A Synopsis of Research on the Ecosystem Services Provided by Large-Scale Oyster Restoration in the Chesapeake Bay

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U.S. Department of Commerce
National Oceanic and Atmospheric Administration
National Marine Fisheries Service

NOAA Technical Memorandum NMFS-OHC-8
January 2021

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U.S. Department of Commerce
Wynn Coggins, Acting Secretary

National Oceanic and Atmospheric Administration
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National Marine Fisheries Service
Paul Doremus, Acting Assistant Administrator for Fisheries

Recommended citation:

Bruce, D. G., J. C. Cornwell, L. Harris, T. F. Ihde, M. L. Kellogg, S. Knoche, R. N. Lipcius, D. N. McCulloch-Prosser, S. P. McIninch, M. B. Ogburn, R. D. Seitz, J. Testa, S. R. Westby, and B. Vogt. 2021. A Synopsis of Research on the Ecosystem Services Provided by Large-Scale Oyster Restoration in the Chesapeake Bay. NOAA Tech. Memo. NMFS-OHC-8, 52 p.

Copies of this report may be obtained from:

NOAA Chesapeake Bay Office
National Oceanic and Atmospheric Administration
200 Harry S. Truman Parkway, Suite 460
Annapolis, MD 21401

Or online at:
http://spo.nmfs.noaa.gov/tech-memos/

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Acknowledgements

Many thanks to Kim Couranz, Mandy Bromilow, and Morgan Corey for editorial assistance.

Executive Summary

Eastern oyster (*Crassotrea virginica*) populations and reef habitat in the Chesapeake Bay have been significantly diminished by disease, overfishing, and habitat loss. Restoring oyster reefs at a large scale is the primary approach used by managers to recover oyster populations and their associated ecosystem service benefits. Understanding and quantifying the ecosystem services provided by restored oyster reefs is important to guiding future restoration.

The 2014 Chesapeake Bay Watershed Agreement called for state and federal partners of the Chesapeake Bay Program to restore native oyster habitat and populations in 10 Bay tributaries by 2025. An additional objective to restoring oyster populations was to recover ecosystem functions provided by oyster reefs within the selected tributaries. NOAA Fisheries funded eight studies focused on quantifying ecosystem services associated with tributary-scale oyster restoration projects occurring around the Bay (see Figure 2 for tributaries). Managed by the NOAA Chesapeake Bay Office, this effort was termed the "Oyster Reef Ecosystem Services (ORES) Project." In general, these studies examined how nutrient cycling rates, macrofaunal abundance, and fish abundance and diet respond to restoration activity. The National Fish and Wildlife Foundation and NOAA Fisheries also provided funding for a ninth study that integrated food web and economic impact models to simulate socioeconomic outcomes linked to oyster reef restoration. This document summarizes and discusses the results of the nine studies.

Key project findings are:

- Nutrient cycling rates increase with oyster density, and are enhanced by biological activity of the entire oyster reef community
- Extrapolated nitrogen removal rates were estimated to be 57 lbs. N acre^{-1} y^{-1} for low oyster biomass (< 75 g DW m^{-2}), which translates to an estimated annual N removal of ~20,000 lbs. of N for the 350 acres of the Harris Creek restoration project.
- Successfully restored reefs are expected to remove about 7 times as much nitrogen each day than unrestored sand/mud bottom areas.
- Observed water clarity improvements are mediated by particle uptake by restored oyster reef communities. Simulation model results suggest that up to 20% of chlorophyll-a (planktonic algae) can be removed per 300 linear meters of restored reef.
- Macrofaunal (benthic invertebrates that may serve as fish prey) density increases with oyster density, and can exceed 5,000 individuals per square meter.
- Self-sustaining oyster populations and habitat can persist even at an elevated risk of shell degradation and mortality in more saline portions of the Bay, when protected from exploitation.
- Macrofauna diversity increases with the structural complexity of restoration sites. Underwater video indicates that oyster restoration has resulted in oyster reefs that are taller and more complex than harvested reefs, providing habitat for a greater diversity of species.
- Abundance of small reef-resident fish species increases with oyster density.
- Survival of juvenile blue crab was three times greater on oyster reefs than on unstructured habitats.
- Thirty-five species of larger transient fishes were collected on oyster reefs; eighteen species have commercial or recreational value.

- Diets of white and silver perch were dominated by oyster-reef dependent macrofauna. Among the most frequently consumed reef prey were sea squirts, mud crabs, polychaete worms, and snapping shrimp.
- If protected from oyster harvest, mature restored reef ecosystems in the Choptank River region are expected to improve fishery landings and associated economic benefits by $23 million annually and support an additional 300 jobs. Blue crab landings account for an annual $11 million of increased economic benefits.

Overall, restored oyster reefs provide hard and structured habitat in an estuary that is otherwise dominated by soft bottom and fine sediments. These complex reef habitats contribute to reductions in nutrients and consequently to enhanced water clarity. They increase fish foraging resources and are used by many adult and juvenile fish species. And, under some conditions, they are expected to positively affect regional economies through enhanced fishery landings.

Introduction

Since the mid-1800s, Chesapeake Bay oyster populations have experienced precipitous declines. Initially, enhanced harvest efficiency led to habitat destruction and stock overfishing (Rothschild et al. 1994). Since the 1950s, oyster disease mortality, coupled with continued harvest pressure and habitat loss, has further depressed oyster populations to all-time low levels (Wilberg et al. 2011). Population declines resulted in the loss of ecosystem services (Grabowski et al. 2005, Fulford et al. 2007, and Kellogg et al 2013) provided by oysters themselves and the hard and relatively complex habitat they create. Population declines also led to decreased commercial harvest value. Oyster habitat restoration employing varied scales and methodologies has been used to offset declines in commercial harvest and ecosystem functions (Luckenbach et al. 1999).

In 2009, Executive Order 13508 and the resulting Chesapeake Bay Protection and Restoration Strategy called for federal agencies to establish specific measurable environmental goals for restoring the Chesapeake Bay and set in motion tributary-scale oyster restoration. Prior to the Restoration Strategy, restoration efforts were generally less targeted and on a smaller reef-level scale. Consequently, the concept of tributary-scale restoration was to significantly increase oyster abundance and reef area in a targeted tributary, facilitating greater oyster population recovery, resilience, and associated ecosystem services relative to initial smaller-scale projects.

In response to the Executive Order and Strategy, the Chesapeake Bay Program's (CBP) Sustainable Fisheries Goal Implementation Team (Fish GIT) convened the Oyster Metrics Workgroup to develop a science-based, shared definition of a successfully restored tributary for the purpose of tracking progress toward tributary-scale restoration. The workgroup was composed of representatives from the state and federal agencies involved in Chesapeake Bay oyster restoration, as well as oyster scientists from academic institutions. The workgroup produced a report (Oyster Metrics Workgroup 2011) defining tributary and reef-scale restoration goals.

According to the Metrics Report, a successfully restored reef should:

- Have a minimum mean density of 50 oysters and 50 grams dry weight/square meter (m^2) covering at least 30% of the target restoration area at 6 years post restoration,
- Have two or more age classes present,
- Exhibit stable or increasing spatial extent, reef height, and shell budget, and
- Have a minimum of 30% of target area covered with added reef material or planted spat-on-shell (juvenile hatchery oysters attached to oyster shell).

A successfully restored tributary is one where:

- A minimum of 50% of restorable area (as defined by current distribution of oyster shell bottom) that constitutes at least 8% of historic oyster habitat within a given tributary meets the reef-level metrics above.

As documented in the Metrics Report, "*the goal of oyster restoration at the tributary-level is to dramatically increase oyster populations and recover a substantial portion of the ecosystem functions provided by oyster reefs within the tributary.*" Implicit in the goal is that working on a tributary scale is required to achieve sufficiently large changes in oyster populations necessary to exceed several threshold values (shell volume, larval supply and survival, disease tolerance, etc.) and achieve a regime shift that supports greater population abundance and enhanced ecosystem services. The cumulative effects of restoration activities are unlikely to be linear (Figure 1), and restoration of oyster populations and the ecological functions they provide may require exceeding threshold improvements. While the immediate goals of restoration projects focus on oyster population and reef area targets, restoring the ecosystem functions of oyster reefs is essential to restoration success but more difficult to measure. The nine studies summarized in this Technical Memorandum aimed to quantify the level of ecosystem services provided or enhanced as a result of tributary-scale restoration implemented to achieve the established Metrics Report goals.

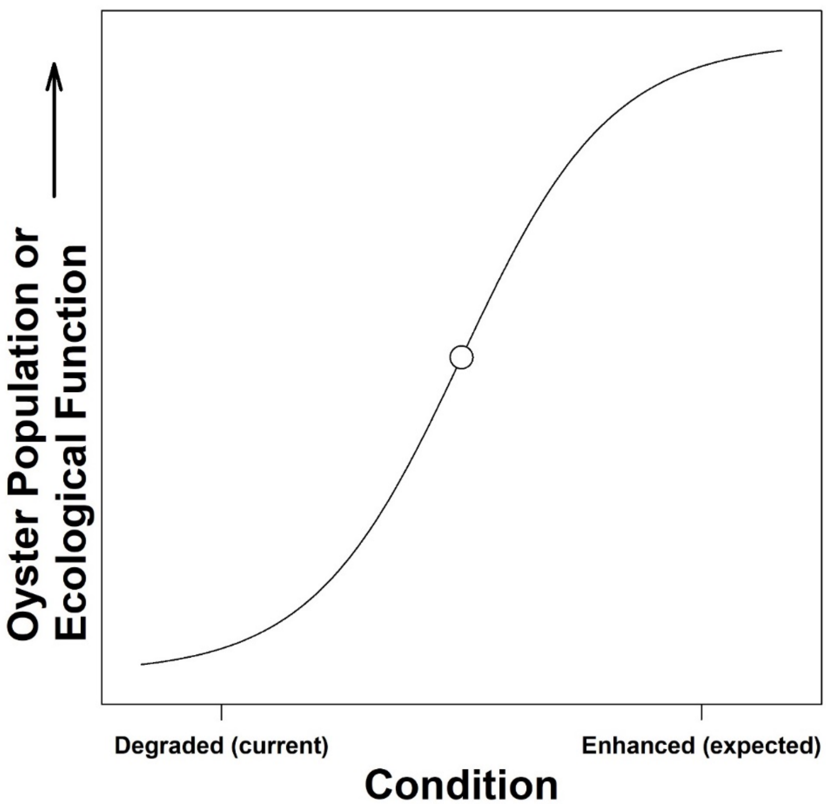

Figure 1. Generalized representation of a threshold response adapted from the restoration metrics report (Oyster Metrics Workgroup 2011). Improvement in conditions (toward the right) must exceed a critical value (open circle) to return the system to stable enhanced oyster population or ecological function (upward).

Goal Implementation

The 2014 Chesapeake Bay Watershed Agreement, drafted subsequent to Executive Order 13508, was signed by governors of the six states of the Chesapeake Bay Watershed, the mayor of Washington, D.C., and officials from the U.S. Environmental Protection Agency and the Chesapeake Bay Commission. The Agreement called for state and federal partners of the CBP to "restore native oyster habitat and populations in 10 Bay tributaries by 2025, and ensure their protection" (Figure 2). As with the Executive Order, responsibility for achieving this goal rests with the Fish GIT. For both Maryland and Virginia, the Fish GIT has convened tributary-specific restoration workgroups that plan, implement, monitor, and track progress toward the restoration success criteria identified by the Oyster Metrics Workgroup Restoration workgroups were formed through partnerships among federal and state agencies, academic institutions, and nongovernmental organizations. Primary funding sources for in-water reef construction and monitoring include the State of Maryland, the Commonwealth of Virginia, NOAA, the U.S Army Corps of Engineers, the National Fish and Wildlife Foundation, and The Nature Conservancy.

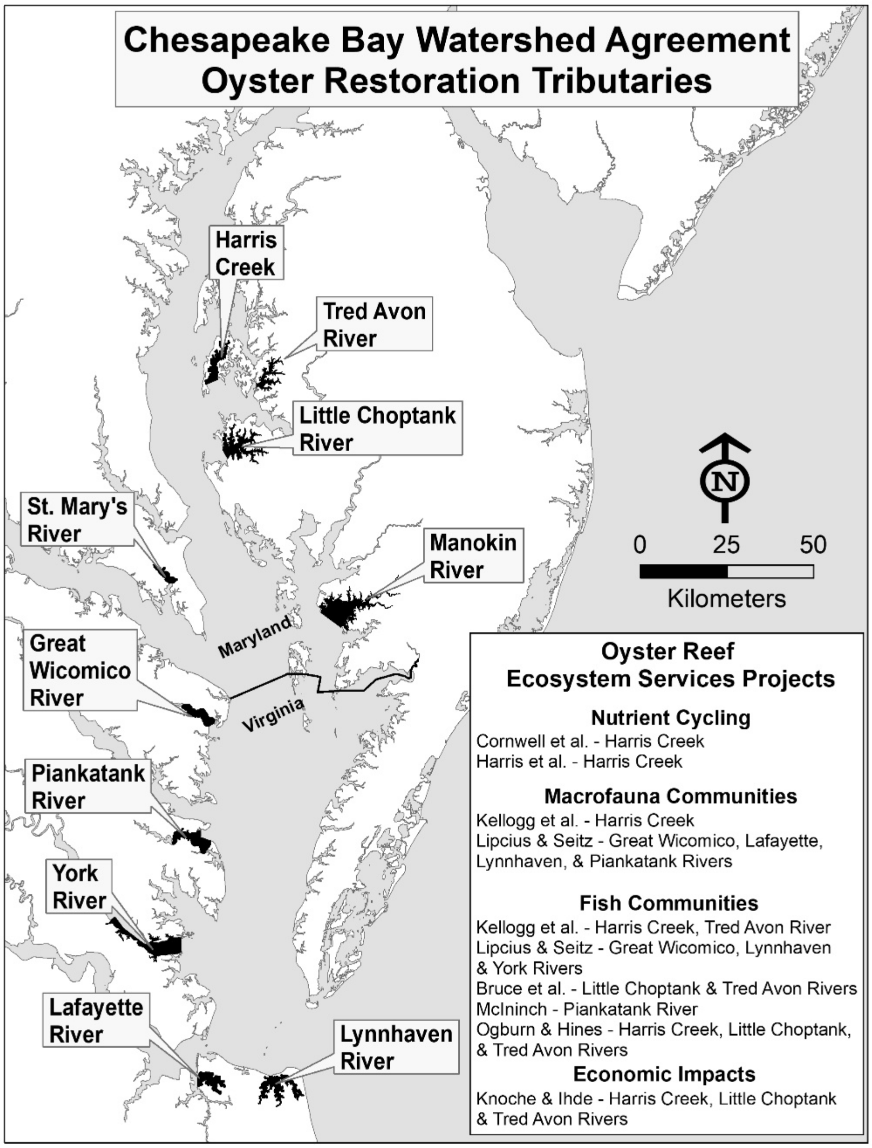

Figure 2. Location of Chesapeake Bay tributary-scale oyster restoration activities and ecosystem services research projects.

Currently (2020), restoration work is complete at Harris Creek and the Little Choptank River in Maryland and the Lafayette River in Virginia; success criteria monitoring is ongoing in these tributaries. Restoration is in the planning or implementation stage in all other tributaries. Although restoration area goals are not firmly set for all tributaries, the total area planned for ten tributaries is nearly 2,000 acres (Table 1). These are formidable restoration goals, and may represent the largest oyster sanctuary (non-harvest) restoration endeavor ever (The Nature Conservancy 2019).

In Maryland, restoration methods typically consist of 1) constructing reefs from a variety of substrate materials and planting the reefs with hatchery-produced oyster spat-on-shell (SOS), or 2) planting SOS on existing natural oyster shell reefs. Because natural spat settlement is more successful in higher salinities, Virginia restoration consists largely of constructing a reef base from various substrates and relying on natural oyster recruitment to populate the reefs; however, some SOS planting also occurs. Constructed reefs in early Chesapeake Bay restoration efforts were made from oyster shell, but because of shell scarcity and the magnitude of tributary-scale restoration, additional materials such as stone, crushed concrete, or clam shell are now used in addition to oyster shell. Intrinsic to their design objectives, constructed reefs generally exhibit greater vertical relief than most naturally existing oyster shell reefs, regardless of the material used.

Table 1. Reef area restored or planned for restoration in the ten Chesapeake Bay tributaries selected for large-scale oyster restoration. Areas exclude restoration activity conducted at these locations before the Chesapeake Bay Program Oyster Restoration Initiative began (2012). Tributary plans can be accessed at: https://www.chesapeakebay.net/who/publications-archive/maryland_and_virginia_oyster_restoration_interagency_teams

Tributary	Planned Restoration Area (Acres)	Status
Harris Creek	351	Complete
Little Choptank River	358	Complete
Manokin River	421	In progress
St. Mary's River	25	In progress
Tred Avon River	147	In progress
Great Wicomico River	22 (draft)	In progress
Lafayette River	12	Complete
Lynnhaven River	63	In progress
Piankatank River	235	In progress
York River	198	In progress

Ecosystem Services

Inherent in the goal of implementing large-scale oyster restoration in multiple Bay tributaries is the idea that, as an ecological keystone species, oysters provide valuable ecosystem services. Accordingly, a component of the oyster restoration outcome in Executive Order 13508 was to "…design a pilot project to quantify the ecosystem services provided by oyster reefs..." (Chesapeake Bay Federal Leadership Committee 2012). In response to the outcome, in 2013, NOAA Fisheries, through the NOAA Chesapeake Bay Office, announced a Federal Funding Opportunity (FFO) requesting proposals to assess ecosystem services of restored oyster reefs with focus on quantifying nutrient cycling (including denitrification, nitrogen sequestration), fish utilization, and trophic interactions on subtidal oyster restoration reefs. A supplementary FFO was announced in 2014 with the same research focus. The 2013 and 2014 NOAA FFOs provided funding awards to the University of Maryland, the Smithsonian Environmental Research Center, Virginia Commonwealth University, and the Virginia Institute of Marine Science for six research projects. The NOAA Chesapeake Bay Office also funded research conducted by its own field science team.

A science gap identified in the fish habitat outcome (Chesapeake Bay Program 2018) of the Chesapeake Bay Watershed Agreement was "[a]n ecosystem services valuation study that quantifies the value of fish habitat would allow us to effectively communicate the economic benefits of restoration and conservation." In 2017, the National Fish and Wildlife Foundation and NOAA funded a Morgan State University regional economics modeling proposal focused on oyster restoration activities within NOAA's Choptank River Habitat Focus Area. In total, nine projects were funded to quantify Oyster Reef Ecosystem Services (ORES) with a specific focus on the benefits supported by subtidal oyster restoration activities throughout the Chesapeake Bay (Figure 2).

The objective of this document is to summarize the findings of ORES research projects. The nine studies were grouped into four general themes: nutrient cycling, macrofaunal communities, fish communities, and economic modeling. Studies within themes are contrasted to identify unified results. Realized and potential relevance to resource managers and policy makers are discussed, and pertinent data gaps are identified within and in addition to the four research themes.

Project Synopses

Nutrient Cycling Research

Integrated Assessment of Oyster Reef Ecosystem Services: Quantifying Denitrification Rates and Ecosystem Services

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Grant Award period: March 2015–February 2019
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Our goal was to improve understanding of the nitrogen (N) removal capability of oyster restoration by measuring nutrient recycling and denitrification rates associated with oyster reef community development. Project objectives were to: 1) quantify changes in denitrification rates in relation to oyster biomass density; 2) assess seasonal patterns in denitrification rates and nutrient fluxes; 3) contrast denitrification rates and nutrient fluxes among non-reef sediments, reef sediments, and oyster clump treatments; and 4) extrapolate research results to tributary scales to assess the utility of large-scale oyster restoration in overall nutrient reduction to better inform management decisions.

Methods

Fluxes of N_2-N (denitrification), dissolved ammonium, nitrate plus nitrite, and dissolved oxygen were determined at the 350-acre oyster restoration project at Harris Creek, Maryland. The *ex-situ* incubation approach involved adding oyster communities to embedded trays for ~1 month, incubating the trays under dark and light conditions for 1-2 hour time courses for gas and solute sampling, and determining the rates of gas and solute exchange for 136 individual reef tray incubations. Reef exchange rates were compared to rates of sediment-water exchange in core incubations from reef-adjacent environments throughout Harris Creek.

To control for the influence of the restoration method employed, we limited our study to sites where oyster spat-on-shell (SOS) were planted directly on existing oyster shell bottom (i.e., areas with substratum conditions suitable for oyster survival and growth, but without the addition of hard substrate prior to planting SOS). To control for the influence of oyster age, we selected only sites that were planted in 2012. Prior to site selection, a baseline patent tong survey of oyster abundance on potential study sites was conducted in 2014 by the Ken Paynter Lab at the University of Maryland. Based upon the resulting data, we delineated eight 3.1-acre study sites for our work. The selected areas provided oyster tissue biomass densities ranging from 2.7 to 98.4 g dry weight (DW) per square meter at the time of initial surveys (Kellogg et al. 2016).

Results

Rates of sediment nutrient exchange, denitrification, and oxygen exchange were variable, but higher rates of denitrification were generally associated with higher oyster biomass (Figure 3) and higher water temperatures (e.g., the warm season). The effects of light on reef denitrification rates were small when the whole data set was examined.

One initial experiment indicated that denitrification rates on oyster reefs are greatly enhanced relative to non-reef core sediments. Two later experiments clearly showed that incubations of reef sediment alone (no oysters or oyster shell) resulted in underestimates of reef denitrification (Figure 4); incubations of oyster clumps alone showed that a considerable proportion of the denitrification was associated with the oyster reef community. A community approach (oysters plus sediment), however, is the most efficacious way to estimate denitrification in an oyster reef. Under warm summer conditions, the total denitrification estimate for oyster biomass < 75 g DW m^{-2} was 57 lbs. $acre^{-1}$ y^{-1}, and increased to 160 lbs. $acre^{-1}$ y^{-1} for biomass > 225 g DW m^{-2}. Denitrification rates observed during colder seasons were lower than in warmer seasons, but do have the potential to increase annual rates up to 25-50% above rates for warmer seasons alone.

In summary, these experiments suggest that nutrient assessments that do not consider the whole benthic community (reef organisms plus sediment) may underestimate nitrogen removal by microbial denitrification considerably. For oyster reefs, the effect of illumination is small relative to the high transformation rates observed for non-photosynthetic biogeochemical pathways. Illumination may be more important for non-reef sediment incubations. The minimum denitrification rate generated in this study for low oyster biomass levels, 57 lbs. N $acre^{-1}$ y^{-1}, would translate to an estimated annual removal of ~20,000 lbs. of N in the 350 acres of restoration in Harris Creek. Higher oyster biomass would be expected to yield higher rates of denitrification, but this conservative estimate is appropriate as a starting point for extrapolation to other restoration sites.

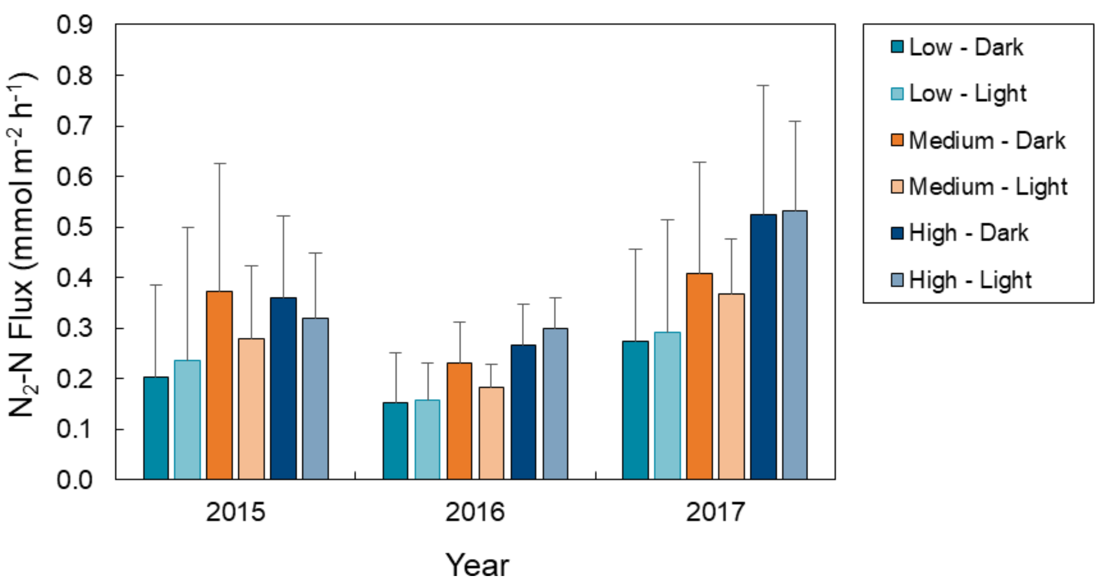

Figure 3. Sediment-water efflux of N_2-N from whole-community incubations for low, medium, and high oyster densities. Averages (± std. dev.) of both dark and light incubations for all May–October incubations are presented.

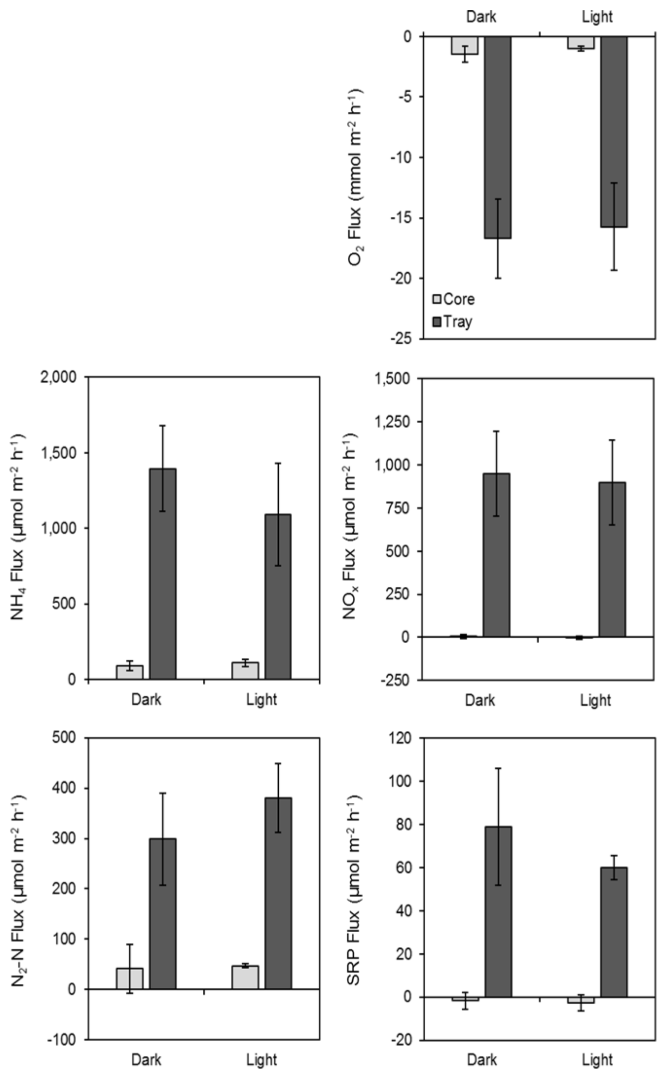

Figure 4. Comparison of fluxes from tray (intact oyster reef segment) and core samples (oyster reef sediments only) collected from a restored oyster reef in Harris Creek, MD (Kellogg et al. in revision). Note the difference in units reported for oxygen and nitrogen fluxes.

Natural Engineers in Ecosystem Restoration: Modeling Oyster Reef Impacts on Particle Removal and Nutrient Cycling

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The overarching goal of this work was to develop and test a modeling tool that can provide quantitative predictions of ecosystem services related to N removal and oyster biomass production using oyster restoration metrics such as reef size and oyster planting densities. N cycling, local primary production, and oyster bioenergetics were coupled with an existing oyster reef particle uptake model. This provided a quantitative link between oyster abundance, reef morphology, and habitat using a simulation framework, supporting an evaluation of these effects on oyster production and N removal. A web-based decision-support tool was created for selecting optimal restoration sites and estimating N removal provided by a given restoration effort.

Methods

To obtain data to validate the oyster filtration component of the model, extensive sampling was conducted at a restored oyster reef in Harris Creek, Maryland, documenting phytoplankton and seston dynamics for the duration of a complete tidal cycle. The hydrodynamic/filtration model is forced by current velocities derived from a Choptank River application of the Regional Ocean Modeling System (ROMS), includes oyster sizes and reef sizes characteristic of Harris Creek. The coupled filtration and biogeochemical processing model (Figure 5) was implemented over a near-annual cycle, and simulations were made to quantify chlorophyll-a removal rates over the reef, spatial patterns of oyster biodeposit accumulation, and associated nitrogen transformations associated with restored oyster reefs versus intact sediments. The model itself connects oyster processes with biogeochemistry via biodeposition. The oysters concentrate particles via filtration, created packets of high organic material in the form of biodeposits that combine with settled material to create inputs that are then processed via a series of detailed, microbially mediated biogeochemical processes.

Results

Field measurements on restored reefs showed a clear signature of oyster filtration at the maximum flood and ebb tides (Figure 6), and provide a snapshot of how water clarity may be enhanced. At these times, both suspended solids and particle volume concentrations decreased over the reef in the direction of the tide. Model simulation results documented the removal of chlorophyll over an oyster reef, with minimum concentrations occurring furthest downstream on an ebb tide and furthest upstream on a flood tide.

Associated with this chlorophyll-a removal is an accumulation of nitrogen-bearing oyster biodeposits along the reef, with highest biodeposit thickness occurring on the upstream near end of the reef with respect to tidal current. Thus, as chlorophyll-a is filtered from the water within the first 100-150 meters of reef, high biodeposit accumulations occur. The magnitude of chlorophyll-a removal by the reef generally varied between 0 and 50%, with the majority of time during April to October simulating 0-20% chlorophyll-a removal. Although these removal fractions are not very large, they do represent a nontrivial estimate of the chlorophyll-a filtering capacity of the reef and associated water column carbon and nitrogen mass removal through biodeposit production. The roughly 100 hours when >50% of chlorophyll-a was removed would represent a substantial loss for ambient phytoplankton material.

Clear patterns emerged from the biodeposition and the subsequent processing of nitrogen on the reef. When simulated oyster densities (100 oysters m^{-2}) were compared to baseline densities (0 oysters m^{-2}), the production of ammonium changed from nearly zero to in excess of 25 mmol N m^{-2} d^{-1}, which is on the same order of magnitude of ammonium fluxes from mid-Bay anoxic sediments where further processing of N (nitrification and denitrification) is inhibited. Although nitrate fluxes were not altered by the presence of oysters and associated biodeposit production, denitrification rates in 100 oysters m^{-2} simulations were three times the rate of baseline levels. This pattern is consistent with elevated denitrification rates observed in restored oyster reefs (Kellogg et al. 2013), but the magnitude predicted in the model is much lower than observed.

It is clear that biodeposit production and remineralization within oyster reefs leads to enhanced nitrogen cycling (both removal and recycling processes), and the model developed here represents those effects. Currently, the model can be applied to simulate a range of oyster densities and reef sizes at Chesapeake Bay restoration sites. Interestingly, the rate of increase of ammonium was not overcome by denitrification fluxes, indicating that in a mass balance context oysters produce a net release of nitrogen from biodeposits back to the water column. This recycled inorganic nitrogen is bioavailable for phytoplankton uptake. A future research question will focus on understanding whether the combined action of reducing phytoplankton concentrations via oyster filtration with the recycling capacity of the reef ultimately results in a whole ecosystem enhancement of nitrogen use efficiency or whether overall productivity is reduced.

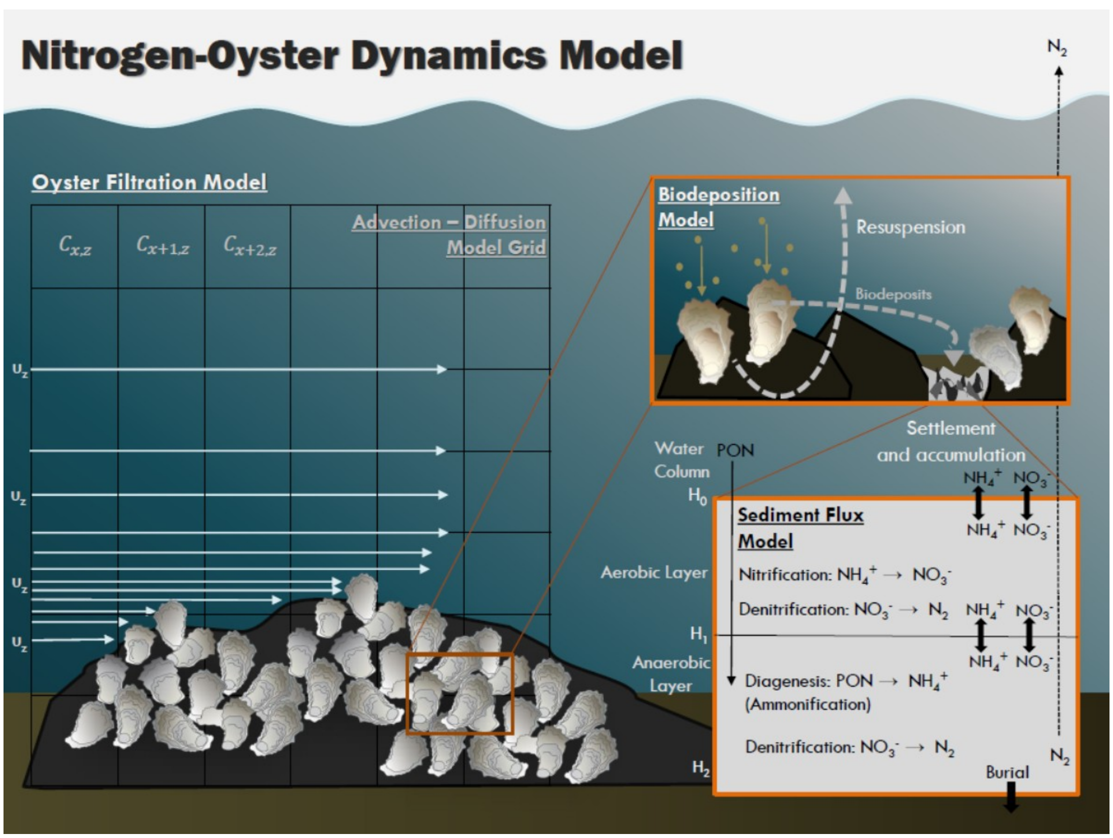

Figure 5. Conceptual model of Nitrogen-Oyster Reef Dynamics Model.

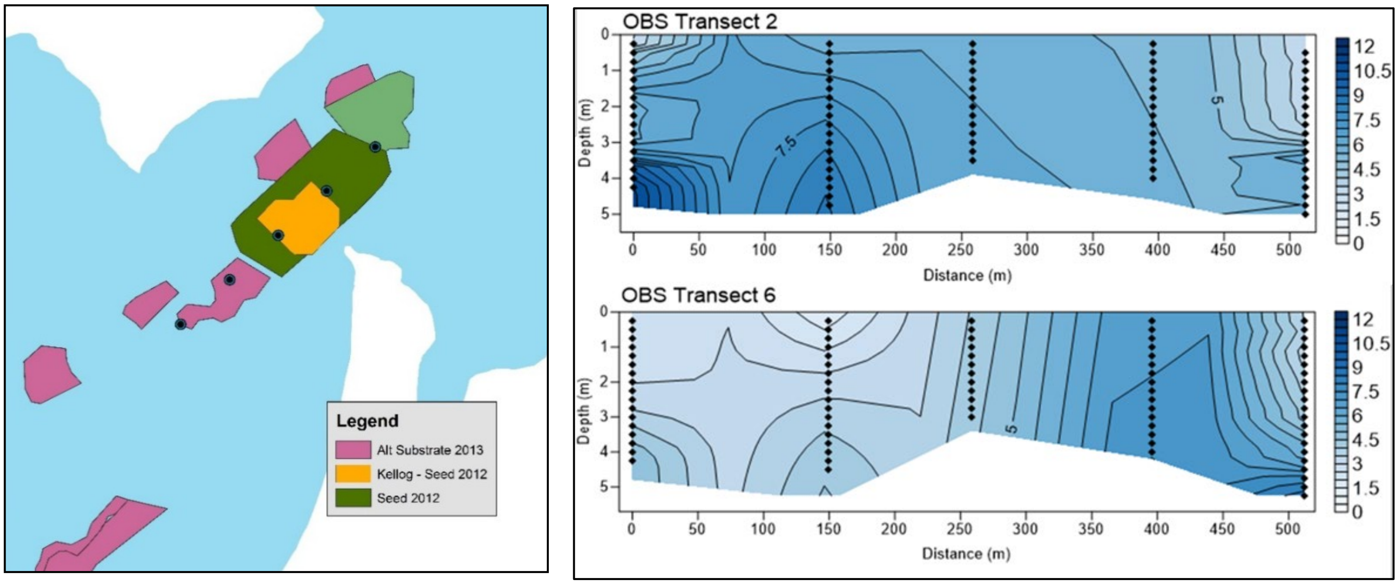

Figure 6. Water column turbidity measurement at Little Neck oyster reef in Harris Creek (left panel). Dotted symbols indicate the five sampling locations, which are located along a transect that is oriented 47° from true north. Optical backscatter turbidity (uncalibrated NTU; right panel) from transects taken on Little Neck Reef at maximum flood (top) and maximum ebb (bottom).

Nutrient Cycling Discussion

The two projects provide oyster reef nutrient cycling information from two different perspectives. One, Cornwell et al., used a fine-scale empirical approach to measure nutrient flux from direct chemical analyses of different habitat treatments and then, using observed flux rates, provides extrapolated estimates of nutrient removal for different areal scales. The other project, Harris et al., used a detailed model system to simulate particle removal from the water column, biodeposit production, transport, and biogeochemical nitrogen processing (Figure 7). Empirical data (chlorophyll-a, suspended sediments, and particle size) were collected over a restored oyster reef to help validate model simulations. The resulting model can be applied to simulate nutrient processing from a range of oyster reef sizes and live oyster densities at restoration sites within the Chesapeake Bay. Assessment of variation in nutrient fluxes relative to oyster restoration methods (e.g., natural shell reefs with planted spat-on-shell versus constructed substrate reefs with spat-on-shell) and restored reef maturity were beyond the scope of either study.

In the empirical study (Cornwell et al.), extrapolated N removal rates were estimated to be 57 lbs. N acre^{-1} y^{-1} for low oyster biomass (< 75 g DW m^{-2}), which translates to an estimated annual N removal of ~20,000 lbs. of N in the 350 acres of restoration in Harris Creek. Using the particle uptake model (Harris et al. 2019), estimated N removal from preliminary model simulations (Harris et al. 2019) was 160 lbs. N acre^{-} yr^{-1} for oyster densities of 100 m^{-2}. In both cases, nitrogen removal rates were higher for oyster reef communities relative to adjacent sediments unoccupied by oyster reefs (Figure 7).

Use of controlled experiments and modeling studies to assess ecosystem services is a valuable component of CBP oyster restoration outcomes (Chesapeake Bay Program 2018). Given that Bay-wide

Total Maximum Daily Load (TMDL) targets for nitrogen have proven difficult to achieve (Chesapeake Bay Program 2019), research studies such as these, which quantify N flux relative to oyster restoration and provide independent estimates of N reduction, have the potential to support general resource policy and management needs.

These projects have provided technical and policy support to specific CBP objectives. Principal Investigators Cornwell, Kellogg, and Sanford actively participate in the CBP Oyster Best Management Practices (BMP) Expert Panel for TMDLs, and have informed the development of oyster BMPs using their empirically determined nutrient flux rates (Cornwell et al 2019). Based on these advances in nutrient cycling science and oyster resource management, the BMP Expert Panel is seeking approval for oyster restoration as a CBP-approved BMP for the removal of pollutant nitrogen and phosphorus. The recommendations are that enhanced denitrification and accumulation of nitrogen and phosphorus in living oyster biomass will add the crediting of oyster restoration nutrient removal to the previously approved BMP for the aquaculture harvest removal of nutrients. Key to this crediting is the assessment of the increase of oyster densities and denitrification above background levels, and an understanding of the relationship between oyster density and nutrient removal. The Harris Creek study is the most comprehensive assessment of water quality improvements associated with large-scale oyster restoration using substrate additions and placement of hatchery-produced oysters.

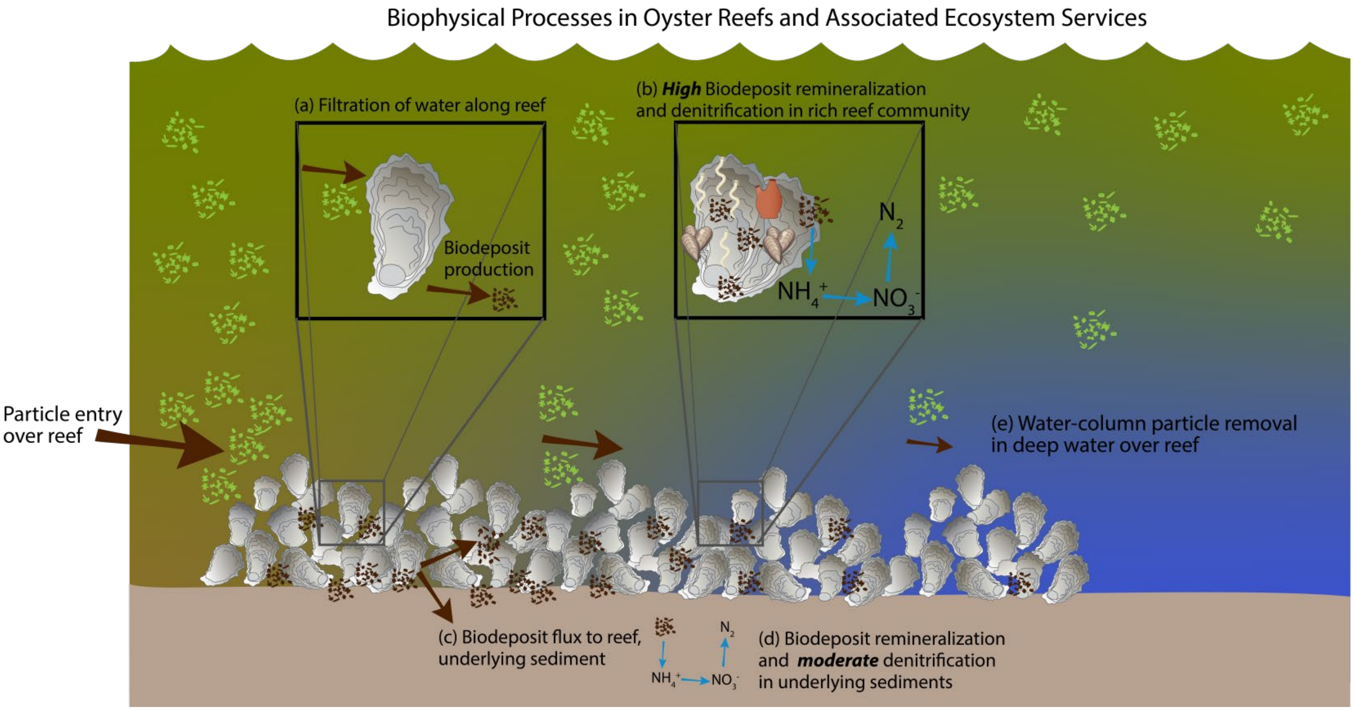

Figure 7. Conceptual diagram of oyster reef impacts on particle concentration and nutrient cycling. Model simulations and observations suggest that oyster communities can enhance particle filtration in a boundary layer just above the reefs, and that this filtration effect is enhanced along the flow path of water as it transits over the reef. A fraction of the filtered particles (those not assimilated by the oysters) are excreted by the oysters, and can be recycled in bare sediments beneath or adjacent to the reef as well as within the shell/reef community itself. Nitrogen recycling rates and nitrogen removal rates via denitrification are enhanced in the oyster reef community relative to bare sediments.

Macrofaunal Communities Research

Oyster Reef Ecosystem Services: Macrofauna Utilization of Restored Oyster Reefs

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Oyster reefs provide habitat for a variety of macrofaunal species that form the prey base of upper-level consumers. Macrofaunal sampling sites encompassed the majority of the area in which restoration activities were conducted within the Harris Creek Oyster Sanctuary in Maryland. Our studies focused on: 1) understanding the relationship between oyster biomass and the abundance and biomass of associated macrofaunal species; 2) assessing how these relationships change with season; 3) evaluating the role of tray-scale (0.1 m^2), plot-scale (10 m^2), and reef-scale (> 5624 m^2) oyster biomass density in determining associated macrofaunal abundance and biomass; and 4) examining larger-scale patterns in macrofaunal biomass density within Harris Creek.

Methods

We studied five restoration sites and three control sites that were suitable for restoration but were not subject to any restoration activities. At restoration sites, juvenile hatchery oysters set on oyster shell (spat-on-shell) were planted directly on the bottom (areas with substratum conditions suitable for oyster survival and growth without adding hard substrate prior to planting). To control for the influence of oyster age, we selected only sites that were planted in 2012. Prior to site selection, a patent tong survey of potential sites was conducted to establish baseline oyster density. We defined the resident macrofaunal community as all sessile and mobile organisms retained on a 1-mm mesh. To assess macrofaunal community abundance, diversity, and biomass, divers excavated a 0.1 m^2 area of the substratum, placed it in life position in a sampling basket lined with 1-mm mesh, replaced it in the excavated area, allowed it to remain in place for a month, and then collected samples. All oysters and attached and mobile macrofauna retained on a 1-mm mesh sieve were identified to species, and their abundance and biomass were assessed. For analyses, oyster biomass density was broken down into three categories: 1) low (< 50.0g DW m^{-2}); 2) medium (50.0-224.9 g DW m^{-2}); and 3) high (≥ 225.0 g DW m^{-2}). Low-density treatments had oyster densities less than the target levels defined by Fish GIT metrics for successful Bay-wide oyster restoration. Medium and high treatments had oyster densities above the target success metric.

Results

Results of our studies demonstrate that restored reefs in Harris Creek provide habitat for ~50 different macrofaunal species (see Appendix 1). The most abundant sessile taxa were the hooked mussel *Ischadium recurvum*, the sea squirt *Molgula manhattensis*, barnacles of the genus *Amphibalanus*, and sea anemones of the genus *Diadumene*. The most abundant mobile species included small reef resident fish (primarily the naked goby *Gobiosoma bosc*, but also striped blenny *Chasmodes bosquianus* and skilletfish *Gobiesox strumosus*), mud crabs *Eurypanopeus depressus*, polychaete worms *Alitta succinea*, and amphipods from several genera (dominated by *Melita nitida* with significant numbers of *Gammarus mucronatus, Apocorophium lacustre*, and *Cymedusa compta*). Two infauna groups, clams of the genus

Macoma and the soft shell clam *Mya arenaria*, were also collected, but abundance estimates may be biased in some cases because of the sampling methods used.

Samples from Harris Creek that had high oyster biomass (>225 g DW m^{-2}) consistently provided habitat for >5,000 non-oyster individuals m^{-2} regardless of season. In spring and fall, non-oyster macrofaunal abundances reached ~10,000 individuals m^{-2}. Biomass of non-oyster macrofauna on high oyster biomass reefs exceeded 60 g ash free dry weight (AFDW) m^{-2} in all seasons and was sometimes as high as 150 g AFDW m^{-2}.

For all sessile and mobile macrofauna, there were significant and complex interactions between the effects of oyster biomass density and season on the biomass density of each species. In all seasons, total macrofaunal biomass was greater at high oyster density than at low oyster density (Figure 8). In general, no consistent seasonal patterns were observed in macrofaunal biomass at medium oyster densities relative to low and high oyster densities.

Comparison of the effects of oyster biomass density on the biomass of mobile macrofaunal species did not reveal significant effects of plot-scale ($10m^2$) oyster biomass density for any species. Tray-scale (0.1 m^{-2}) and reef-scale (5625 m^{-2}) oyster biomass had a significant effect on all species. In general, macrofaunal density relative to oyster density was similar at intermediate (plot) scales, but was different and variable on small (tray) and large (reef) scales. Dividing macrofaunal biomass density by oyster biomass and plotting the resulting ratio against distance from the mouth of the creek revealed a significant effect of position within the creek on three of the four sessile macrofaunal groups, one mobile macrofaunal species, and both of the infauna groups. In general, when significant effects were observed, macrofaunal density relative to oyster density decreased moving upriver from the mouth of the creek.

Overall, our studies confirmed that oyster reef restoration especially when high biomass densities of oysters are achieved—leads to increased biomass of macrofaunal species; however, local oyster biomass density is only one of the factors that significantly influences macrofaunal community structure and abundance.

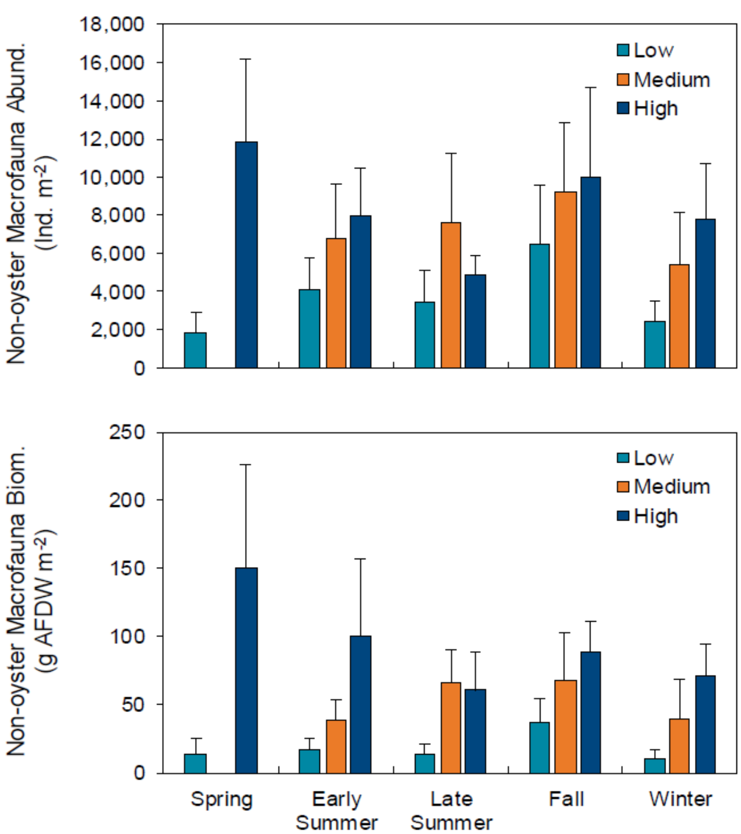

Figure 8. Seasonal non-oyster macrofaunal abundance and biomass density relative to low (< 50.0g DW m^{-2}), medium (50.0-224.9 g DW m^{-2}), and high oyster density (≥ 225.0 g DW m^{-2}). In spring, none of the samples collected fell in the medium oyster biomass category. Error bars represent one standard deviation. Refer to text for results of statistical analyses of biomass data.

Ecosystem Services of Restored Oyster Reefs in the Lower Chesapeake Bay: Oyster Populations and Benthic Macrofaunal Communities

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Oysters are vital to the health of Chesapeake Bay. Their reefs create a rich habitat for other species (Harding & Mann 2001) that are essential prey for predators of higher trophic levels (Quan et al. 2010, Abeels et al. 2012). This project aimed to determine oyster abundance, oyster biomass, and benthic prey utilization of oyster reefs in relation to reef characteristics, environmental conditions, and geographic location. Samples were collected in the Great Wicomico, Lynnhaven, Piankatank, and Lafayette rivers of the lower Western Shore of the Bay in Virginia. Oyster populations in U.S. Army Corps Engineers-constructed sanctuary reefs have been successful for over a decade. A thriving network of relict oyster reefs was discovered in the Lafayette River. And, benthic macrofaunal communities were enhanced by restored reefs.

Methods

Oyster population sampling was conducted in the Great Wicomico, Lafayette, and Lynnhaven rivers using patent tongs. Oysters were enumerated and measured to estimate density and biomass and to assess age structure. Sample data were used to determine reef performance relative to the Fish GIT restoration success reference points. The success threshold reference points are 15 oysters and 15 g dry weight (DW) per m^2, with multiple year classes; and the success target reference points are 50 oysters and 50 g DW per m^2 with multiple year classes.

Macrofaunal sampling was conducted on restoration reefs constructed of planted oyster shell that had been naturally colonized by wild oysters in the Lynnhaven, Great Wicomico Rivers, Piankatank, and Lafayette rivers. Benthic trays were embedded in restored reefs and retrieved after seven weeks, and all organisms were removed to estimate macrofaunal species diversity, density, and biomass. All collected macrofauna were retained with a 1.0 mm-mesh liner. Salinity and fine-scale reef rugosity (habitat complexity) were recorded at sampling sites to serve as environmental correlates. Benthic samples were sorted and individual organisms were identified, measured, and biomassed. Lastly, oyster volume (dead, live, boxes, clumps) and biomass were measured for each sample.

Results

Most of the constructed shell reefs in the Lynnhaven and Great Wicomico rivers that were sampled in 2015 and 2017 met the oyster restoration target density (15 and 50 oysters m^{-2}) and biomass (15 and 50 g DW m^{-2}) reference points (Table 2). Exceptions included a few sanctuary reefs in the Great Wicomico that may have been poached and a small group of reefs in the Lynnhaven that were in a high-energy area where the reefs were destroyed by a tropical storm. The reefs in the Great Wicomico were nearly 15 years post construction, and those in the Lynnhaven were nearly 10 years old. Oyster populations on the reefs were composed of multiple year classes and, with the observed density and biomass, thereby met Fish GIT metrics for successful restoration performance. In the Lafayette River, we identified, for the first time, a network of natural relict subtidal oyster reefs composed of multiple year classes at high density and biomass (50-100 oysters and > 50 g DW m^{-2}). Oysters on these reefs have persisted for more than five decades, contrary to the paradigm that oyster shell accretion cannot compensate for shell degradation of oyster reefs. Sample extrapolation suggests that the reef network was composed of more than 15 million live adult oysters.

Analysis of benthic tray samples identified 66 species of macrofauna (bivalves, crabs, shrimp, worms, tunicates, amphipods, slipper shells, and fish) on the reefs, and on average 75.6 g AFDW m^{-2} and 6356 individuals m^{-2}. Polychaetes (particularly *Alitta succinea*) were most abundant (45.9% of the total number of organisms collected), followed by amphipods (13.7%) and gastropods (9.8%). Macrofaunal density and biomass were positively related to local reef oyster density (Figure 9). Macrofaunal biomass and total density (as well as density of reef resident fish, polychaetes, mud crabs, and mussels) were positively related to live oyster volume, but not with rugosity measurements or salinity. Salinity was negatively related to macrofaunal density.

Restored oyster reefs have the potential to be productive habitats, and this potential varies with salinity. Our results suggest that habitat quality and utilization of reefs will be enhanced when habitat complexity of restored oyster reefs is high (Karp et al. 2018). Restored oyster reefs can thus serve as productive habitats by enhancing a diverse suite of invertebrates that subsequently subsidize upper trophic levels, including commercially valuable finfish and the blue crab.

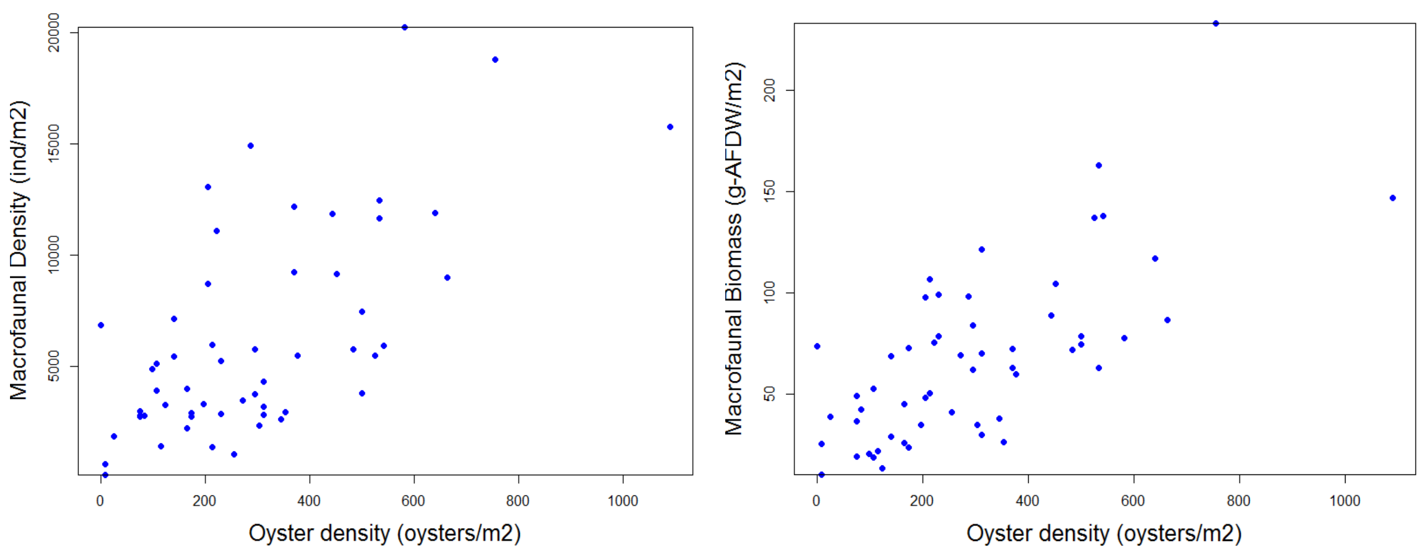

Figure 9. Relationship between oyster density and (left) macrofaunal density and (right) macrofaunal biomass, a strong predictor from the mixed-model analysis.

Table 2. Average estimates of live oyster density and biomass for each reef within the rivers (Lafayette, Lynnhaven, Great Wicomico) in 2015 and 2017. Yellow cells indicate compliance with Fish GIT threshold goal (15 oysters per m^2, 15 g DW per m^2), green cells indicate compliance with Fish GIT target goal (50 oysters per m^2, 50 g DW per m^2).

Tributary	Reef	2015		2017	
		Number per m^2	Biomass (g) per m^2	Number per m^2	Biomass (g) per m^2
Great Wicomico	1	480.40	21.32	145.03	35.54
	2	9.59	3.11	53.54	13.46
	3	297.26	9.15	355.99	93.45
	4	394.74	25.58	660.03	96.22
	8	64.72	21.34	19.71	5.95
	9	226.14	47.24	142.24	36.97
	10	28.77	9.18	64.72	19.39
	11	277.21	54.59	194.83	41.67
	12	426.71	11.89		
	13	977.67	62.01	775.50	90.65
	15	19.18	8.07	22.37	7.82
	16	411.12	45.47	979.66	151.85
Lafayette	1	30.68	10.00	28.77	11.46
	2	124.31	35.99	162.33	104.80
	3	95.89	34.63	79.11	45.09
	4	50.82	17.83	89.04	49.29
	5	150.23	70.18	178.46	144.78
	6	105.48	39.19	220.54	153.64
	7	77.91	32.00	105.48	93.68
	8	121.30	42.76	55.62	69.60
	9	55.94	32.45	57.53	37.04
	10	47.94	33.92	47.94	56.96
	11	56.73	35.84	62.33	60.24
Lynnhaven	BB1	184.24	94.60	347.60	125.46
	BB2	206.16	101.27	209.36	77.24
	BB3	118.26	61.61	131.05	59.31
	LB1	188.58	105.06	63.70	45.81
	LB2	109.37	63.63	145.03	59.90
	LB3	220.54	134.98	60.73	43.04
	LB4	357.98	199.69	258.90	155.83
	LB5	139.04	113.00	1.60	0.15
	UEB	349.99	151.91		

Macrofaunal Communities Discussion

Both macrofaunal community studies addressed spatial variability and found significant effects of oysters on macrofaunal communities, but the spatial scales were different. Kellogg et al. examined variability in the macrofaunal community along a single 7-km river continuum, and Lipcius et al. studied macrofauna in four lower-Bay tributaries along an approximately 100-km reach of the Bay mainstem. Aside from the oyster population assessment conducted by Lipcius et al., similar sampling methods were used in both projects to quantify macrofaunal communities (namely, benthic settlement trays embedded in the reef) relative to oyster abundance and biomass metrics, and a similar suite of macrofaunal organisms was encountered. Additional differences in the two projects were the examination of seasonal effects by Kellogg et al. and habitat-complexity effects by Lipcius et al.

Although both studies sampled restored oyster shell reefs, the restoration methods were not necessarily equivalent. Kellogg et al. worked on reefs that had been planted with spat-on-shell (SOS) three years prior, and Lipcius et al. sampled shell reefs 10 to 15 years old that had been colonized by wild oysters. Due to differences in reef maturity and environmental conditions (e.g., salinity), it is impossible to compare the effect of oyster restoration methodology (planted hatchery SOS vs. natural recruitment on new reefs) on the macrofaunal community. Neither study examined macrofaunal communities on reefs that had been restored with alternative (non-oyster shell) substrate material. A seven-fold difference in macrofaunal productivity has been observed on stone riprap revetments compared to infaunal productivity in soft sediment, with non-oyster macrofaunal diversity and production positively related to oyster production (Seitz et al. 2019).

Most important to oyster restoration is that both studies found that overall macrofaunal biomass increased with oyster biomass (Figure 10). This suggests that if restoration is successful at sustaining elevated oyster biomass, then elevated macrofaunal biomass would be expected. Both oyster and non-oyster biomass are key factors in assessing reef productivity, because they represent the amount of prey tissue available to higher trophic levels. In addition, increased oyster biomass leads to increased biodeposition, which in turn supports deposit-feeding organisms. Because benthic macrofauna form a large proportion of the diet of demersal fish, increased macrofaunal biomass could directly increase production of fish species by expanding foraging opportunities. Thus, relative to habitat management and policy objectives in general, and specific to CBP fish habitat and oyster outcomes, both studies indicate that oyster restoration provides enhanced foraging habitat and associated macrofauna, which implies that increasing the biomass of oysters through restoration activities could provide added fish production benefits. These findings may be useful in supporting ecosystem-based fishery management in the Chesapeake Bay (Chesapeake Bay Program 2018).

A significant component of the Lipcius et al. work was focused on assessment of oyster populations on restoration sites in selected Virginia tributaries, which is directly aligned with Chesapeake Bay oyster restoration policy goals and objectives. Overall, observed oyster densities at most sites exceeded the Fish GIT restoration success target of 50 oysters m^{-2}. This study also showed that in Virginia, settlement of wild oysters on restored sites can sustain elevated oyster densities for long periods of time if restoration sites are designed correctly and are protected from commercial exploitation. High densities and multiple year classes of wild oysters were also observed on higher-salinity unrestored reef habitat that had been protected from anthropogenic disturbance for several decades. This finding was significant because it indicates that native oyster populations can indeed persist for long time periods, which is contrary to the paradigm that oyster shell accretion cannot compensate for shell degradation or disease mortality in lower portions of the Chesapeake Bay.

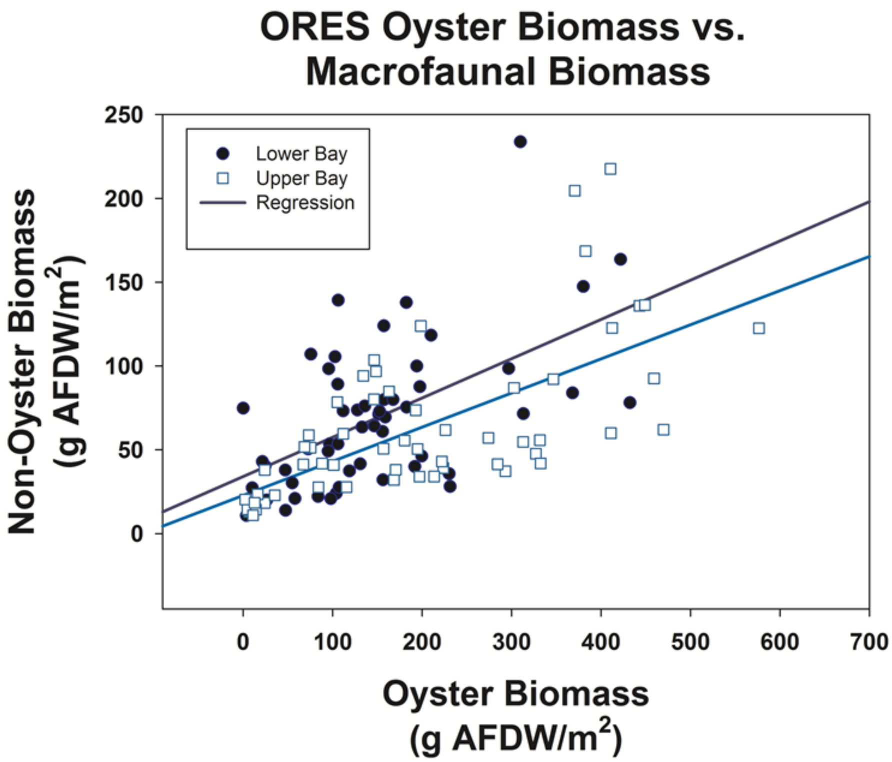

Figure 10. Relationship between oyster biomass and non-oyster macrofaunal biomass with linear regression lines from two studies, lower Chesapeake Bay (filled circles, dark blue line) and upper Chesapeake Bay (open squares, light blue line). Using log-transformed data, regression lines differed significantly by lower vs. upper Bay (General Linear Models and Aikaike's Information Criterion), presumably driven by the overall salinity gradient.

Fish and Blue Crab Communities Research

Fish Utilization of Subtidal Mesohaline Oyster Restoration Sites in the Chesapeake Bay

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This study took advantage of two planned large-scale subtidal restoration projects to assess how fish community composition and abundance may vary on restoration sites and on unrestored reference sites before and after restoration. We hypothesized that after restoration, fish abundance would be greater on treatment sites than on reference sites. Fish were collected at oyster sanctuaries within the Little Choptank and Tred Avon rivers, two mesohaline tributaries on Maryland's Eastern Shore of the Chesapeake Bay.

Methods

Two types of restoration treatment sites were sampled: 1) existing oyster shell bottom planted with hatchery oyster spat-on-shell (SOS restoration) and 2) reefs constructed with alternative substrates (SR restoration) and planted with SOS. Corresponding control sites were: 1) existing shell bottom with no hatchery oysters and 2) hard unstructured bottom with no hatchery oysters. Fish were collected with five different trap types to maximize the diversity of fish species collected. Traps were baited with macerated fish and clams. Five traps connected by a line were considered a single observation unit, and replicate lines were fished on treatment and reference sites sampling sites for 24 hours. A limited pilot study was conducted in 2013 in the Tred Avon River. Full trap sampling began in 2014 at both locations before the onset of restoration activity. Reefs were constructed in 2015 prior to the sampling season, and all treatment sites were planted with hatchery spat-on-shell in 2016 prior to the sampling season. Treatment and control sites were sampled monthly during summer. A total of 544 trapline samples were collected throughout the 2014-2017 study period.

Results

The 2013 pilot study determined that fish trap catch was lowest in May and October, so sampling in ensuing years occurred June-September. Mean salinity during fish sampling ranged from 9.9 to 13.8 PPT. Overall, a total of 10 reef-resident and transient species were collected on restoration sites (Appendix 1). Eighty-five percent of the total catch (1,867 fish) was composed of adult American eel, blue crab, oyster toadfish, and white perch. Blue crab was the only taxon with appreciable numbers of juveniles collected. Relative abundance estimates were generally low and ranged from 0 to 10.0 fish trap set^{-1} (mean = 1.28; se =0.03).

No before/after fish community composition responses to restoration were observed. Responses of species-specific abundance to restoration were mixed for the four dominant species. Overall, fish abundance on SOS restoration sites did not vary relative to before/after or treatment/control effects. We did observe restoration effects for constructed SR reef sites, but the results were inconsistent relative to fish species and location.

American eel abundance varied relative to SR restoration status in the Little Choptank (Kruskall-Wallis test; $p = 0.0202$) with only marginal increases on constructed reefs than on reference sites; abundance did not vary relative to restoration ($p=0.5456$) in the Tred Avon. Blue crab and oyster toadfish abundance varied relative to SR restoration status at both locations ($p \leq 0.0281$), and abundance was generally lower on constructed reefs than on reference sites. When juvenile and adult blue crabs were separated, abundance for both life stages on unstructured SR reference sites was significantly greater ($p \leq 0.0003$) than on constructed reefs in the Little Choptank, but there was no difference ($p \geq 0.2270$) in the Tred Avon. It is possible that for blue crabs and oyster toadfish, the traps themselves may serve as structured habitat on unrestored sites and may be become less attractive when placed on restored reefs. Abundance of white perch did not vary relative to SR restoration ($P \geq 0.3294$) at either location.

To gain insight on structural attributes of oyster restoration, we used multibeam sonar bathymetry data to assess habitat complexity at sample sites. In both the Little Choptank and Tred Avon sanctuaries, habitat roughness for SOS-only reef treatment sites and all reference sites was low and similar (Figure 11). However, unlike SOS treatment sites, for the four SR reefs sites at both locations, the average increase in habitat complexity after reef construction was 1232.2%. For American eel, greater abundance values were associated with greater complexity values (Spearman Rank Correlation; $r = +0.29$; $p = 0.0021$; Figure 12) on SR sites. Conversely, lower abundance was associated with lower complexity for both oyster toadfish ($r = -0.23$; $p < 0.0013$) and blue crab ($r = -0.45$; $p < 0.0001$). White perch relative abundance was generally similar across the range of complexity values ($r = +0.01$; $P= 0.8685$) at experimental sites.

An unintended consequence of the habitat complexity information is that from a structural perspective there were only a small number of restoration sites that differed from unrestored conditions, resulting in a relatively low sample size of four replicate reference sites and four replicate constructed reef treatments at the two locations.

In summary, the response of mobile species to oyster restoration is complex and may vary relative to restoration methodology, location, and by species-specific foraging behaviors or general habitat preferences. Results suggest that even among the benthic-oriented species collected in this study, inherent mobility linked to foraging or other behaviors, and gear selectivity, make habitat and site affinities difficult to quantify.

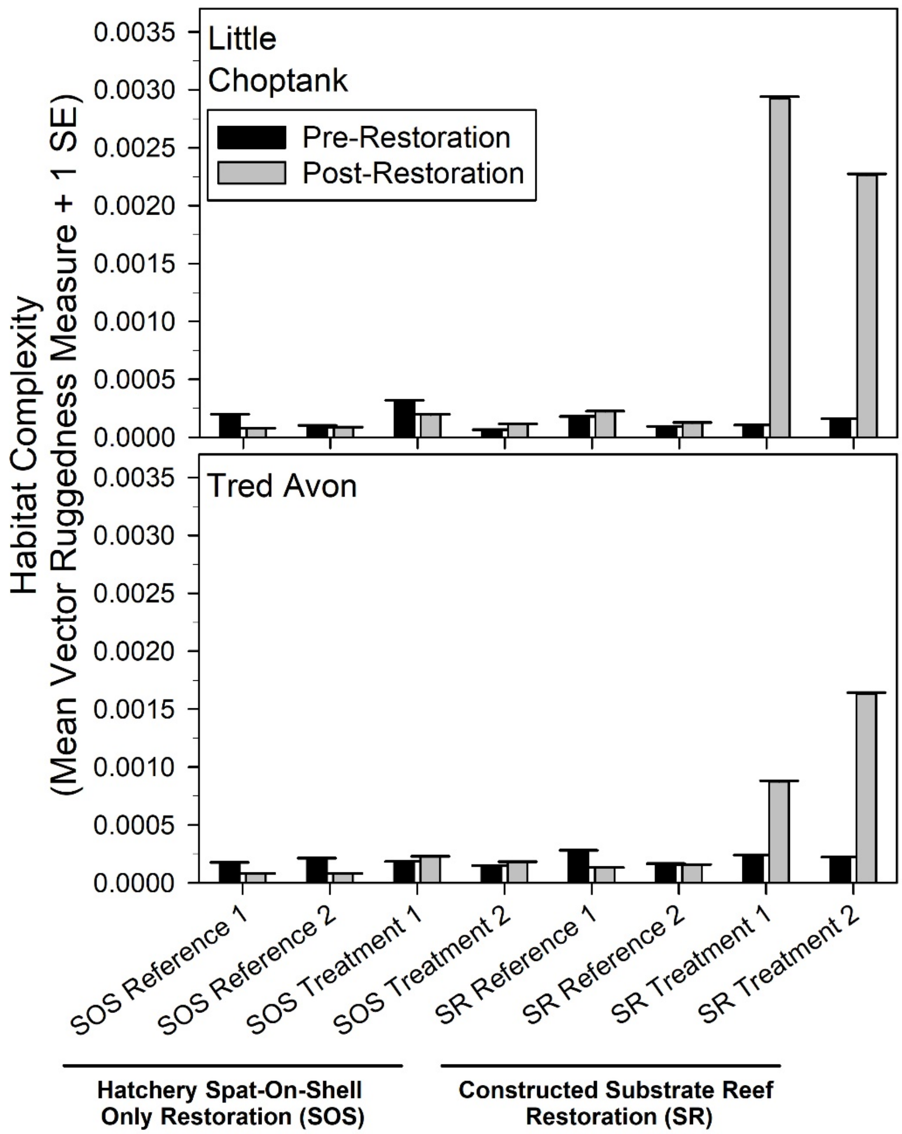

Figure 11. Structural habitat complexity at restoration and unrestored reference sites in the Little Choptank River and Tred Avon River oyster sanctuaries. The Vector Ruggedness Measure was derived from multibeam sonar bathymetry grids. Both Little Choptank Substrate Reef treatments and Tred Avon Substrate Treatment 2 were constructed of stone (152 mm min. dimension). Tred Avon Substrate Reef Treatment 1 was constructed of double crushed mixed shell from commercial seafood processors.

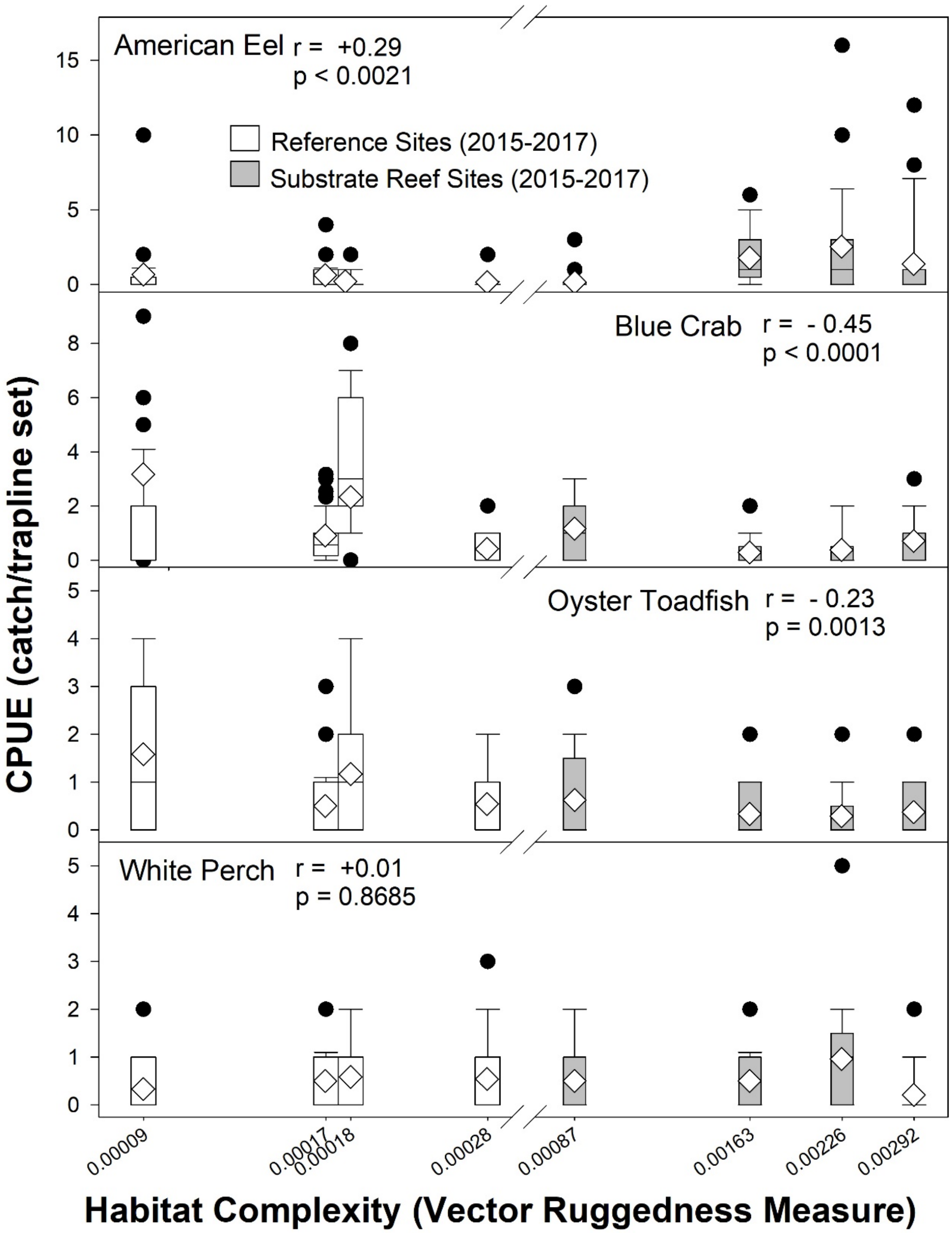

Figure 12. Relative abundance (CPUE) of selected species relative to habitat complexity at constructed substrate reefs and reference sites 2015–2017. Diamond symbols are mean values. Statistical parameters are for the Spearman Correlation test.

Oyster Reef Ecosystem Services: Finfish Utilization and Trophic Linkages

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Our project focused on determining the impacts of oyster reef restoration on finfish in the Harris Creek oyster sanctuary in the Maryland portion of the Chesapeake Bay. As a preliminary step, we examined the utility of using trawls in place of gillnets to sample finfish. The primary focus of our study was to examine patterns in finfish utilization and finfish diets on restored reefs, non-restored reef sites, and adjacent soft sediment habitats. Our study sought to answer two fundamental questions: 1) Are transient fish species found in greater abundance on restored oyster reefs than on non-restored sites or adjacent soft sediment habitats, and 2) Are the fish caught on oyster reefs feeding on the prey species commonly found in oyster reef habitats?

Methods

Small resident finfish were sampled with benthic trays embedded in reefs with low, medium, and high oyster densities in Harris Creek as part of the related macrofaunal study described above. Trawl and gillnet gear comparison sampling occurred in May, September, and October 2015 in Harris Creek and the nearby Tred Avon River oyster sanctuary. Habitat-specific gillnet sampling occurred in Harris Creek, May through October, in 2016 and 2017. Collections were made on 1) restored shell reefs that were planted with hatchery oyster SOS in 2012, 2) unrestored shell reefs, and 3) adjacent non-reef (sand, sand/mud) habitat. White perch and striped bass were selected for diet studies because they are commercially and/or recreationally important species, benthic organisms frequently form a significant portion of their diets, and sample sizes were sufficient to make diet analyses meaningful. For the diet studies, a minimum of 25 fish were measured and weighed in each sample, and guts were excised and preserved for laboratory analyses. All species found in guts were identified to lowest practical taxonomic level and their wet weight was determined.

Results

We found that trawl samples were highly variable and that the diets of finfish caught in trawls tended to be different than those caught in gillnets. In trawl samples, prey taxa associated with oyster reefs were either absent from fish guts, or at orders of magnitude lower than in gillnet samples. These data, combined with the fact that gillnet samples are collected directly from oyster reef habitats rather than from adjacent sites, suggest that gillnet sampling is more appropriate than trawl sampling for determining the effects of oyster reef restoration on finfish abundance and diet.

For small reef resident fish (blennies and gobies) collected in reef-embedded benthic trays, biomass alone was consistently higher in samples with medium and high oyster biomass density. Fish biomass was also significantly higher in fall than in all other seasons. Gillnets collected 12 transient and no reef-resident species on restored oyster reefs. White perch and striped bass were the dominant demersal species collected on reef habitats, and spot was the most frequent species collected on non-reef habitat. Of the species captured, only white perch tended to have higher relative abundance in reef habitats than in adjacent non-reef habitats. Using only data from shell-reef sites (restored and unrestored), we found that restoration status had no significant effect on relative abundance of white perch or striped bass.

The diets of both striped bass and white perch differed from those commonly reported for these two species in the Chesapeake Bay. In contrast to previous studies of striped bass diets in the Chesapeake Bay, fish prey commonly accounted for <20% of their diet in Harris Creek. Mysids formed a substantial part of the diet of smaller (≤ 200 mm) striped bass but were rarely found in larger fish (> 200 mm). In contrast, blue crabs were a significant part of the diet of larger striped bass but not of smaller ones. White perch in Harris Creek commonly consumed the sea squirt, *Molgula manhattensis,* a species reported as part of in their diet. White perch diets also relied heavily upon other species commonly found on oyster reefs including mud crabs, mussels, gobies, and blennies (Figures 13 and 14). Overall, our data suggest that restored oyster reefs provide significant prey resources for white perch, and may alter the foraging habits of striped bass.

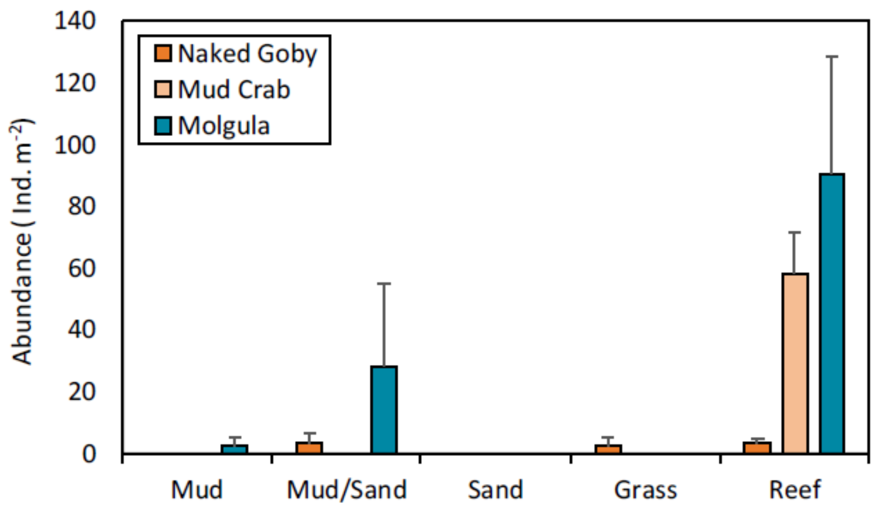

Figure 13. Mean abundance of selected reef-resident prey species across habitats in Harris Creek in October 2017. Error bars represent one standard deviation.

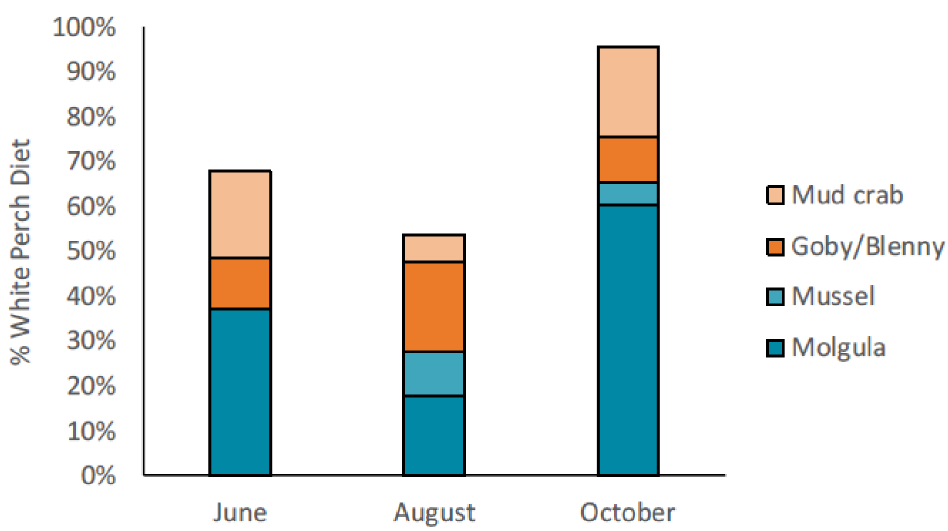

Figure 14. Seasonal diet composition of white perch based on data from 2016 and 2017.

Ecosystem Services of Restored Oyster Reefs in the Lower Chesapeake Bay: Importance for Blue Crabs and Finfish

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This project examined the importance of restored oyster reef habitats for finfish and blue crabs in tributaries of the lower Western Shore of the Chesapeake Bay. Our specific objectives were to 1) examine juvenile blue crab survival on oyster reefs, 2) quantify finfish diet and use of oyster reefs and non-reef habitats, and 3) investigate scavenging of oysters by reef predators under the hypothesis that oyster carrion move up the food web to higher trophic levels rather than being decomposed by bacteria.

Methods

Relative survival of juvenile blue crabs was quantified on structured oyster reef habitat and unstructured soft-bottom in the York River, Virginia, in the summer of 2017. In this field experiment, juvenile crabs were tethered to the bottom at shallow subtidal sites, and an underwater camera system was used to record predation activity during 24-hour trials.

Relative abundance and finfish diet metrics were determined from multi-mesh experimental gillnet samples on constructed oyster shell reefs and unstructured bottom in the Lynnhaven River. Fish were sampled 2-3 times per month from April to October 2016. Three sites were fished simultaneously (1 net per site), and the order in which sites were visited was randomized on each sampling date. Nets were left to soak approximately 2 hours. We recorded the length and weight of all individuals captured, and the stomachs of a subset of individuals (5-10 individuals per species per gill net) were preserved for laboratory diet analysis. To estimate daily consumption, we conducted two 24-hour sampling events. Multiple gill nets were deployed at one representative oyster reef and one representative control site. Gill nets were set and checked repeatedly within 4-hour periods for approximately 24 hours. Upon each net retrieval, non-filter-feeding fishes were collected and stored on ice for later gut content analysis. Consumption rates were modeled from stomach fullness data and literature based gastric evacuation parameters.

To test the role of scavengers in dead oyster consumption, we created a study emulating different methods of death to oysters and examined scavenger feeding behavior using an underwater four-camera video system. The dead oyster treatments were 1) crushed shells and 2) unbroken but gaping shell valves. For both treatments, intact oyster tissue was retained with the shells.

Results

Juvenile blue crab survival was more than three-fold higher in oyster reef habitat (52.6%) compared to bare sand (15.0%). The major successful predators were the northern pufferfish in the oyster reef trials and adult blue crabs in the sand trials. Juvenile crab survival also tended to increase with size, as expected. The high survival rate on oyster reefs suggests that reefs provide refuge from predation pressure. With continued seagrass depletion in the Chesapeake Bay, restored oyster reefs could provide an alternative nursery to sustain blue crab populations.

In the Lynnhaven River fish sampling, the most abundant benthic-feeding fishes were spot (*Leiostomus* *xanthurus*), silver perch (*Bairdiella chrysoura*), and Atlantic croaker (*Micropogonias undulatus*). Overall catch of these species in oyster reef habitat was reduced relative to unstructured bottom, but species-level dietary responses to habitat type varied. For example, benthic prey dominated the diet of all three species in both habitats (>75% by weight), and prey items enhanced by restored reefs contributed prominently to silver perch diet (30% by weight), but six times less for spot (< 5% by weight; Figure 15). The estimated consumption rate of silver perch foraging in oyster reef habitat significantly exceeded that in unstructured bottom habitat, whereas other fish species were unaffected. Restored oyster reefs act as valuable foraging habitat for silver perch (Figure 15), and promote a key trophic link in coastal systems. Estimating enhancement of fisheries production by reefs requires considering species-specific trophic dynamics and habitat use.

In experiments examining video footage of oyster scavenging, there was a similar suite of scavengers for every trial regardless of oyster size or treatment. The most common scavengers were naked gobies (*Gobiosoma bosc*), striped blennies (*Chasmodes bosquianus*), feather blennies (*Hypsoblennius hentz*), mud crabs (*Eurypanopeus depressus* and *Panopeus herbstii*), blue crabs (*Callinectes sapidus*), and eastern mud snails (*Tritia obsoleta*). Gobies were always the first species to arrive at a trial, closely followed by blennies, mud crabs, and snails. Blue crabs were consistently the last species to arrive and consumed the most total oyster tissue. In crushed oyster treatments, gobies, blennies, and mud crabs typically tore off small pieces of oyster flesh, and when blue crabs appeared, they usually consumed the remaining flesh. In gaping oyster treatments, gobies, blennies, mud crabs, and snails would approach gaping oysters but were unable to open the shell. Nearly all gaping trials required a large blue crab to facilitate oyster consumption by smaller scavengers. With only a few exceptions, total trial duration means indicated that oysters were generally consumed within two hours for gapers and under half an hour for crushed oysters. In opposition to the paradigm that oyster carrion falls to the detrital pool, dead and dying oysters are consumed within one day (or less) by scavengers. This has major implications for analyses of the Chesapeake Bay food web. Consumption of dead and dying oysters by fish, crabs, and snails demonstrates that oyster reefs can significantly enhance blue crab and finfish production at higher trophic levels.

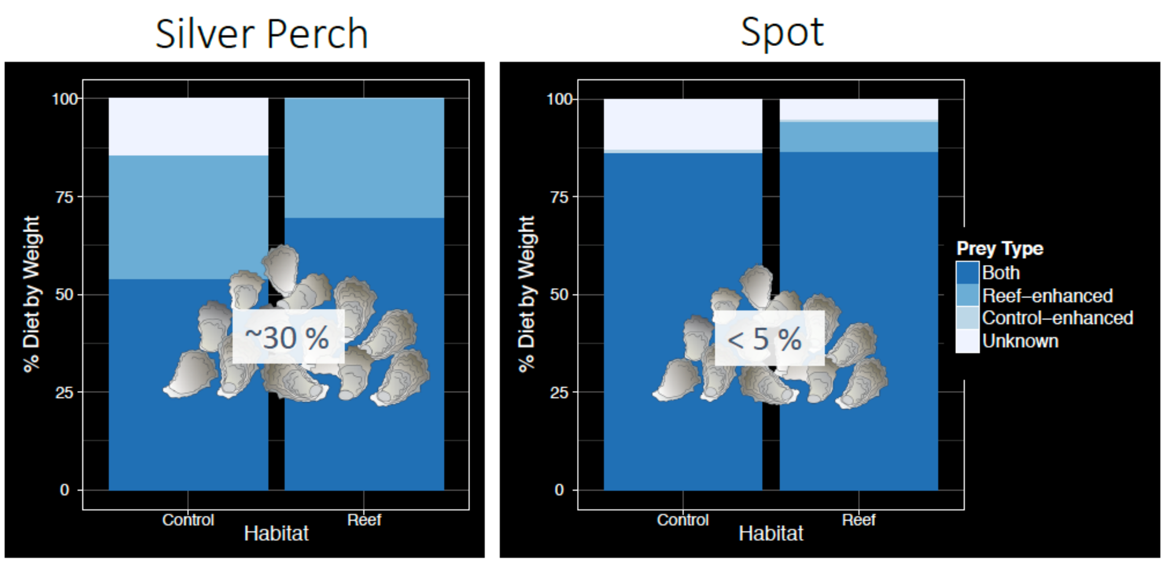

Figure 15. Percent contribution by weight of prey-habitat categories to the diet of silver perch *(Bairdiella chrysoura)* and spot *(Leiostomus xanthurus),* estimated from stomach content data taken during peak feeding hours (1 a.m.–9 a.m.; 24-hour survey). 'Both' indicates prey types found in both habitats types; 'Reef-enhanced' indicates prey types found in higher abundance or biomass on oyster reefs compared to unstructured control bottom; 'Control-enhanced' indicates prey types found in higher abundance or biomass in unstructured control bottom. 'Unknown' used for unidentified material with uncertain habitat origin.

Pathways to Production: An Assessment of Fishery Responses to Oyster Reef Restoration and the Trophic Pathways That Link the Resource to the Reef

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Oyster reefs throughout the Chesapeake Bay watershed make up a small fraction of the benthic habitat they once covered. This has an obvious negative impact on the oyster fishery but also reduces other ecosystem services supplied by robust reefs. Our research was designed to understand the relationship between constructed/restored reef habitats and fish communities. Our objectives were to document changes in fish diversity, density, size, and diet relative to restored oyster reef habitat. Quantifying impacts of oyster restoration on fish community parameters would benefit the policy makers and managers that strive to manage and protect our resources.

Methods

A combination of traditional and novel approaches to data collection was used to assess fish community dynamics associated with different habitat types. Benthic fish traps and multipanel gillnets were used to assess fish diversity and density on three different restored reefs, off-reef habitats (unstructured habitat near the associated reef habitats), and outside habitat (unstructured habitat outside the reef complex). Restored reefs were constructed from various combinations of stone and oyster shell rubble, reef balls, and shell mounds. Three unbaited fish traps containing oyster shell substrate were set for two weeks on the different habitat treatments. Multipanel experimental gillnets were set on the habitat treatments for three hours during day and night periods approximately every three weeks from April–October, 2015–2017 (n=84 gill net sets).

Captured fishes were identified, weighed, and measured before release or processing. Hydroacoustic data were collected (same site locations) to acquire a better understanding of fish density variation among habitat types and during day and night conditions. Hydroacoustic density data and the gillnet species composition data were analyzed to assess species structure, diversity, and abundance on and off restored oyster reefs. An additional 137 hydroacoustic sites were randomly selected to assess fish density as it relates to distance from reef habitat. Trophic assessments were made from a subsample of net-captured fishes representing different feeding guilds (planktivores, benthivores, and piscivores). Stable isotope analysis was also performed on fishes and decapods to assess variation in carbon source and trophic levels within the oyster reef community.

Results

Benthic fish trap results indicated that relative abundance of reef-resident fish and total organisms (inclusive of crabs and shrimp) was significantly greater on restored reef habitats than either of the non-structured habitats (off-reef and outside-reef complex). On-reef fish diversity was significantly greater than the fish diversity in off-reef and outside-reef habitats. Numerically, mud crabs, naked gobies, blue crabs, silver perch, and oyster toadfish made up 87% of the total trap catch.

Southern kingfish was the only demersal species that showed significant abundance differences between habitat types, being found in higher numbers on unstructured habitat. Fish relative abundance from gillnet samples did vary significantly on a diel cycle, with greater catch during night-time sets. Species richness was highest on reef habitat (23 species), followed by off-reef (20 spp) and outside-reef (16 spp). Reef habitat had seven unique species associated with it, while off-reef habitat had four, and the outside-reef habitat had one (Figure 16). However, the three habitat types shared 14 species, demonstrating similarity in the overall fish community.

Shannon-Weiner diversity index from gillnet samples varied significantly by habitat type and temporal period. The greatest diversity of fishes was observed on outside-reef complex sites followed by restored reefs and off-reef sites. Nighttime samples had the greatest species diversity at all habitats, and the greatest difference between night and day samples was observed on restored reefs. Numerically, menhaden and Atlantic thread herring composed 79% of the total gillnet catch. For the non-clupeid species, striped bass, Atlantic croaker, bluefish, spot, and southern kingfish composed 81% of the catch. Relative abundance of large and small (total length </> 46 mm) hydroacoustic targets did not vary relative to temporal period or by habitat type. However, proximity analysis suggests a higher abundance of large acoustic targets within the reef complex compared to outside.

Of the 599 gillnet caught specimens, 25% had empty stomachs. Of stomachs containing prey items, 39% contained fish, 34% detritus/sediment, 11% crustaceans, 9% polychaetes, 5% bivalves, and 2% contained miscellaneous non-prey material. Fish caught on unstructured habitat had approximately the same percentage of empty and full stomachs, whereas more than 60% of fish caught on reef habitat had empty stomachs. Overall, identification of gut contents (especially fish tissue) was difficult to resolve due to variable stages of digestion. This increased the difficulty in forming the direct connection from the many available reef residents (gobies, blennies, etc.) to the predatory fishes that may frequent reef habitats. Species containing items commonly inhabiting oyster reefs (mud crabs, mussel, polychaetes) include Atlantic croaker, black seabass, bluefish, cobia, spadefish, and striped bass. All of the bluefish, striped bass, and cobia with reef-associated items consumed were in the juvenile/subadult size range.

Stable isotope analyses suggest there are at least two major sources of carbon (C) in the trophic pathway. The close proximity of piscivores to planktivores ($\delta 13C$) suggest a shared organic matter source of likely autochthonous primary productivity. Signatures from crabs, shrimps, and benthivores suggest other pathways that may include an allochthonous C source from upriver or adjacent wetland/marsh source, and/or from an oyster reef source.

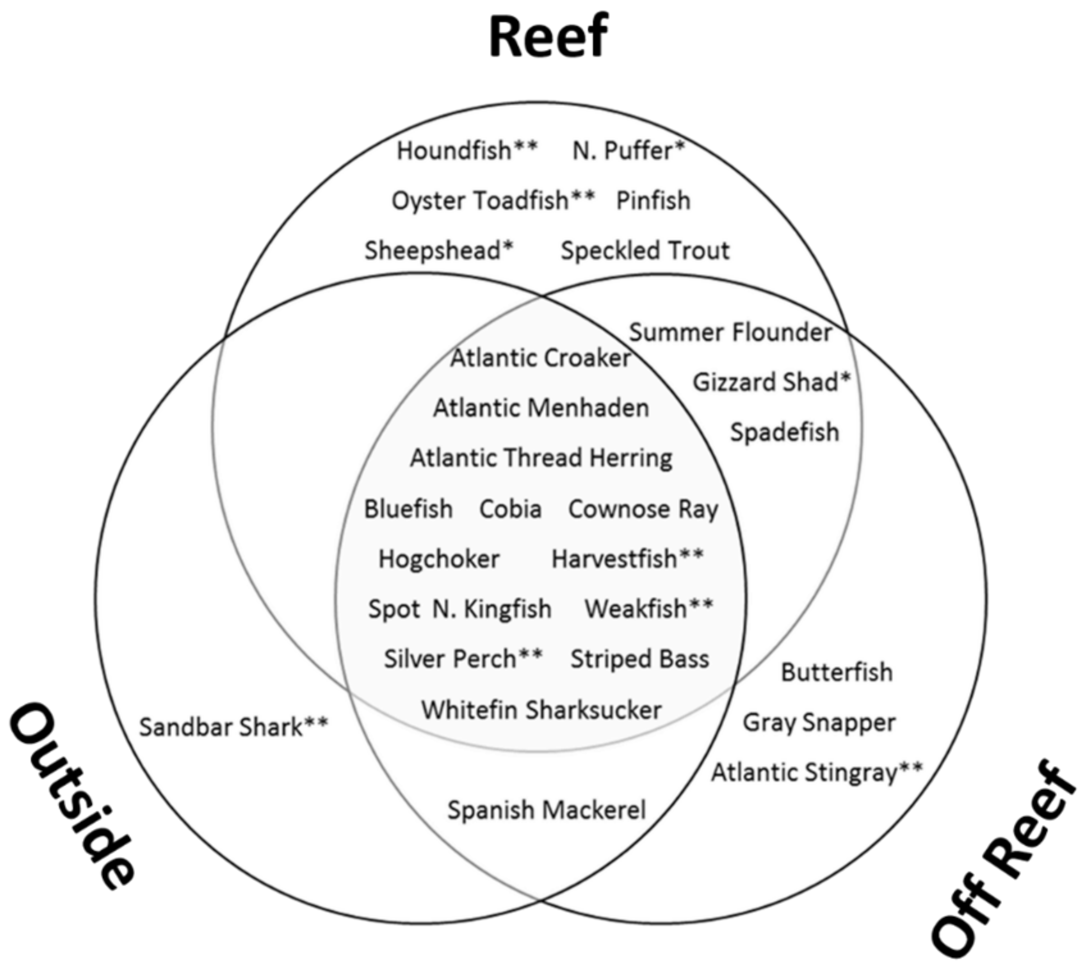

Figure 16. Species composition from gillnet collections by habitat type.
*Denotes species only caught during the day.
**Denotes species only caught at night.

Application of Dual-Frequency Identification Sonar to the Study of Oyster Reef Ecosystem System Services

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The value of oyster reefs as habitat for other species, including commercially and recreationally important finfish and crabs and the forage species they depend on, is a critical ecosystem service that remains poorly understood in the Chesapeake Bay. Furthermore, assessing the habitat quality of oyster reefs in comparison with fished reefs and unrestored sanctuary reefs is critical to understanding the effectiveness of oyster restoration. Several studies have focused on assessing the value of oyster habitat using traditional fisheries sampling methods. Our aim was to apply a different technology, high-resolution Dual Frequency Identification Sonar (DIDSON acoustic camera), to conduct 1) a study of fish trap encounter and capture efficiency rates and 2) a before-after, control-impact (BACI) study of trap-independent finfish and crab abundance on experimental restoration sites. We also developed a qualitative index of oyster reef habitat quality from photographic images and compared habitat metrics on restored and unrestored locations inside and outside of three oyster sanctuaries and in one harvested tributary in the Choptank River Complex, Maryland.

Methods

We used the DIDSON system to record encounters of finfish and blue crabs with baited black sea bass traps in the Tred Avon River oyster sanctuary, Maryland. We conducted 2.5-hour daytime and 24-hour deployments. Once traps were retrieved, the contents were counted and measured. For DIDSON videos, we recorded the rate of occurrence of fish >15 cm total length and crabs >12.7 cm carapace width (individuals hour $^{-1}$ within the video frame), the trap encounter rate (individuals hour $^{-1}$ passing within 0.5 m of the trap), the trap entrance rate (individuals hour^{-1} entering the trap), and the capture efficiency (percent of individuals entering the trap that remained when the trap was retrieved).

For trap-independent studies of restoration sites, the DIDSON was deployed monthly from June to October 2015–2017 to record finfish and crab abundance on Tred Avon River restoration reefs and control sites. Restoration treatments included two DIDSON replicates at 1) reefs constructed of alternative substrates and 2) natural shell reefs, both planted with hatchery oyster spat-on-shell. Corresponding control treatments included two replicates of 1) unstructured sand/mud sites and 2) natural shell reefs, both with no planted oysters. Substrate reefs were constructed in 2015 prior to data collection, and all restoration sites were planted with oysters in 2016. Two replicate DIDSON recordings were conducted on each of the eight sites per month.

Qualitative video-based habitat scoring was conducted at the Harris Creek oyster sanctuary, where restoration is complete; at the Little Choptank River and the Tred Avon River sanctuaries, where restoration is in progress; and at Broad Creek, a non-restored but productive commercial harvest area. In each tributary, stratified-random sampling was used to select 25 sites expected to be naturally occurring oyster reef and 25 sites expected to be anthropogenic oyster reef based on available oyster habitat GIS layers. With this sampling strategy, the survey was not biased by only selecting restored reef sites. For example, the Harris Creek sites were located both inside and outside the sanctuary boundary, and on both restored and unrestored habitat. Video and still imagery were collected with three frame-mounted

GoPro cameras. Sites were assigned a habitat score of 0-3 (Figure 17) based on the percent cover of hard substrate and fouling organisms, and the height of hard substrate observed in the imagery.

Results

The DIDSON system provided novel data on finfish and crab behavior and abundance that we could not have obtained using other gear types, including much higher numbers of fish and crabs than were captured in traps. There was a positive relationship between occurrence rate and trap encounter rate, but trap catch and capture efficiency were very low in both the 2.5-hour and 24-hour deployments. The rate at which individuals visible in the camera frame encountered the trap was positive for both fish (r^2=0.50) and crabs (r^2=0.60), suggesting that trap encounter rate was associated with the local abundance of fish and crabs. Fish (r^2=0.61), but not crabs, also entered traps more frequently when they were more abundant. Nothing was collected in the 2.5-hour daytime deployments, and for the 24-hour deployments, only one white perch of 13 fish (8%) and one blue crab of 16 crabs (6%) were observed entering a trap remained when the trap was fished. These results suggest that black sea bass traps provided relative abundance data that reflected the local abundance of fish and possibly crabs, but catch rates and capture efficiency were low for species occurring in the Tred Avon River.

There were no consistent patterns in DIDSON video counts of fish and crabs relative to oyster restoration in the Tred Avon. Counts from both constructed substrate reefs and natural shell reefs with spat-on-shell were generally similar to control sites during all years. Seasonal patterns were observed, however, as counts on all sites and years were generally greatest July through September. Although finfish species were not easily identified in the sonar data, GoPro camera deployments indicated that the most common fish species >15 cm total length observed were striped bass, white perch, and northern puffer (especially in 2015). The lack of relationship between fish and crab abundance and restoration may be related in part to minimal differences between habitat structure of restored and unrestored reefs at the study site (see Bruce et al.) and the lack of reef-resident fish recorded in sonar videos.

Findings from our work with the DIDSON acoustic cameras indicated that demersal finfish and blue crabs are using restored and natural oyster reefs, but are also using adjacent habitats such that there are not strong patterns in abundance relative to habitat type. Nevertheless, methods are valuable for documenting the abundance of commercially and recreationally important species in a way that is independent of the biases inherent in trap and net sampling.

Video-based habitat scoring demonstrated that Harris Creek had the highest percentage of randomly selected sites with high-quality reef habitat (a score of 3; Figure 18) with 40%, followed by the Little Choptank (14%), Tred Avon (6%), and Broad Creek (2%). Overall, habitat quality scoring varied substantially within each tributary, such that 31 sites had the highest-quality habitat score of 3, 34 scored a 2, 97 scored a 1, and 36 scored a 0. These results clearly show that a fully restored sanctuary tributary (Harris Creek) contains substantially more high-quality oyster reef habitat than harvest areas (Broad Creek) and partially restored sanctuaries (Little Choptank and Tred Avon). Additionally, the number of sites with vertical reef structure at least as tall as the shell height of a harvestable oyster was 20 times higher in the Harris Creek sanctuary than in the adjacent commercially fished Broad Creek.

The rapid qualitative assessment method for oyster reef habitat quality we developed has great potential to inform monitoring and management of oyster reefs in the Chesapeake Bay and in other regions with subtidal oysters. Using these techniques, we were able to detect clear differences in habitat-quality-based oyster reef restoration and fishery management status, but additional applications could include documenting temporal changes, new site selection, more efficient monitoring effort, and communication of actual ground conditions.

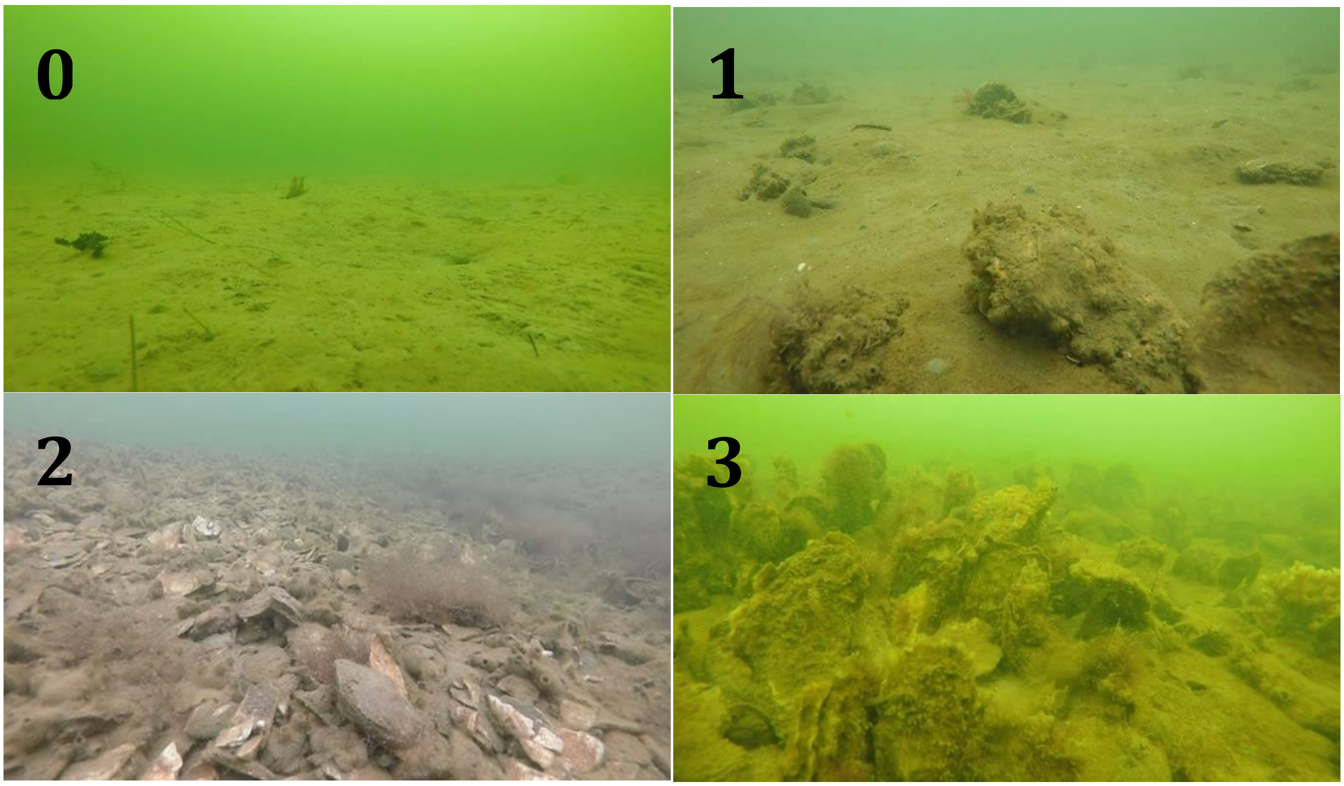

Figure 17. Examples of qualitative benthic habitat scoring based on underwater imagery. Scores are numerals in upper left corner of these images.

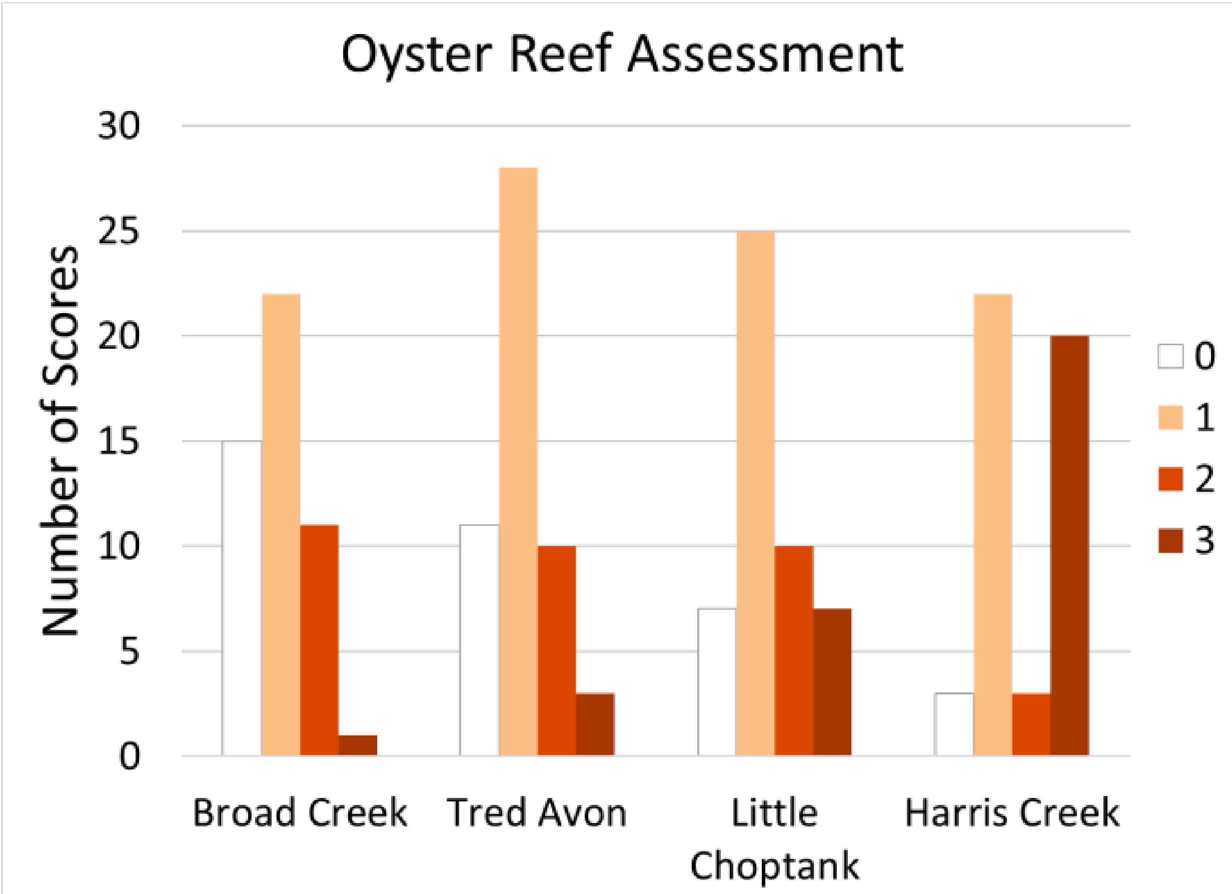

Figure 18. Qualitative benthic habitat scores for one fished tributary (Broad Creek) and three tributaries containing oyster sanctuaries in the Choptank River Complex, Maryland, in 2017. Note that only Harris Creek had fully constructed restored reefs at the time of sampling.

Fish Communities Discussion

There is considerable management value in understanding the affinity of fishes to specific habitat types and how vital rates and fish production may vary relative to habitat type (NMFS 2010, Chesapeake Bay Program 2019). Documentation of the relative quality of different habitats can support protection or conservation designations and restoration activities, and can be incorporated into regional stock assessments. All five of the studies presented here examined fish utilization of oyster restoration sites relative to other habitat types. As a preliminary step to understanding the value of oyster habitat relative to fish production, three studies examined how fish diets may be linked to restored oyster reefs.

Oyster reef sampling collected reef-resident and transient species. Resident species use reefs for foraging, reproduction, and as nursery habitat; the most frequently collected taxa were naked goby, oyster toadfish, skilletfish, and striped blenny. Transient species primarily use reef habitat for foraging; the most frequent taxa collected on reefs were Atlantic croaker, blue crab, silver perch, spot, and striped bass. Although sampling was not focused on collecting early life stages, some juveniles were collected; these included black seabass, cobia, gray snapper, summer flounder, and white perch.

There were spatiotemporal scale differences among the different studies. Locations of fish studies were distributed throughout the long axis of the Chesapeake Bay (Figure 2). Of the six study sites, Harris Creek, Little Choptank, Piankatank, and Tred Avon rivers are in the mesohaline zone, and the York and Lynnhaven rivers are in the polyhaline zone. Spatial variation in fish abundance or diet relative to oyster restoration was not a specific focus of these studies; however, Bruce et al. observed different abundance responses to restoration at two different locations. Restoration reef age was not a specific response variable in these studies, but age did vary within and among them. Among studies, restoration site age ranged from 0 years (pre-restoration) to up to 10 years post restoration. Kellogg et al. observed significant and complex interactions among seasonal, annual, and restoration (restoration/control) effects, but aside from generally greater white perch catch rates in September and October samples, there were no consistent seasonal patterns in abundance of other species sampled. Bruce et al., Lipcius et al., and Ogburn and Hines generally observed maximal fish abundance in mid- to late-summer samples.

All five studies compared relative abundance of fishes on restored reefs and on unrestored sites. Using benthic tray sampling on control sites and restoration sites with different oyster densities, Kellogg et al. observed that numbers of small reef-resident fish generally increased with live oyster abundance, indicating that if restoration successfully increases oyster numbers, then reef-resident species will also increase. McIninch, using small-mesh fish traps containing oyster shell, also observed greater abundance of small reef-resident species on restoration reefs than on control sites.
For larger transient fish sampled with traps, gillnets, and acoustics, there was no strong and consistent demonstration of greater abundance on restoration reefs than on unrestored control sites. Variability in the response to restoration may depend on habitat preferences of different fish species, season, restoration type, location-specific environmental conditions, and sampling gear selectivity. From gillnet samples, Kellogg et al. observed that white perch had the most consistent pattern of enhancement associated with oyster reef restoration. For all months except May, white perch catch per unit effort (CPUE) tended to be higher for on-reef samples than for off-reef samples with significantly higher values in both September ($p = 0.001$) and October ($p = 0.029$). No other species showed any consistent trends across sampling periods. Also using gillnets, Lipcius, Seitz, and Pfirrmann observed overall reduced catch on restoration sites with some species-specific variation, and McIninch only observed

significance with one species, and it had a negative response to restoration. Bruce et al., using baited traps, did not find any differences in abundance between natural shell reefs restored with hatchery oysters and control sites; however, for constructed substrate reefs in two different tributaries, significant positive, negative, and neutral responses to restoration were observed for different species at one location but not the other.

Positive results from oyster restoration were most visible in the increased foraging of some epibenthic fishes on restored reefs compared to reference conditions (Table 3). Diet and predation studies indicate that the trophic value of restored reefs may also vary by species. Restored reefs support dense populations of both mud crabs and small reef-associated fish including gobies and blennies. In Harris Creek, mud crabs tended to account for a greater portion of the diets of both striped bass (19.10%) and white perch (17.90%) caught on restored oyster reefs those caught adjacent to reefs (0.00% and 2.96%, respectively; Table 3). In addition, gobies and blennies accounted for 14.50% of the diet of white perch caught on reefs compared to 0.96% for fish caught adjacent to the reef (Kellogg et al.). However, due to high variance in the data and the need to account for the number of comparisons made (i.e., Bonferroni correction), these differences were not statistically significant. In the Lynnhaven River, Virginia, diets of silver perch were linked to restored reefs, as silver perch on reefs consumed more than 10 times more smaller fish than did silver perch in nearby unstructured habitats; they consumed snapping shrimp on reefs but none in unstructured habitats (both fish and snapping shrimp are reef-associated prey) (Table 3). However, diets of spot and Atlantic croaker were not strongly linked to reefs, as Atlantic croaker fed on prey unassociated with reefs, e.g. polychaetes, in equal percentages in both reef and unstructured habitats (Table 3). Estimated size of fish, stomach fullness of silver perch, and daily consumption rates of silver perch were also greater on reefs than on nearby unrestored control sites, suggesting that oyster reefs may increase foraging of important fisheries species.

Controlled experiments suggest that oysters themselves may support reef community production, as blue crabs and reef-resident fish species rapidly consume dead oysters, and juvenile crabs survive better on reefs than unstructured habitats. A survival rate of juvenile blue crab that was three times higher on oyster reef habitats compared to nearby unstructured habitats suggests that reefs have the potential to serve as predation refuges for juvenile blue crabs, as reefs include physical habitat complexity. Thus, as an alternative to seagrass, oyster reefs could provide an alternative nursery habitat for juvenile blue crabs, expanding the ecosystem services provided by oyster reefs.

These studies demonstrate that quantifying the relative value of restored oyster reefs as fish and crab habitat can be accomplished for small reef-resident species but generally not for transient species. For this reason, habitat-focused management objectives for larger commercial species may not be fully realized by this work. Fish species, functional groups, and life stages may interact with habitat in different ways, and fish sampling gears are notoriously biased (Biro 2013) relative to these elements. Furthermore, sampling methods and experimental designs that successfully quantify habitat utilization by a suite of fishes may not necessarily provide adequate estimates of trophic parameters and vice versa. Species of commercial or recreational interest are usually generalists in their foraging habitats, and this makes linking reef prey production to fish diet and production especially problematic.

Overall, these studies suggest that future work should focus on specific taxa, functional groups, or life stages and use sampling methodologies with the fewest biases to address the particular research question.

Table 3. Fish Communities Discussion. Percent contribution by weight of fish gut contents for top 2 or 3 fish species collected at restored reef sites compared to either adjacent unstructured sites (50-200 m distant, upper Bay study), or nearby unstructured bottom (> 750 m distant; lower Bay study). Upper Bay fish were collected monthly May–October 2016 and 2017, whereas lower Bay fish were collected monthly April–October 2016 (modified from Pfirrmann & Seitz 2019). Bold values indicate substantial differences by habitat (e.g., the %weight of that prey type in one habitat was outside of the 95% confidence interval for the %weight of that prey type in the other habitat).

	Upper Bay: Harris Creek, MD				**Lower Bay: Lynnhaven River, VA**					
	Striped Bass		***White Perch***		***Silver Perch***		***Spot***		***Croaker***	
Prey Type	*Rest Reef*	*Adj Unstr*	*Rest Reef*	*Adj Unstr*	*Rest Reef*	*Near Unstr*	*Rest Reef*	*Near Unstr*	*Rest Reef*	*Near Unstr*
Crustaceans										
Amphipods/Isopods	0.01	6.35	0.95	1.75	0.00	**21.77**	0.10	0.01	0.00	0.00
Blue Crabs	22.10	43.10	6.84	0.00	0.00	**6.35**	0.00	0.00	0.00	**2.50**
Mud Crabs	19.10	0.00	17.90	2.96	0.00	0.00	0.00	0.00	0.00	0.00
Mysids	0.19	0.11	2.63	3.07	4.40	**35.75**	0.71	0.59	0.00	0.01
Snapping Shrimp	0.00	0.00	0.00	0.00	**21.90**	0.00	0.00	0.00	0.00	0.00
Other Shrimps	0.02	0.00	0.00	0.00	0.27	**3.23**	0.00	0.00	**3.73**	0.00
Other/Unknown	1.55	0.00	1.27	1.56	5.46	3.61	**6.11**	2.16	0.00	0.00
Fish										
Bay Anchovy	10.10	5.31	0.25	0.00	NA	NA	NA	NA	NA	NA
Gobies/Blennies	5.73	10.20	14.50	0.96	**2.82**	0.00	0.00	0.00	**0.35**	0.00
Other/Unknown	24.30	10.00	5.58	1.15	**11.27**	1.39	**2.00**	0.00	2.39	2.84
Mollusks										
Various	5.83	6.19	9.32	5.18	0.00	0.00	0.36	**0.89**	14.60	**30.78**
Tunicates										
M. manhattensis	4.06	0.01	35.10	49.20	0.00	0.00	**7.54**	0.00	0.00	0.00
Worms										
Polychaetes	7.09	18.70	2.88	34.10	**53.89**	13.58	77.87	83.56	67.05	60.98
Other										
Other/Unknown	0.00	0.14	2.86	0.01	0.00	14.32	5.31	**12.80**	11.89	2.89

Rest = Restored
Adj Unstr = Adjacent unstructured habitat
Near Unstr = Nearby unstructured habitat
NA = Data not available because Bay Anchovy were included in the "Fish - Other & Unknown" category.

Ecosystem and Economic Modeling

Estimating Ecological Benefits and Socioeconomic Impacts from Oyster Reef Restoration in the Choptank River Complex, Chesapeake Bay

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Award period: January 2017–November 2018
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The objective of this project was to explore potential changes in commercial fisheries harvest and regional economic impacts resulting from large-scale oyster reef restoration efforts, within the context of alternative policy options for managing these new oyster reefs. This work focuses on three Maryland tributaries initially chosen for large-scale oyster restoration—Harris Creek, the Little Choptank River, and the Tred Avon River. An ecosystem-based trophic (i.e., food-web) model was developed and 15-year projections were run under management policies that range from preserving the prohibition on oyster harvest in the restored areas to opening these areas to harvest leading to the oyster population returning to prerestoration levels. For each policy, estimated commercial fisheries harvests are converted into dockside revenues. These revenues are then used in regional economic impact modeling to generate key economic impact measures. This enables a predictive analysis that explores the effect of different management approaches on seafood harvests and regional economic impacts.

Methods

Ecopath with Ecosim (EwE) software was used to develop a trophic model that included the main producers and consumers, including commercial seafood harvesters as top consumers. The EwE software uses a mass-balance approach to estimate group productivity, and accounts for predator-prey interactions along with fishery removals.

The region modeled (Figure 19, inset hashed area) includes the areas (445.0 km^2) where most natural oyster settlement has historically occurred in the lower Choptank River. Ecopath was used to estimate a snapshot of the trophic flows (Figure 20) and this balanced model was used as a starting point for Ecosim scenario simulations.

Commercially harvested species in the model include American eel, Atlantic croaker, Atlantic menhaden, blue crab, eastern oyster, striped bass, catfish (channel, bullhead, and white combined), gizzard shad, and white perch. Twelve gear-specific commercial fisheries were modeled based on occurrence in Maryland Department of Natural Resource catch records (2006-2015). These included the trotline, eel pot, pound net, gillnet, oyster (power dredge, skipjack, hand tongs, dive), and clam (bait) fisheries.

Seafood harvests were estimated for those groups targeted by commercial fisheries. Landed weight was based on 2006 Maryland Department of Natural Resource landings (unpublished data, C. Lewis, MD DNR) corresponding to the start of the modeled timeframe. Landings dollar value was based on 2015 data for all species. Average price/pound was calculated for each fishery by summing the average price by species weighted by the proportion of each species caught in that gear over a 10-year span (2006-2015).

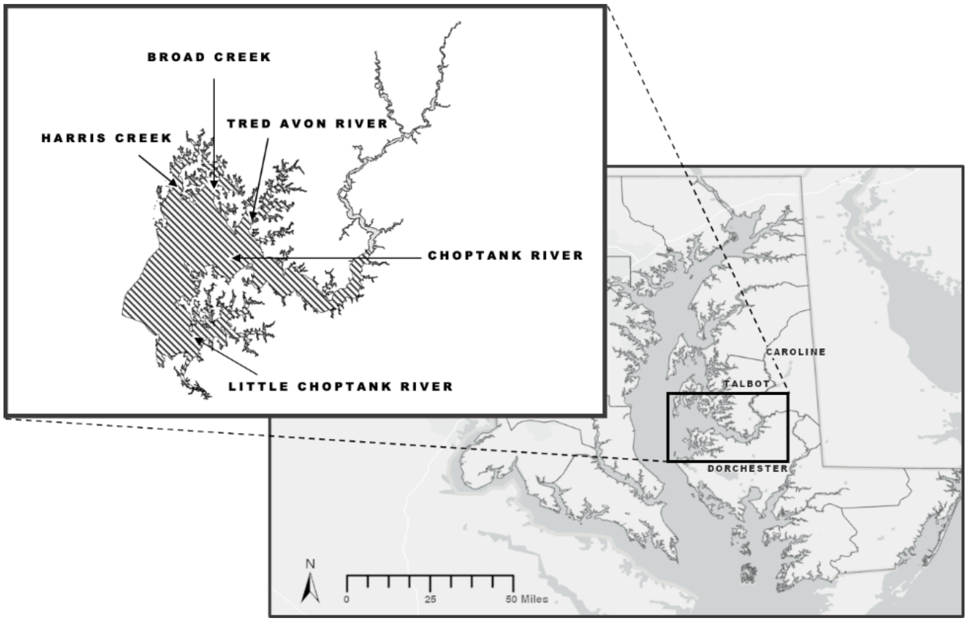

Figure 19. Study Area. Oyster reef restoration projects in Harris Creek, the Tred Avon River, and the Little Choptank River are the focus for this analysis and the area included in the model (inset hashed area). Predator-prey relationships and life history information (e.g., growth, age at maturity) of the balanced EwE base model were based on input from a range of sources including field data specific to the region (Kellogg et al., C. Bonzek, unpublished ChesMMAP data), an existing EwE model of the Chesapeake (Christensen et al. 2009), and an existing Atlantis ecosystem model of the Chesapeake (Ihde et al. 2016) in order of preference.

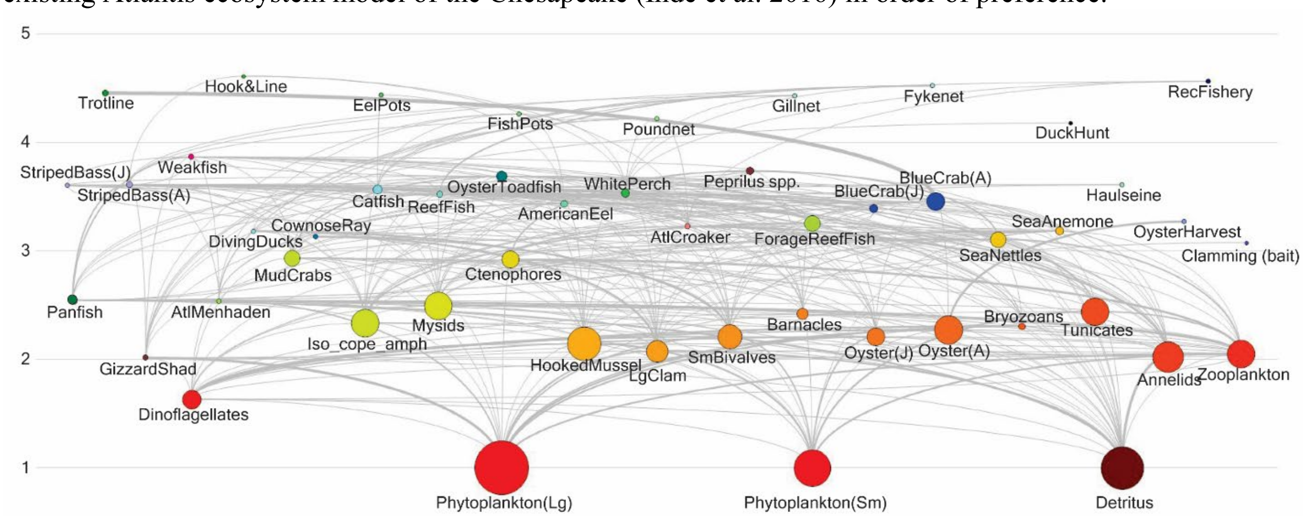

Figure 20. Energy flow diagram of the balanced Ecopath model, including all ecological groups and commercial fisheries. Relative group node size and line width are quantitative indicators of energy flow through that group and trophic pathway, respectively. Numbers on y-axis indicate trophic levels.

The abundance of oysters and associated filter feeders (i.e., animals that depend on the surface area provided by oyster growth: anemones, barnacles, hooked mussels, and tunicates) were manipulated across five scenarios (Table 4) to examine the effect of these organisms on ecological production, seafood harvested, and regional economic impacts. Harvested biomass estimates from these scenarios were converted to dockside revenues by applying mean, species-specific prices by fishery to the biomass harvest estimates. Dockside revenues were linked to IMPLAN regional economic impact modeling software with a custom set of cost functions for the major fisheries in the region. Cost functions were developed for the regional fisheries through semi-structured interviews of 12 commercial seafood harvesters active in the region. IMPLAN estimates of direct, indirect, and induced economic effects were then made for each of four key economic measures: sales, labor income, value-added, and employment.

Table 4. Ecological and management scenarios used in economic impact simulations.

Scenario	Condition
S1	Young restoration reefs in current oyster sanctuaries
S2	Mature reefs with increased oyster biomass in sanctuaries
S3	Mature reefs with increased oyster and associated filter feeder biomass in sanctuaries
S4	Fished down oyster biomass, sanctuaries opened to harvest, and oyster density at prerestoration levels
S5	Fished down with decreased biomass of oysters and associated filter feeders, sanctuaries opened to harvest, and oyster density at prerestoration levels

Results

Mature oyster reefs (Scenario 2—S2) support an increase in annual commercially harvested finfish and shellfish biomass of about 45% relative to the current young reef (S1). Mature reefs are predicted to increase total harvested biomass by about 80% relative to the scenario (S4) in which restored oyster reef sanctuaries have been fished down to a level that reflects the prerestoration status.

Scenarios 3 and 5 simulate how changes in oyster abundance and associated filter feeders affect fisheries harvests, and inclusion of filter feeders on oyster reefs increases fisheries harvest by 11% to 17% relative to the analogous scenarios (S2 & S4) that account for change in oyster biomass alone.
The ecological model predicts large increases in harvests for some commercially important species in the region. The mature reef with filter feeders scenario (S3) projects an 80% increase in blue crab harvest relative to the young reef scenario (S1), and a 160% increase in harvest relative to the fished-down scenario (S5) where the biomass is reduced for both oysters and their associated filter feeders. Scenario S3 also predicts that white perch harvests will be about 110% greater than that of the young reef scenario (S1), and more than 650% greater relative to the fished-down with other filter feeders scenario (S5). The effects on striped bass harvest across all scenarios is predicted to be negligible.

The commercial harvest changes predicted here only account for changes of food availability in the system, and does not account for the value of the reef structure itself as refuge from predators. Harvest is entirely driven by the modeled, scenario-specific changes in the food availability of oysters and the filter feeders that depend on the increased surface area of oyster shells. Increases in blue crab, for example, are driven by an increase in prey such as mud crabs, with mud crabs benefitting from increases in their prey groups (e.g., young oysters). White perch increases are largely driven by the abundance of a tunicate that is important in the white perch diet—and tunicates are one of the filter feeding groups that increased due to additional oyster shell surface area to grow on.

The changes in commercially harvested biomass have the potential to contribute millions of dollars in additional sales for commercial seafood harvesters each year. The mature reef with associated filter feeders scenario (S3) is projected to increase annual dockside sales by more than $4.5 million relative to the young reef scenario (S1) and by about $11 million relative to the fished-down with filter feeders scenario (S5). These predicted changes in dockside sales are primarily driven by increased blue crab harvest.

Each dollar generated through the dockside sales received by commercial seafood harvesters has an economic multiplier effect of 2.07. That is, for each $1.00 of dockside sales, an additional $1.07 of economic activity is generated in Dorchester and Talbot Counties through inter-industry transactions and additional spending generated through the increases in employee wages and business owner income. Accounting for both the initial direct effects of dockside sales and the additional economic activity in Dorchester and Talbot counties generated by these initial sales, the mature reef with associated filter feeders scenario (S3) is projected to increase total regional sales by about $10 million relative to the young reef scenario (S1) and by about $23 million relative to the fished-down with filter feeders scenario (S5).

Fisheries managers, commercial seafood harvesters, and other stakeholders are increasingly seeking information regarding the regional economic impacts resulting from fisheries management decisions. This modeling effort predicts sizable increases in harvest and regional economic impacts from oyster reef restoration. Harvest increases and potential regional economic impacts predicted in this project are specific to the Choptank River region and local economies. Caution is urged with respect to assumptions about the transferability of these predicted gains to other areas, where other factors not present in the Choptank ecosystem or surrounding economy may affect harvest and economic impacts.

Summary

The primary goal of oyster restoration is to increase oyster abundance; however, given their nature as ecosystem engineers, successful oyster restoration provides numerous additional ecosystem services. Oyster reefs, and consequently their restoration, provide structured benthic habitat critical to various life stages of ecologically and economically important species. In estuaries dominated by fine-grained sediments, for example, oyster reefs may be the only stable hard bottom that can support primary and secondary production in addition to other biogeochemical processes, such as nutrient cycling. Ecosystem services research aims to quantify the added benefits of increasing oyster abundance and reef habitat. Chesapeake Bay oyster restoration metrics documents (Oyster Metrics Workgroup 2011) have acknowledged the ecosystem benefits of oyster reefs, but left the designation of specific services as restoration metrics for a future time, thereby relying primarily on oyster abundance as an indicator for restoration success. Components of research in the ORES projects have demonstrated that by enhancing oyster densities and oyster reef habitats, ecosystem services will respond accordingly.

The nine studies in NOAA’s Oyster Reef Ecosystem Services project used both empirical and modelling techniques to assess the ecosystem services provided by large-scale oyster restoration. Some studies demonstrated significant restoration benefits, but for others, the benefits were less evident. For empirical studies (those that require biological sampling), quantifying linkages between ecosystem services and restoration is more challenging at upper trophic levels. For example, microbially mediated nutrient cycling rates and macrofaunal abundance responded to restored oyster density, but abundance and diet of transient finfish were at best loosely linked to oyster restoration activity overall.

Experimentally derived nutrient cycling rates increased in response to enhanced oyster densities on restoration sites. Field observations, modelling simulations, and extrapolations also demonstrated elevated particle processing and nutrient cycling relative to oyster density and areal extent of restoration. From a management perspective, this work suggests that if restoration successfully increases oyster densities, then phytoplankton uptake and nutrient processing from biologically available to unavailable forms will also increase. In turn, this provides benefits to water quality, and the expected result is increased localized water clarity on scales proportional to the extent of restoration. A tangible potential outcome of this work is inclusion of activities that enhance oyster abundance as Chesapeake Bay nutrient reduction best management practices.

In general, abundance of both invertebrate macrofauna and small reef-resident fishes was found to increase with oyster density. However, for larger transient species—even those generally associated with bottom habitats—strong linkages between abundance and oyster restoration activity were not observed. Quantifying the significance of oyster restoration sites for larger transient fishes has consistently been problematic (Harding and Mann 2001, Gregalis et al. 2008, Geraldi et al. 2009, Pierson and Eggleston 2014), and is likely due to sampling gear inefficiency coupled with the mobile nature of these fishes. These studies were successful at documenting species present on reefs throughout the Chesapeake Bay (see Appendix), but were less successful at identifying consistent utilization patterns of restored sites relative to unrestored sites. For fish species such as black seabass, bluefish, cobia, silver perch, spadefish, striped bass, and white perch, diets or consumption rates were linked to oyster reef prey. Diets of Atlantic croaker were linked to reef prey in one study but not in another. For other species, diets were either linked to other habitat types or habitat linkages could not be quantified. Benthic infauna, such as clams, may respond negatively to restoration, persisting at higher abundances in softer sediments, and, as a result, predators that rely on infaunal prey (e.g. spot, Atlantic croaker) may also exhibit a negative response to restoration. It is clear that if oyster restoration successfully increases oyster density and the amount of structured habitat, then the abundance and diversity of macrofaunal prey will increase. This provides enhanced foraging opportunities and potential growth and production of some commercially important predator species such as American eel, black seabass, spotted seatrout, striped bass, summer flounder, and weakfish. Although estuary-specific temperature and salinity may dictate exactly which species use oyster reef habitat, these community-level responses would be expected at restoration sites outside of the Chesapeake Bay.

Coupled food web and economic models provided estimates of the regional aggregated economic impact of three oyster restoration projects in the vicinity of the Choptank River, Maryland. Economic output was compared among simulated management and ecosystem scenarios that varied reef age, filter feeder biomass, and oyster sanctuary status. These simulations are significant, as they place estimated dollar values relative to restoration and management options. Simulations suggested that relative to commercially exploited oyster reef ecosystems, total regional output of fishery production by mature and fully functional reef ecosystems in these three oyster sanctuaries would increase by an estimated $22.8 million. Estimated increases in blue crab harvest were the main driver of enhanced aggregate economic measures such as dockside landings, labor income, value-added, and employment.

Information Gaps

Notwithstanding the volume of work summarized here, several information gaps remain that are relevant to fully understanding the ecosystem services provided by oyster restoration. These gaps identify the limitations of the current body of knowledge and may suggest areas for future research. Among these gaps are how services provided by restoration may vary relative to reef age, aquaculture, and commercial harvest activities; and the spatial applicability of research findings, variability attributable to different restoration practices, and significance of restoration for production of juvenile fishes.

Ecosystem services benefits may vary relative to reef maturity. Oyster reef communities, from microorganisms to fish, would be expected to become established in about five years; however, it would be important to know at what reef age ecosystem services are maximized, especially for benefits such as nutrient cycling and suspended particle processing. Restoration sites studied in Maryland were up to six years old and Virginia study sites were up to ten years old; none of the studies presented here considered reef age as an explanatory variable for ecosystem services.

Relative to spatial coverage, oyster reef macrofauna and fish communities are adequately documented on restoration sites throughout the Bay. However, due to temperature and salinity differences, estimated nutrient cycling rates derived from Harris Creek restoration sites alone may not necessarily be applicable to reefs in the lower Bay or elsewhere within the range of the oyster.

Sonar and video monitoring (Figs. 11 and 17) demonstrates that from a structural perspective, not all oyster habitats are equivalent. Subtidal restoration reefs vary in height, construction material composition and particle size, and whether they are planted with hatchery oysters or colonized by wild oysters. Variability in these factors can alter currents and food delivery for filter feeders (Lenihan 1999); determine the amount and size of interstitial spaces that may serve as refuge, foraging, or reproductive habitats for mobile organisms (Humphries et al. 2011, Brown et al. 2014); and influence the amount of surface area potentially available for photosynthetic and microbial activity and for higher sessile organisms. It is likely that these factors also regulate ecosystem services, though the benefits provided by different restoration methodologies have not been adequately examined. We know how nutrient cycling, macrofauna, and reef-resident fish communities respond to increased oyster abundance, but we do not know the effects of factors such as reef height, material, and surface area. Further exploration of the linkages between biological processes and structural metrics may support the application of remote sensing to provide rapid assessment of the relative value of benthic habitats or restoration sites.

Estuaries provide significant nursery habitats for numerous fish species (Wingate & Secor 2008), many with commercial value. Largely dependent on sampling gear used, the studies summarized here did not collect many juvenile fishes or directly address the use of restored reefs by younger life stages. Enhanced abundance of macrofauna and small reef-resident fishes on restored oyster reefs presumably could serve as a superior foraging resource that could increase production of juvenile fishes. Structurally complex reefs could also provide predation refuge for juvenile fishes, further improving recruitment success and production. Quantifying positive relationships between oyster reefs and vital rates of juvenile stages of commercially significant fish species would increase the ecosystem services value of oyster restoration.

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Appendix: Organisms Collected at Chesapeake Bay Oyster Restoration Sites during Ecosystem Services Sampling

Group	Name	Species	Location
Anemone	**Anemone**		
	Orange Striped Anemone	*Diadumene lineata*	1
	White Anemone	*Diadumene leucolena*	1
Tunicate	**Sea Squirt**		
	Sea Grape	*Molgula manhattenensis*	1,4,5,6,7
Worm	**Flatworm**		
	worm	*Stylochus ellipticus*	1
	Other Worm		
	worm	*Mediomastus sp.*	1
	Polychaete		
	Clam Worm	*Alitta succinea*	1
	Ice Cream Cone Worm	*Pectinaria gouldii*	1
	Rock Worm	*Marphysa sanguinea*	4,5,6,7
	worm	*Hydroides dianthus*	5,6,7
	worm	*Terebellidae spp.*	6,7
	worm	*Phyllodocidae spp.*	1
	worm	*Spionidae spp.*	1
Mollusk	**Clam**		
	Baltic Macoma	*Macoma balthica*	1
	Dwarf Surf Clam	*Mulinia lateralis*	1
	False Angelwing	*Petricolaria pholadiformis*	1
	Gem Clam	*Gemma gemma*	1
	Hard Clam	*Mercenaria mercenaria*	6,7
	Mitchell Macoma	*Macoma mitchelli*	1
	Soft-shell Clam	*Mya arenaria*	1
	Mussel		
	Dark False Mussel	*Mytilopsis leucophaeata*	1
	Hooked Mussel	*Ischadium recurvum*	1,4,5,6,7
	Ribbed Mussel	*Guekensia demissa*	6,7
	Snail		
	Brown-band Wentletrap	*Gyroscala rupicola*	1
	Convex Slippershell	*Crepidula convexa*	5,6,7
	Eastern White Slippershell	*Crepidula plana*	5,6,7
	Impressed Odostome	*Boonea impressa*	1
	Lunar Dove	*Astyris lunata*	6,7
	Rams Horn	*Planorbidae spp.*	1

	Sea Slug	*Corambe obscura*	1
	Solitary Glass Bubble	*Haminoea solitaria*	1
	Truncated Marsh Hydrobia	*Ecrobia truncata*	1
	snail	*Anachis spp.*	4,5,6
	snail	*Odostomia sp.*	4,6,7
Crustacean	**Amphipod**		
	Scud	*Apocorophium lacustre*	1
	Scud	*Gammarus mucronatus*	1
	Skeleton Shrimp	*Caprellidae spp.*	1,6
	amphipod	*Corophium sp.*	6,7
	amphipod	*Cymadusa compta*	1,4,5,6,7
	amphipod	*Dulichiella appendiculata*	5,6,7
	amphipod	*Melita nitida*	1,4,5,6,7
	amphipod	*Microdeutopsus gryllotalpa*	6,7
	amphipod	*Monoculodes edwardsi*	1
	Barnacles		
	barnacles	*Amphibalanus spp.*	1
	barnacles	*Barnacles*	4,5,6,7
	Crab		
	Blackfingered Mud Crab	*Panopeus herbstii*	4,5,6,7
	Blue Crab	*Callinectes sapidus*	1,2,3,4,5,7
	Oyster Crab	*Zaops ostreus*	6,7
	mud crab	*Dyspanopeus sayi*	6,7
	mud crab	*Eurypanopeus depressus*	4,5,6,7
	mud crab	*Xanthidae spp.*	4,5,6,7
	Isopod		
	isopod	*Cassidinidea lunifrons*	1
	isopod	*Chiridotea almyra*	1
	isopod	*Cyathura polita*	1
	isopod	*Erichsonella attenuata*	1
	isopod	*Probopyrus pandicola*	11
	isopod	*Synidotea laevidorsalis*	1
	Shrimp		
	Bigclaw Snapping Shrimp	*Alpheus heterochaelis*	4,6,7
	Brackish Grass Shrimp	*Palaemonetes intermedius*	1
	Daggerblade Grass Shrimp	*Palaemonetes pugio*	1
	Marsh Grass Shrimp	*Palaemonetes vulgaris*	1,4,5,6,7
	shrimp	*Lubinia dubia*	6
	Tanaidacean	*Hargeria rapax*	1

Insect	**Fly**		
	midge	*Chironomidae spp.*	1
Fish	**Fish**		
	American Eel	*Anguilla rostrata*	1,2,3,4,5
	American Harvestfish	*Peprilus paru*	5
	Atlantic Croaker	*Micropogonias undulates*	5,7
	Atlantic Menhaden	*Brevoortia tyrannus*	1,5,7
	Atlantic Thread Herring	*Opisthonema oglinum*	5,7
	Bay Anchovy	*Anchoa mitchilli*	1
	Black Sea Bass	*Centropristis striata*	5
	Bluefish	*Pomatomus saltatrix*	5,7
	Cobia	*Rachycentron canadum*	5
	Cownose Ray	*Rhinoptera bonasus*	5
	Feather Blenny	*Hypsoblennius hentz*	5
	Gizzard Shad	*Dorosoma cepedianum*	5,7
	Gray Snapper	*Lutjanus griseus*	5
	Hogchoker	*Trinectes maculatus*	5
	Houndfish	*Tylosurus crocodilus*	5
	Inland Silversides	*Menidia beryllina*	1,5
	Lined Seahorse	*Hyppocoampus erectus*	5
	Mullet	*Mugil sp.*	7
	Naked Goby	*Gobiosoma bosc*	1,2,3,4,5,6,7
	Northern Kingfish	*Menticirrhus saxatilis*	5,7
	Northern Pipefish	*Syngnathus fuscus*	5
	Northern Puffer	*Sphoeroides maculatus*	3,5
	Northern Searobin	*Prionotus carolinus*	7
	Oyster Toadfish	*Opsanus Tau*	1,2,3,4,5,6,7
	Pigfish	*Orthopristis chrysoptera*	5
	Pinfish	*Lagodon rhomboides*	5,7
	Red Drum	*Sciaenops ocellatus*	5
	Sheepshead	*Archosargus probatocephalus*	5
	Silver Perch	*Bairdiella chrysoura*	1,3,5,7
	Skilletfish	*Gobiesox strumosus*	1,5
	Southern Kingfish	*Menticirrhus americanus*	5
	Spadefish	*Chaetodipterus faber*	5
	Spot	*Leiostomus xanthurus*	1,2,3,5,7
	Spotted Seatrout	*Cynosion nebulosus*	3,5,7
	Striped Bass	*Morone saxatillis*	1,2,5
	Striped Blenny	*Chasmodes bosquianus*	1,2,3,4,5,7
	Summer Flounder	*Paralichthys dentatus*	5
	Three-spined Stickleback	*Gasterosteus aculeatus*	1

Weakfish	*Cynosion regalis*	1,5,7
White Perch	*Morone americana*	1,2,
Whitefin Sharksucker	*Echeneis neucratoides*	5

1-Harris Creek, MD
2-Tred Avon River, MD
3-Little Choptank River, MD
4-Great Wicomico River, VA
5-Piankatank River, VA
6-Lafayette River, VA
7-Lynnhaven River, VA