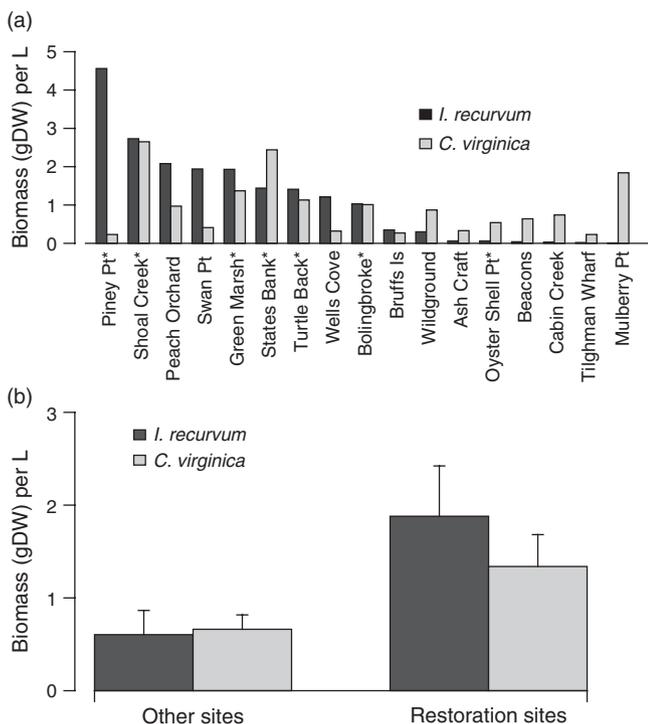


Figure 2. Biomass per liter of reef material of *Ischadium recurvum* and *Crassostrea virginica* at (a) 17 sampled sites in the eastern Chesapeake Bay, with asterisks after the site name indicating restoration activity between 2006 and 2011, and (b) shown as the mean biomass (+SE) at sites with restoration activities relative to all other sites.

as were all model parameters (Table 2). Maximum filtration rates were $7.0 \text{ L}\cdot\text{hour}^{-1}\cdot\text{gDW}^{-1}$ ($\pm 0.5 \text{ SE}$) for oysters and $4.6 \text{ L}\cdot\text{hour}^{-1}\cdot\text{gDW}^{-1}$ ($\pm 0.3 \text{ SE}$) for mussels. As expected, rates estimated based on filtration of the 4–5 μm size class were close to those based on the 7–10 μm size class, which were 6.0

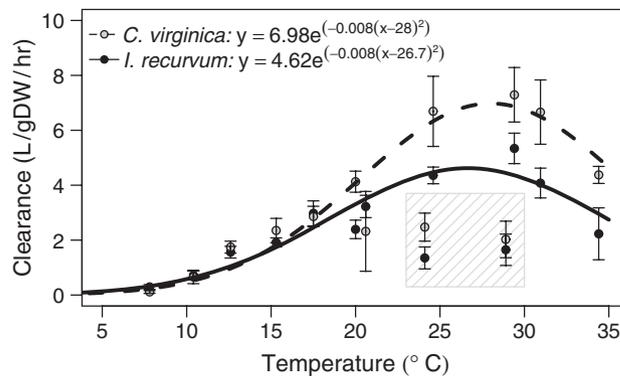


Figure 3. Clearance rates of *Crassostrea virginica* and *Ischadium recurvum* over a range of temperatures based on their clearance of *Phaeodactylum tricornutum*, size range 4–5 μm . Maximum clearance rates were used to fit the curve; points in the shaded box were excluded from curve fitting. Each point represent $N = 5$ replicates \pm SD.

and $4.3 \text{ L}\cdot\text{hour}^{-1}\cdot\text{gDW}^{-1}$ for oysters and mussels, respectively (figure in Appendix S1). While the general response to temperature change was similar for the two bivalves (shape of the curves, Fig. 3), oysters filtered optimally at a slightly higher temperature, 28.0°C , than mussels, 26.6°C . Both bivalves fed minimally at less than 10°C , which corresponds to the winter months in the region. For oysters, these rates are in the range of other estimated clearance rates ($6.8 \text{ L}\cdot\text{hour}^{-1}\cdot\text{gDW}^{-1}$ in seawater approximately 32 ppt and $27\text{--}29^\circ\text{C}$, Riisgaard 1988, $8\text{--}9.6 \text{ L}\cdot\text{hour}^{-1}\cdot\text{gDW}^{-1}$ in $12\text{--}15$ ppt salinity water at 25°C , Newell & Koch 2004). For hooked mussels, there have been no prior measurements.

The two species also differed in their clearance efficiency of picoplankton, with mussels exhibiting greater efficiency than oysters (Fig. 4). Factorial ANOVA indicated a significant interactive effect of trial and species identity ($F_{5,28} = 3.32$, $p = 0.0177$). This was primarily due to high variation in mussel

Table 1. Modeled restoration scenarios for Harris Creek.

Scenario	Description and Rationale	Segment Oyster Biomass (mt)	Segment Mussel Biomass (mt)
Present	Present day abundance of oysters and mussels*	59.71	75.99
Scenario 1: Restoration of existing reefs	A 2-fold increase in oyster biomass and a 3-fold increase in mussel biomass, based on the greater biomass per unit area observed at sites with previous restoration activities (Fig. 2b)	119.42	227.98
Scenario 2: Reef plantings, no mussels	A 15-fold increase in oyster biomass from Scenario 1 to represent the 15-fold increase in restored oyster reef area in Harris Creek; no mussel filtration included	1,791.35	0.00
Scenario 3: Reef plantings	A 15-fold increase in oyster and mussel biomass from Scenario 1 to represent the 15-fold increase in restored oyster reef area in Harris Creek	1,791.35	3,419.69

*Present day biomass is based on segment level data for oysters (Fulford et al. 2007) and mussel biomass as the mean proportion of mussel:oyster biomass found at all non-restored sites, including Tilghman Wharf in Harris Creek.

Table 2. Summary of *F*-tests of the effect of species identity on nonlinear regression models and model parameters.

	4–5 μm			7–10 μm		
	<i>df</i>	<i>F</i>	<i>p</i>	<i>df</i>	<i>F</i>	<i>p</i>
Model	99, 96	9.61	<0.0001	98, 95	7.60	0.0001
Parameter						
$F_{r_{\max}}$	99, 97	5.33	0.0063	98, 96	5.64	0.0048
K_{tg}	99, 97	14.51	<0.0001	98, 96	11.40	<0.0001
T_{opt}	99, 97	13.58	<0.0001	98, 96	9.69	0.0001

df, degrees of freedom. Bolded values are significant at the $p < 0.05$ level.

$F_{r_{\max}}$ (maximum filtration rate), K_{tg} (the effect of temperature on filtration), and T_{opt} (the temperature of optimal clearance) for models of clearance rates based on clearance of 4–5 μm phytoplankton and 7–10 μm phytoplankton. *F*-tests were performed by comparing a model without species identity to one that included species as a factor for each parameter.

filtration in Trial 1 (Fig. 4). In all other trials, mussels exhibited greater clearance efficiency of picoplankton. Averaging across all trials, mussels exhibited 88% efficiency in filtering picoplankton, whereas oysters were 45% efficient (species effect: $F_{1,28} = 42.2$, $p < 0.0001$, Fig. 4).

Phytoplankton Control Model

Sites varied greatly in their abundance of mussels and oysters, and there was no correlation between mussel and oyster abundance ($p = 0.3128$; Fig. 2a). Both bivalves were more abundant on reefs where restoration activities had occurred (effect of restoration: $F_{1,30} = 9.2$, $p = 0.005$, Fig. 2b). This observed increase in bivalve biomass on restoring reefs defined Restoration Scenario 1 (Table 1).

Differences in clearance rates and efficiencies between the species translated into differences in top-down control between regional models. On average, adding mussel filtration into the oyster phytoplankton control model more than doubled control of phytoplankton (Fig. 5). Oysters alone were capable of filtering 0.02–0.04% of phytoplankton in March and 0.89–1.65% of phytoplankton in August, depending on the site, whereas the combination of oysters and mussels were capable of filtering 0.03–0.47% of phytoplankton in March and 1.09 to over 13% of phytoplankton in August (mean = 2.75%, Fig. 5), depending on the site (Table S4). At the site where *Ischadium recurvum*

was most abundant, Piney Point in the Chester River, the proportion of phytoplankton control in August increased 15-fold when mussels were included in the model.

Using our phytoplankton control model to estimate restoration effects in Harris Creek, we found that the control of phytoplankton varied among restoration scenarios (Fig. 6). Restoration of existing reefs (Scenario 1) increased phytoplankton control 2.5-fold across all months. A 15-fold increase in restored habitat (Scenario 3) resulted in a 38-fold increase in phytoplankton control across all months, 39% of which was due to mussels alone (Scenario 3 versus Scenario 2, Fig. 6). In Scenario 3, bivalves consumed more than the entire standing stock of phytoplankton in the summer months (values over 100%, Fig. 6).

Discussion

In laboratory experiments, the hooked mussel *Ischadium recurvum* cleared phytoplankton at 66% the rate of the eastern oyster *Crassostrea virginica*, a species widely renowned for its filtration capabilities (Loosanoff 1958; Newell 1988; Riisgaard 1988). *Ischadium recurvum* more efficiently cleared particles in the picoplankton size class, representing a unique niche in the oyster reef community. The two species exhibit niche complementarity in their use of phytoplankton resources. However, their resource use overlaps for larger size classes

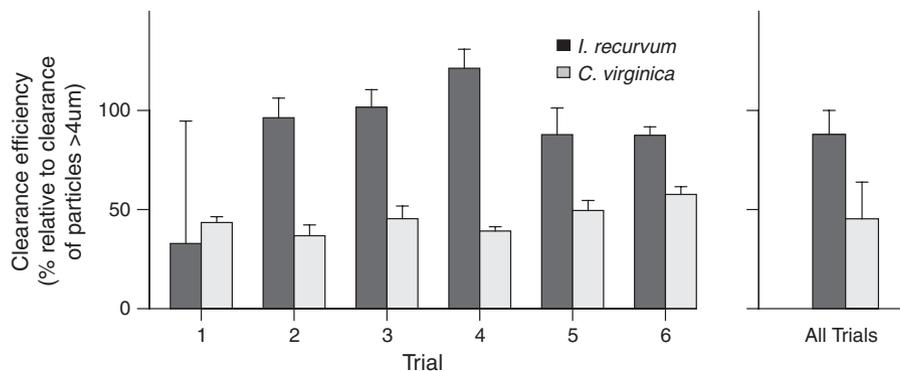


Figure 4. Clearance efficiency by *Ischadium recurvum* and *Crassostrea virginica* of small *Nannochloropsis oculata* cells, size range 1.5–3 μm , relative to complete clearance of larger *Phaeodactylum tricorutum*, size range 4–5 μm in six experimental trials. Each bar represents between 2 and 4 individuals; non-feeding individuals were excluded from the analysis.

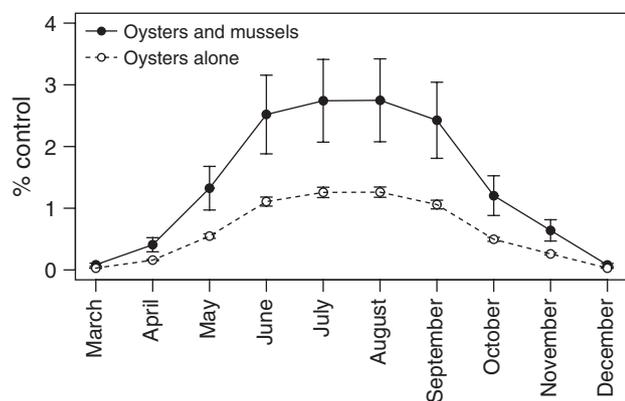


Figure 5. Average modeled percentage reduction of phytoplankton loads (\pm SE) by *Crassostrea virginica* (oysters) alone and by *Crassostrea virginica* and *Ischadium recurvum* (oysters and mussels) at eastern Chesapeake Bay field sites throughout the year, based on empirical measurements of the two species' clearance rates and clearance efficiencies and environmental data on water temperature, phytoplankton composition, and mussel and oyster abundances.

of phytoplankton, resources for which they would compete at times or in places where phytoplankton resources are limiting.

These resources are not limiting, however, in the eastern Chesapeake Bay, where less than 15% of phytoplankton is being consumed by the two species at sites of high bivalve biomass, according to our model. In most sites, less than 3% of the standing biomass of phytoplankton is consumed by the two species (table in Appendix S1). According to our model, a 15-fold increase in oyster habitat would increase phytoplankton control to 100% at a site where it is presently less than 2%. Admittedly, the model is simplistic in that it does not account for filter feeders depleting phytoplankton in near-reef waters, does not include movement of water, assumes animals are filtering 24 hours a day, and uses inflated clearance rates due to the elimination of non-feeding mesocosms in the rate estimation. While the elimination of nonfeeders is standard practice in lab-collected datasets, the nonfeeders might also represent variable feeding behavior within a population. In our data, bivalves in 7 of 130 mesocosms (5%) did not detectably feed.

Nonetheless, this prediction highlights the potential for oyster reef restoration to greatly affect water quality. Moreover, with numerous other filter-feeding organisms in these brackish water communities that depend on oyster and mussel shells for hard benthic structure to which to attach (e.g. the tunicate *Molgula manhattensis*, encrusting bryozoans), the effects of oyster habitat restoration on phytoplankton could be even greater. The large effect of incorporating a single oyster reef associate into filtration models inspires investigation into the water quality effects of the oyster reef community as a whole, measurements that would be most informative if measured in field or field-simulated conditions to avoid some of the assumptions of our modeling approach. Given scientific understanding of the Chesapeake and other estuaries (Cloern 2001, Kemp et al. 2005), reduced phytoplankton loads should increase water quality in terms of greater light transmission and nighttime dissolved

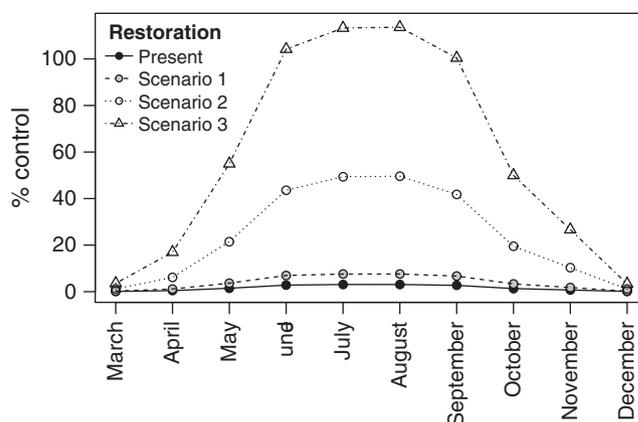


Figure 6. Modeled percentage reduction of phytoplankton loads by *Crassostrea virginica* and *Ischadium recurvum* at the Harris Creek site under present conditions and three restoration scenarios (Table 1).

oxygen, which will further benefit benthic communities like oyster reefs and seagrass beds within the Harris Creek tributary.

Studies of picoplankton seasonal dynamics have found it to be a key component of the Chesapeake's summer phytoplankton assemblage (Ray et al. 1989; Sin et al. 2000; Gaulke et al. 2010). Ray et al. (1989) found that picoplankton comprised 3–14% of the phytoplankton biomass during summer in the York River, a euhaline Chesapeake Bay tributary. Some have suggested that oysters' inability to filter this portion of the phytoplankton may limit the effectiveness of oyster restoration on phytoplankton control and light transmission (Fulford et al. 2007). In exerting greater top-down control on picoplankton, hooked mussels, therefore, contribute in an important way to oyster habitat restoration's water quality services.

In this study, picoplankton made up a smaller proportion of summer phytoplankton biomass, 2–7%, relative to Ray et al.'s (1989) York River dataset. Hooked mussels may have an even greater effect on water quality regulation in tributaries where picoplankton represents a larger component of the phytoplankton community.

We conclude that because oyster reef habitats frequently have primary and secondary foundation species, they will likely provide greater water quality ecosystem services than previous modeling efforts suggest. The ecosystem services provisioned will depend, in a large part, on interactions between these foundation species. A dearth of research on *I. recurvum* has left many outstanding questions about the interactions between hooked mussels and oysters, which may be net positive or negative and are likely context-dependent. For example, do hooked mussels use oysters as a recruitment cue or vice versa, and do the species consume one another's larvae? Most common at brackish salinities, *I. recurvum* is more likely to have an effect on water quality there. However, does the presence of one of these foundation species reduce or increase predation mortality on the other? By documenting their joint and complementary impacts on phytoplankton, we have demonstrated the relevance of these interactions for predicting restoration outcomes. Greater study will determine the overall effect of hooked mussels on oyster reef

ecosystem function and ecosystem service provision. If hooked mussels are found to enhance oyster reef restoration, it would be worthwhile to encourage their colonization of restored sites or consider introducing the two species jointly (see Implications for Practice).

Following biodiversity and ecosystem function theory, multiple foundation species will likely enhance the ecosystem services delivered by restored habitats due to niche complementarity relative to single foundation species restoration. Additionally, environmental conditions may dictate when and where multiple foundation species will be most effective in providing specific ecosystem services. For example, the extreme stress tolerance of some foundation species (e.g. blue mussels' resistance to wave exposure) may make them more effective than associated species at providing ecosystem services in stressful environmental conditions, whereas higher biodiversity of foundation species in areas of intermediate environmental stress may make them fruitful ground for multi-species ecosystem service provision (Crain & Bertness 2006). Oyster reefs and many other habitats targeted for restoration are likely to benefit from accounting for multiple foundation species in planning and performance.

Implications for Practice

- In evaluation of habitat restoration projects and establishing pre-activity baselines, it is important to quantify the abundance of multiple foundation species, not solely that of the focal restoration species. In oyster habitat restoration projects, hooked mussels or other foundation species can be present in high abundance, provide valuable ecosystem services, and may change in abundance over the course of restoration activities.
- Restoration practitioners should consider facilitating the presence of multiple foundation species. This could include seeding or planting multiple species or providing substrate that is more likely to be colonized by multiple species.

Acknowledgments

For assistance with models and graphics, we thank Virginia Clark and Keira Heggie. For donations of datasets, materials, and equipment, we thank Chris Judy, Sharyn Hedrick, Pat Neale, Mitch Tarnowski, and Odi Zmora. We thank the David H. Smith Conservation Research Fellowship for funding to K. Gedam, the Oyster Recovery Partnership for funding sample collection in the Choptank River, and numerous volunteers for collecting and analyzing those samples.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Appendix S1. Supplementary information about the phytoplankton control model and bivalve biomass estimates, clearance rates based on *T. chuyi*, 7–10 µm size class, and modeled phytoplankton control at each site.