

Non-Federal Funding Sources and total dollar amounts anticipated for replenishment and restoration in 2025.

NON-FEDERAL FUNDING SOURCES	AMOUNT
General Funds Replenishment (GF)	\$2,500 ,000
General Funds Restoration (GF)	\$1,500,000
Non-General Funds (NGF) Oyster Resource User Fees	\$300,000
Other Non-General Funds	Up to \$500,000
Total	\$4,800,000

Federal Funding Sources and total dollar amounts available restoration in 2025.

FEDERAL FUNDING SOURCES	AMOUNT
NOAA	Up to \$750,000
Total	\$750,000

SEED TRANSFER:

James River

Initially the majority of the transported seed from the James River was harvested from the Hand Tong Seed Areas. However, the cost of harvesting and then transporting this seed has continued to increase. As a result, the SMD has not received responses to the notices to transport and plant seed at the price that has been offered in most recent years. Fortunately, seed of equal quality can be moved for a significantly lower price from areas that have received consistent and very good spat sets in the lower James River. These areas are then re-shelled and were expanded in 2018, 2019 and again in 2020. Most have continued to receive good spat sets. As a result of the lower cost, and as a way of increasing productivity in low recruitment areas beyond the Potomac tributaries, staff has transported some of this seed to multiple areas for the last 5 years. The SMD again intends to transport seed taken from these areas of the lower James River to up to three areas that do not consistently receive high spat sets from shell planting alone. The areas recommended for planting are the Potomac River Tributaries, Areas 7 and 8 in the Rappahannock River, and a portion of the Pocomoke Sound several miles from the Maryland Virginia state line. The areas planted with seed may not be opened for immediate harvest. Staff would evaluate the seed plant areas prior to opening them to harvest. The cost for each bushel of seed to be harvested from the Lower James River, transported, and planted in will be at least \$7.00/bushel. Funds from Oyster Resource User Fees and replenishment GFs will be used for this project.

A notice to transport seed oysters from hand tong areas will again be put out to solicit persons who may be willing to conduct this work at the price offered. If no positive responses are received this

funding will be used to plant additional high recruitment areas with shell that can then be moved later as seed. The cost to harvest transport and plant will be no more than \$15.00/bushel.

Great Wicomico River

The Shellfish Management Advisory Committee (SMAC) requested that staff contract for the movement of seed from the traditional seed areas in the Great Wicomico River. This project would look to move up to 5000 bushels of seed from these areas to a harvest area in the Chesapeake Bay south of Smith Point known as Black Berry Hangs.

Proposed Project	Up to 20,000 bushels of seed oysters @ ~\$7.00-\$15.00/bu.
Estimated Cost	\$300,000
Funding Sources	NGF and GF (Replenishment)

SHELL PLANTING:

Bay and Tributaries:

Shells on public beds naturally degrade over time and lose their effectiveness as a substrate for oyster larval attachment. In most of the mid-salinity areas in Virginia, the half-life of shells appears to be 3 to 4 years. Additional shell is lost and degradation intensified by the harvest and removal of market oysters. The density of living oysters and shell volume are determined from the results of the VIMS-VMRC annual hydraulic patent tong survey and this information is used to determine what areas are in the most in need of shell. If the mean volume of shell observed in the fall survey does not fall below 5 liters per square meter, a reasonable degree of productivity can be maintained. Maintaining areas at a mean shell volume closer to 10 liters per square meter or above is ideal.

Most of the harvest areas in the Chesapeake Bay and tributaries are experiencing a period of relatively consistent and high recruitment. However, there is strong evidence to suggest that extreme weather events, such as those seen in 2018, could become more frequent, resulting in the possibility of localized high oyster mortality and low recruitment. Replenishment should continue in areas that are determined to need additional substrate. This will prevent further substrate degradation of the public ground that is opened to harvest and provide an additional buffer for localized high mortality events and low spat sets should they occur. In addition, should a good spat set occur, more substrate will be available for spat to settle on and the areas will be able to more quickly recover from harvest or unpredictable natural causes.

The majority of the replenishment specific General Funds appropriation for FY2025 will be used for adding new shell to those areas in most need of shell and/or those that have been recently opened to public oyster harvest. Some restoration General Funds will be used to maintain or expand sanctuary areas. Funds for oyster replenishment are not likely to be enough to maintain the

public beds at maximum productivity but will be used to maintain a minimum volume of shell, as observed in the fall survey, above 5 liters per square meter where possible and practical, with a goal of maintaining 10 liters per square meter or more. In Table 1 there is a list of all of the areas and acreages of oyster beds that staff has determined to be in need of shell in 2025. In total, nearly 7,000 acres of bottom is in need of replenishment, based on shell volume. However, a considerable portion of the areas most in need of replenishment are in the upper James River and are not practical or feasible to replenish on a large scale. These areas should continue to be monitored to assess their decline.

The CRD will seek to plant the largest quantity of comparable shells for the lowest area dependent per-unit price. This will likely be a combination of house, reef and dredged shells. There is currently one location permitted for hydraulic shell dredging (reef shells) in the lower James River, the SMD intends to seek permit authorization for a second location in the vicinity of the Craney Island Eastward Expansion. The currently permitted site has an estimated 10-15 years of shell resource remaining at the current rate of use.

Proposed Project	600 – 800 acres of oyster shell restoration @ 750-1,000 bushels/acre @ \$2.50 - \$5.50/bushel
Estimated Cost	\$2,500,000-\$4,000,000
Funding Sources	GF

Eastern Shore:

The CRD-SMD and The Nature Conservancy (TNC) have consistently collaborated on Seaside replenishment and restoration efforts. Last year, for the sixth year in a row, TNC funds were used on areas both closed and open to harvest. The SMD will contract for shell planting for a Nature Conservancy project, assist with the site selection, and shell planting monitoring. If funding allows additional locations will be planted using General Funds for restoration.

Up to 30 acres will be planted with shells harvested from local shell deposits or purchased from local sources.

Proposed Project	Up to 30 acres @ 2,000 to 10,000 bushels of shells/acre @ ~\$2.50-\$5.50/bushel
Estimated Cost	Up to \$425,000
Funding Sources	NGF-TNC and GF (restoration)

ALTERNATIVE CULTCH PROJECTS:

The supply of shell for restoration, replenishment, and aquaculture will always be limited. The demand for shells in most years tends to be higher than the supply leading to increasing prices. Over the last several years, the CRD-SMD and other restoration partners have begun using alternative substrate in certain areas. Non-harvest locations have been planted with larger sized substrate. In the Rappahannock, several harvest areas have been planted with a smaller sized material. The first planting used crushed concrete that was slightly larger than ideal. Some oysters were crushed during harvesting. The other areas that were planted used a slightly smaller size. These areas have been open to harvest recently, and it appears that the size of the alternative substrate is no longer an issue. Not all areas are suitable for planting with stone or concrete. The bottom needs to be firmer than areas that can be planted with shell.

The SMD has identified a number of locations that could have suitable bottom for alternative cultch plantings. These areas tend to have sandier bottoms and low oyster densities. Staff has existing permits (JPAs) for several locations. The locations would be near the Deep Rock Area, two locations in the Lower Rappahannock, the Lower James River near Nansemond Ridge, and the lower Pocomoke Sound adjacent to Onancock Rock. Only a small portion of the permitted areas would be planted at any given time. In the event that issues with acquiring shell arise, these areas could be expanded as needed and as suitable for planting.

In addition to these harvest areas, VMRC in partnership with NOAA will continue alternative cultch projects that will primarily focus on the restoration of non-harvest areas. Current efforts are focused in the Mobjack Bay. The CRD-SMD will continue to carefully select locations in these areas for alternative substrate planting that will minimize potential user conflict. The intent is to create “new oyster reefs” that will have multiple benefits to adjacent areas, through improved water quality, increased fish habitat, and oyster larval transport to both public and private ground.

Proposed Project	0-100 acres @250 tons/acre @ ~\$70.00/ton Up to 100 acres @ 250-1000 tons/acre
Estimated Cost	\$750,000-\$4,500,000
Funding Sources	GF Restoration and Replenishment, Federal, Non- General Fund

Summary of proposed projects and costs for oyster replenishment and restoration for 2025.

Proposed Project	Estimated Cost	Funding Sources
Seed Oysters - Up to 20,000 bushels @ ~\$7.00-\$15.00/bu.	\$300,000	NGF and GF (Replenishment)
Shell Planting - 600 – 800 acres of oyster shell restoration @ 1,000-750 bushels/acre @ \$2.50 - \$5.50/bushel	\$2,500,000	GF Replenishment
	\$0-\$1,500,000	GF Restoration
Eastern Shore Shell Planting	\$425,000	GF Restoration and TNC
Alternative Cultch Projects: 0-50 acres @250 tons/acre @ ~\$50.00/ton Up to 100 acres @ 250-1000 tons/acre	\$750,000-\$4,500,000	GF Restoration and Replenishment and Federal

Table 1. Summary of potential areas of oyster replenishment and restoration activity for the 2025 Oyster Replenishment Plan.

	Acreage	Maximum Bushels Needed (1,000 bu/ac)	Cost Estimate (\$/bu)
Total Most in Need of Replenishment (Shell Volume less than 5L)	4,338	4,338,000	\$ 17,352,000
Total in Need of Replenishment (Shell volume less than 10L)	6,371	6,371,000	\$ 25,484,000
Total Targeted	885	885,000	\$ 3,540,000

COLOR LEGEND	
Most in need	Shell volume less than 5L
In need	Shell volume less than 10L
Not in need unless open to harvest	Shell volume greater than 10L

Table 2. All areas available for oyster replenishment and restoration activity for the 2025 Oyster Replenishment Plan.

Notes:

- This cost estimate is based on an average cost of planting shell and material that can range from \$2.50-\$5.50 per bushel.
- The average markets and Brown Shell Volume are derived from the annual VIMS/VMRC Joint oyster assessment survey.
- Areas are targeted based on criteria outlined in the ORP that include brown shell volume and open harvest status.

Area Name	Average Number of Markets	Average Brown Shell Volume (L)	Acreage	Minium Bushels Needed (7,500 bu/acre)	Maximum Bushels Needed (1,000 bu/ac)	Cost Estimate (\$/bu)	Notes (S=Sanctuary, H=Harvest Area, O=Open Area 24/25, T=Target for 2025 planting)
James River							
LOWER JAIL ISLAND	1.2	1.0	150	112,500	150,000	\$600,000	H,O,T
UPPER JAIL ISLAND	0.8	1.4	612	459,000	612,000	\$2,448,000	H,O
OFFSHORE SWASH	1.1	1.7	641	480,750	641,000	\$2,564,000	H,O
SWASH MUD SLOUGH	1.2	1.7	1,230	922,500	1,230,000	\$4,920,000	H,O
OFFSHORE JAIL ISLAND	2.6	2.0	1,017	762,750	1,017,000	\$4,068,000	H,O
DAYS POINT	1.4	3.2	275	206,250	275,000	\$1,100,000	H,O
SWASH	1.8	3.9	201	150,750	201,000	\$804,000	H,O
WRECK INSHORE	7.6	5.2	585	438,750	585,000	\$2,340,000	S
LONG ROCK also Cross Rock	4.0	7.8	41	30,750	41,000	\$164,000	H,O
CRUISER'S SHOAL	8.5	8.3	55	41,250	55,000	\$220,000	H,O,T
NANSEMOND RIDGE	9.8	8.5	100	75,000	100,000	\$400,000	H,O,T
SHANTY ROCK	5.5	8.5	3	2,250	3,000	\$12,000	H,O
MULBERRY POINT	11.7	9.5	48	36,000	48,000	\$192,000	H,O
White Shoal	14.6	9.8	26	19,500	26,000	\$104,000	H,O
DOG SHOAL LOWER	21.4	10.6	35	26,250	35,000	\$140,000	H,O
HIGH SHOAL	13.6	11.2	44	33,000	44,000	\$176,000	H,O
THOMAS ROCK LOWER	21.4	11.2	93	69,750	93,000	\$372,000	H,O
BALLARD'S MARSH	23.7	11.3	78	58,500	78,000	\$312,000	H,O
UPPER DEEP WATER SHOAL	46.9	11.6	313	234,750	313,000	\$1,252,000	H,O
HOTEL ROCK	8.8	12.6	14	10,500	14,000	\$56,000	H,O
V-ROCK	20.1	13.3	76	57,000	76,000	\$304,000	H,O
THOMAS ROCK UPPER	37.0	13.3	103	77,250	103,000	\$412,000	H,O
Lower Brown Shoal	25.8	13.8	82	61,500	82,000	\$328,000	H,O
LOWER HORSEHEAD	14.6	14.2	21	15,750	21,000	\$84,000	H,O
SNYDER'S ROCK	26.7	14.3	9	6,750	9,000	\$36,000	H,O
DRY LUMPS	29.0	16.0	6	4,500	6,000	\$24,000	H,O
POINT OF SHOALS	31.5	16.0	155	116,250	155,000	\$620,000	H,O
DOG SHOAL UPPER	32.6	17.4	13	9,750	13,000	\$52,000	H,O

Upper Brown Shoal	32.8	18.4	23	17,250	23,000	\$92,000	H,O
MOON ROCK	24.7	19.0	3	2,250	3,000	\$12,000	H,O
TRIANGLE ROCK	36.0	19.0	7	5,250	7,000	\$28,000	H,O
LOWER DEEP WATER SHOAL	37.5	19.3	20	15,000	20,000	\$80,000	H,O
MIDDLE HORSEHEAD	53.1	21.6	44	33,000	44,000	\$176,000	H,O
UPPER HORSEHEAD	58.5	28.0	5	3,750	5,000	\$20,000	H,O

Area Name	Average Number of Markets	Average Brown Shell Volume (L)	Acreage	Minium Bushels Needed (7,500 bu/acre)	Maximum Bushels Needed (1,000 bu/ac)	Cost Estimate (\$4/bu)	(S=Sanctuary, H=Harvest Area, O=Open Area 24/25, T=Target for 2025 planting)
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York and Mobjack

Tow Stake East	4.0	2.8	6	4,500	6,000	\$24,000	H,O,T
Sarah's Creek 2	4.8	4.4	14	10,500	14,000	\$56,000	S,T
PULTZ BAR	6.7	5.5	14	10,500	14,000	\$56,000	H,O,T
Brown's Bay #2	6.6	5.7	22	16,500	22,000	\$88,000	S
Tow Stake West	4.8	6.0	3	2,250	3,000	\$12,000	H,O,T
Timberneck	3.8	6.9	47	35,250	47,000	\$188,000	H,O,T
Sarah's Creek 1	12.4	8.1	9	6,750	9,000	\$36,000	S
Cheatham PG 1	8.0	8.5	2	1,500	2,000	\$8,000	S
Brown's Bay #1	15.3	8.7	83	62,250	83,000	\$332,000	S
Pages Rock	8.8	10.8	116	87,000	116,000	\$464,000	H,O
Aberdeen Rock	11.0	10.9	45	33,750	45,000	\$180,000	H,O
Indian Field PG 2	26.7	17.0	1	750	1,000	\$4,000	S

Area Name	Average Number of Markets	Average Brown Shell Volume (L)	Acreage	Minium Bushels Needed (7,500 bu/acre)	Maximum Bushels Needed (1,000 bu/ac)	Cost Estimate (\$4/bu)	(S=Sanctuary, H=Harvest Area, O=Open Area 24/25, T=Target for 2025 planting)
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Piankatank/Deep Rock

THOMPSONS	1.0	1.3	1	750	1,000	\$4,000	S
SHIPLEYS EDGE	0.0	1.5	1	750	1,000	\$4,000	S
PALACE BAR B also PALACE B	2.0	2.2	7	5,250	7,000	\$28,000	S
DOCS VIEW	3.3	5.0	1	750	1,000	\$4,000	S
Iron Point Reef - TNC	6.3	5.0	4	3,000	4,000	\$16,000	S
BURTON POINT B	10.3	5.4	8	6,000	8,000	\$32,000	S
ISLAND BAR	2.7	6.1	5	3,750	5,000	\$20,000	S
Cape Toon NOAA Stone Plant	7.0	6.6	5	3,750	5,000	\$20,000	S
Burton Point NOAA Stone Plant	9.5	7.0	16	12,000	16,000	\$64,000	S
Fishing Point	8.6	7.0	2	1,500	2,000	\$8,000	S
HERON ROCK	9.6	7.0	13	9,750	13,000	\$52,000	S
COBBS CREEK	9.3	7.2	4	3,000	4,000	\$16,000	S
DEEP ROCK 4	8.4	7.2	8	6,000	8,000	\$32,000	H,O
HILLS BAY	12.0	7.3	5	3,750	5,000	\$20,000	S,T
BURTON POINT	10.4	7.5	39	29,250	39,000	\$156,000	H,O,T
CAPE TUNE	6.9	7.5	41	30,750	41,000	\$164,000	S,T
PALACE BAR also PALACE BA	6.1	8.1	38	28,500	38,000	\$152,000	H,O
STOVE POINT	8.4	8.8	5	3,750	5,000	\$20,000	S
Palace Bar NOAA Stone Plant	8.3	9.0	9	6,750	9,000	\$36,000	S
Island Bar NOAA Stone Plant	7.3	9.0	2	1,500	2,000	\$8,000	S
Ginney Point NOAA Stone Pla	9.0	9.1	6	4,500	6,000	\$24,000	S
BLAND POINT	6.4	9.6	11	8,250	11,000	\$44,000	S
Stove Point NOAA Stone Plant	19.9	10.4	9	6,750	9,000	\$36,000	S
GINNEY POINT	15.5	11.5	4	3,000	4,000	\$16,000	S
Heron Rock NOAA Stone Plan	20.3	11.5	3	2,250	3,000	\$12,000	S
Bland Point NOAA Stone Plan	14.1	13.0	11	8,250	11,000	\$44,000	S

BEVERLYS 4	19.4	13.6	15	11,250	15,000	\$60,000	H
BEVERLYS 3	20.8	14.3	7	5,250	7,000	\$28,000	H
BEVERLYS 1	24.0	14.7	14	10,500	14,000	\$56,000	H
THREE BRANCHES	24.0	15.3	1	750	1,000	\$4,000	S
BEVERLYS 2	26.8	15.4	7	5,250	7,000	\$28,000	H
DEEP ROCK	24.8	15.6	38	28,500	38,000	\$152,000	H
MILFORD HAVEN	50.0	18.7	1	750	1,000	\$4,000	H
Area Name	Average Number of Markets	Average Brown Shell Volume (L)	Acreage	Minium Bushels Needed (7,500 bu/acre)	Maximum Bushels Needed (1,000 bu/ac)	Cost Estimate (\$4/bu)	(S=Sanctuary, H=Harvest Area, O=Open Area 24/25, T=Target for 2025 planting)
Rappahannock River							
Mosquito Island	0.7	0.2	2	1,500	2,000	\$8,000	H
Drumming Ground sanctuary	0.3	1.3	3	2,250	3,000	\$12,000	S,T
Mill Creek sanctuary	18.8	4.8	4	3,000	4,000	\$16,000	S,T
Bush Park	5.0	5.2	4	3,000	4,000	\$16,000	H,O,T
Bush Park 2018 (Stone)	7.6	5.3	6	4,500	6,000	\$24,000	H,T
Drumming Ground sanctuary	9.5	5.4	7	5,250	7,000	\$28,000	S,T
Butler's Hole West	9.0	6.6	7	5,250	7,000	\$28,000	H,O,T
Broad Creek Inshore	9.0	6.9	8	6,000	8,000	\$32,000	H,O,T
Ferry Rock	7.3	7.0	4	3,000	4,000	\$16,000	H
Parrot Rock sanctuary	11.0	7.3	10	7,500	10,000	\$40,000	S,T
Lower Edge Broad Creek Midd	9.9	7.4	13	9,750	13,000	\$52,000	H,O,T
Larsons Bay	11.7	7.5	2	1,500	2,000	\$8,000	S
Broad Creek	10.2	7.8	16	12,000	16,000	\$64,000	H,O,T
Lower Edge Broad Creek Wes	13.7	8.1	22	16,500	22,000	\$88,000	H,O,T
Sturgeon Bar West (S.P. 552)	14.4	8.2	8	6,000	8,000	\$32,000	H
Big Wicks B	7.3	8.3	24	18,000	24,000	\$96,000	H
Corrotoman Point C-3	10.4	8.4	8	6,000	8,000	\$32,000	H
MORATTICO BAR	7.2	8.6	121	90,750	121,000	\$484,000	H,O
Larson's Lower sanctuary	18.3	8.7	3	2,250	3,000	\$12,000	S
Lower Edge Broad Creek East	11.7	9.6	18	13,500	18,000	\$72,000	H,O
Temple Bay 5	15.0	9.6	18	13,500	18,000	\$72,000	H,O,T
Spike B offshore	13.0	9.8	6	4,500	6,000	\$24,000	H,O
Little Wicks A	14.0	10.0	6	4,500	6,000	\$24,000	H,O
Little Wicks B	19.3	10.0	7	5,250	7,000	\$28,000	H,O
STOVE POINT	15.5	10.2	30	22,500	30,000	\$120,000	H,O
Whiting Creek	16.8	10.3	13	9,750	13,000	\$52,000	H
Corrotoman sanctuary	23.3	10.3	9	6,750	9,000	\$36,000	S
Temple Bay sanctuary	12.3	10.3	9	6,750	9,000	\$36,000	S
Corrotoman Point C-1	14.0	10.4	9	6,750	9,000	\$36,000	H
Corrotoman Point C-2	18.0	10.4	9	6,750	9,000	\$36,000	H
Temple Bay 2 (S.P. 136)	19.8	10.6	6	4,500	6,000	\$24,000	H,O,T
Butler's Hole East	14.8	11.0	6	4,500	6,000	\$24,000	H,O
Whitehouse East	15.6	11.0	13	9,750	13,000	\$52,000	S
Sturgeon Bar East (S.P. 551)	21.0	11.3	11	8,250	11,000	\$44,000	H
Parrot's Rock West	16.0	11.3	9	6,750	9,000	\$36,000	H,O,T
Monaskin Bluff	22.8	11.4	162	121,500	162,000	\$648,000	H,O
Middle Ground	8.2	11.4	5	3,750	5,000	\$20,000	H,O,T
Spike	19.8	11.6	7	5,250	7,000	\$28,000	H,O
Parrot's Rock East	22.2	12.1	11	8,250	11,000	\$44,000	H,O,T
Butler's Hole gravel plant	19.0	12.3	5	3,750	5,000	\$20,000	H,O
Drumming Ground Inshore	16.8	12.8	29	21,750	29,000	\$116,000	H
North End S.P. 553	4.2	12.8	10	7,500	10,000	\$40,000	H
Butler's Hole sanctuary	25.5	13.3	2	1,500	2,000	\$8,000	S
Broad Creek sanctuary	25.5	14.0	8	6,000	8,000	\$32,000	S
Waterview C	14.8	14.0	19	14,250	19,000	\$76,000	H,O

Smokey Point	21.2	14.2	26	19,500	26,000	\$104,000	H,O
Big Wicks C	27.0	15.3	24	18,000	24,000	\$96,000	H,O
Temple Bay 3	28.8	15.5	5	3,750	5,000	\$20,000	H,O,T
Larson's Upper sanctuary	28.5	15.8	4	3,000	4,000	\$16,000	S
Spike A	30.5	15.8	2	1,500	2,000	\$8,000	H,O
Waterview B	24.0	16.0	20	15,000	20,000	\$80,000	H,O
Whitehouse West	22.4	16.4	14	10,500	14,000	\$56,000	S
Temple Bay 4	24.0	16.5	12	9,000	12,000	\$48,000	H,O,T
Drumming Ground Offshore	39.8	18.2	28	21,000	28,000	\$112,000	H
Hog House Inshore	40.5	18.5	4	3,000	4,000	\$16,000	H
Hog House Offshore	39.8	19.5	6	4,500	6,000	\$24,000	H
Temple Bay 1 (S.P. 138)	33.0	19.5	6	4,500	6,000	\$24,000	H,O,T
Lower Sturgeon sanctuary	48.7	20.7	1	750	1,000	\$4,000	S
Drumming Ground Offshore A	76.0	22.6	7	5,250	7,000	\$28,000	H
Upper Sturgeon sanctuary	58.7	23.0	5	3,750	5,000	\$20,000	S

Area Name	Average Number of Markets	Average Brown Shell Volume (L)	Acreage	Minium Bushels Needed (7,500 bu/acre)	Maximum Bushels Needed (1,000 bu/ac)	Cost Estimate (\$4/bu)	(S=Sanctuary, H=Harvest Area, O=Open Area 24/25, T=Target for 2025 planting)
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Great Wicomico/Black Berry

VMRC 12/GW Corps 17	0.0	0.0	2	1,500	2,000	\$8,000	S
Mill Creek East	1.3	0.6	2	1,500	2,000	\$8,000	H,O
VMRC 15/GW Corps 21	2.3	1.3	3	2,250	3,000	\$12,000	S
Cockrell Creek Expansion Stone	15.8	3.8	10	7,500	10,000	\$40,000	S
VMRC 10/GW Corps 12, 13	10.3	5.3	5	3,750	5,000	\$20,000	S
VMRC 8/GW Corps 9	3.1	5.4	14	10,500	14,000	\$56,000	S
VMRC 9/GW Corps 10	6.3	5.5	7	5,250	7,000	\$28,000	S
VMRC 3/GW Corps 4	1.7	5.7	3	2,250	3,000	\$12,000	S
VMRC 13/GW Corps 18 & 19	2.0	6.3	6	4,500	6,000	\$24,000	S
VMRC 11/GW Corps 14,15 & 16	4.8	6.7	14	10,500	14,000	\$56,000	S
HILLY WASH	7.6	7.1	3	2,250	3,000	\$12,000	S
HARCUM FLATS	7.5	7.5	6	4,500	6,000	\$24,000	S
Dameron Marsh East	14.5	7.8	12	9,000	12,000	\$48,000	S
ROGUE POINT	5.8	7.8	3	2,250	3,000	\$12,000	S
INGRAM'S Bay South	9.2	10.0	9	6,750	9,000	\$36,000	H,O
SANDY POINT	10.6	10.4	12	9,000	12,000	\$48,000	H,O
VMRC 4/GW Corps 5	18.7	11.3	3	2,250	3,000	\$12,000	S
Rogue Point Expansion Stone	9.3	11.5	5	3,750	5,000	\$20,000	S
Shell Creek Expansion Stone	34.8	12.3	5	3,750	5,000	\$20,000	S
Back Yard Stone 2021	6.3	12.5	5	3,750	5,000	\$20,000	S
SHELL BAR	12.7	12.6	18	13,500	18,000	\$72,000	H,O
VMRC 1/GW Corps 1&2	17.3	12.8	6	4,500	6,000	\$24,000	S
CRANES CREEK also WHALEY	16.8	12.8	13	9,750	13,000	\$52,000	H,O
Cockrell Creek	33.3	13.0	4	3,000	4,000	\$16,000	H,O
HAYNIE POINT	23.4	13.0	5	3,750	5,000	\$20,000	H,O
FLEET POINT	32.0	13.3	15	11,250	15,000	\$60,000	H,O
VMRC 16/GW Corps 22, 23 & 24	20.0	14.0	7	5,250	7,000	\$28,000	S
BLACKBERRY HANG	43.7	15.3	11	8,250	11,000	\$44,000	H,O
INGRAM'S Bay North	15.0	18.0	22	16,500	22,000	\$88,000	H,O

Area Name	Average Number of Markets	Average Brown Shell Volume (L)	Acreage	Minium Bushels Needed (7,500 bu/acre)	Maximum Bushels Needed (1,000 bu/ac)	Cost Estimate (\$4/bu)	(S=Sanctuary, H=Harvest Area, O=Open Area 24/25, T=Target for 2025 planting)
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Tangier/Pocomoke

Public Ground #10 H-2	0.8	0.9	21	15,750	21,000	\$84,000	H,O
Public Ground #10 H-1	4.0	3.8	70	52,500	70,000	\$280,000	H,O
PG17 Parker's Rock A	2.2	4.4	34	25,500	34,000	\$136,000	H,T
Public Ground #9 H-2	4.6	4.7	32	24,000	32,000	\$128,000	H,O
Marshalls Rock	9.3	5.8	40	30,000	40,000	\$160,000	H,T
Public Ground 11-1	6.7	6.1	37	27,750	37,000	\$148,000	H,O,T
PG13 H-2	8.6	6.5	40	30,000	40,000	\$160,000	H,O,T
PG13 H-5	6.0	6.5	19	14,250	19,000	\$76,000	H,O,T
Public Ground #9 H-1	6.3	6.8	21	15,750	21,000	\$84,000	H,O
PG07 H-3 Thoroughfare	10.8	6.9	26	19,500	26,000	\$104,000	H,O
PG13 H-1	6.7	8.6	31	23,250	31,000	\$124,000	H,O,T
PG13 H-4	9.8	8.8	28	21,000	28,000	\$112,000	H,O,T
PG18 Onancock Rock A	5.3	9.0	10	7,500	10,000	\$40,000	H
Byrd Rock	4.8	9.5	65	48,750	65,000	\$260,000	H
PG08-H4 California Rock	15.0	10.0	15	11,250	15,000	\$60,000	H,O
Island Rock	20.1	10.8	47	35,250	47,000	\$188,000	H
PG13 H-3	19.8	10.8	24	18,000	24,000	\$96,000	H,O,T
PG08-H2 California Rock	17.8	11.0	9	6,750	9,000	\$36,000	H,O
PG07 H-5 Thoroughfare	14.8	11.8	9	6,750	9,000	\$36,000	H,O
PG07 H-1 Thoroughfare	22.0	11.8	14	10,500	14,000	\$56,000	H,O
PG04 Johnson's Rock	10.5	12.0	40	30,000	40,000	\$160,000	H
PG05 H-1 Fox Island Rock	14.5	12.0	6	4,500	6,000	\$24,000	H
PG08-H3 California Rock	10.3	12.3	7	5,250	7,000	\$28,000	H,O
PG07 H-2 Thoroughfare	28.2	12.6	15	11,250	15,000	\$60,000	H,O
PG08-H1 California Rock	24.0	13.3	9	6,750	9,000	\$36,000	H,O
PG01 Hurley's	19.3	13.3	7	5,250	7,000	\$28,000	H,O
PG07 H-4 Thoroughfare	23.0	14.3	4	3,000	4,000	\$16,000	H,O
Cod Harbor	32.8	15.2	5	3,750	5,000	\$20,000	S

A Final Report:

Impacts of rotational harvest areas and replenishment: A test case from the Rappahannock River

Submitted to:

Virginia Marine Resources Commission's Shellfish Management and Advisory Committee
Fisheries Improvement Fund Grant #CF 23-04

**Lead investigators:**

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What are the impacts of rotational harvest areas and replenishment on oysters and the fishery? Evidence from the Rappahannock River.

Key Findings and Recommendations

- Current management strategies enhance oyster reefs *and* the oyster fishery
- Shell replenishment supports oyster reef structure and provides juvenile oyster habitat
- A 3-year harvest area rotation increases market sized oyster density
- Focus replenishment efforts on reefs with low shell volume ($<10 \text{ L m}^{-2}$) to maximize benefits
- Future fine scale harvest report monitoring will help target replenishment efforts

BACKGROUND

Eastern oysters (*Crassostrea virginica*) create critical habitat and are a valuable fishery species in the Chesapeake Bay; however, oyster populations collapsed in the Chesapeake Bay in the mid-1980s leading to extensive restoration efforts. The Virginia Marine Resources Commission (VMRC) manages the public oyster fishery and coordinates oyster restoration efforts in the Virginia portion of the Chesapeake Bay. Oyster restoration in Virginia and throughout the Chesapeake Bay focuses on shell replenishment, where clean oyster shells are added to reefs to increase reef height and provide habitat for juvenile oysters. Shell for replenishment is a limited and expensive resource, which limits how much and where replenishment can occur. Further, prior research on oyster replenishment focuses on marine protected areas, where fishing is not allowed. There is a critical need to evaluate the best way to apply limited shell to maximize the benefits to the overall oyster population and support a successful fishery.

The Rappahannock River is a major oyster producer in Virginia. VMRC manages the Rappahannock using a combination of rotational harvest areas and shell replenishment. Since the 2007-2008 harvest season, over 500,000 bushels of oysters worth over \$24 million (2023 USD) in dockside value were harvested in the Rappahannock River alone. Since 2000, VMRC has invested over \$14 million (2023 USD) towards replenishment in the Rappahannock. Long term monitoring data in the Rappahannock was used to evaluate how current management strategies impact oyster reefs and fisheries success.

METHODS

The analyses presented in this document incorporated data collected and maintained by the VMRC and Virginia Institute of Marine Science (VIMS). Data sources included the annual fisheries independent oyster patent tong survey (2003-2021), daily oyster harvest records (2007-2008 to 2020-2021 seasons), and shell replenishment records (2000-2021) from the Rappahannock River. Using generalized linear mixed effects models, this project examined how **rotational harvest area timing**, **marine protected areas (MPAs)**, and the **volume of shell** used for replenishment impacts oyster reefs and the oyster fishery. To understand the broad impacts from current management strategies, analyses considered four metrics: brown shell volume (L m^{-2}), spat density (m^{-2}), market oyster density (m^{-2}), and fisheries efficiency (meeting the daily bushel limit or not).

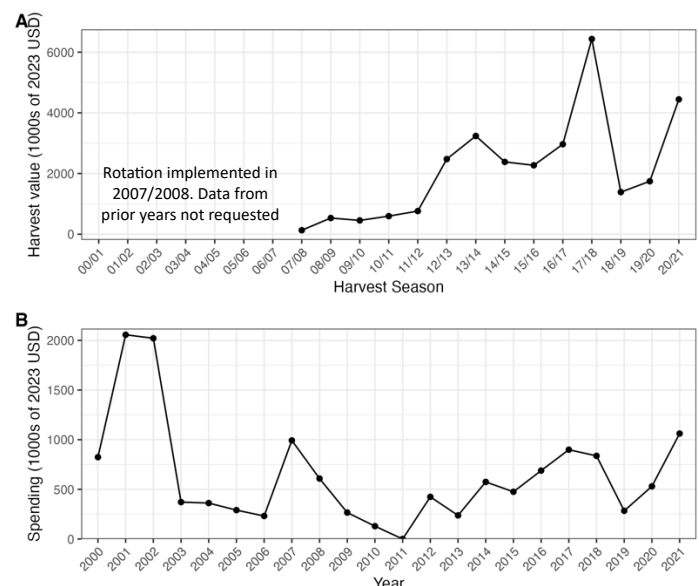


Fig. 1. Dockside value for harvest (A) and amount spent on replenishment efforts (B) in the Rappahannock.

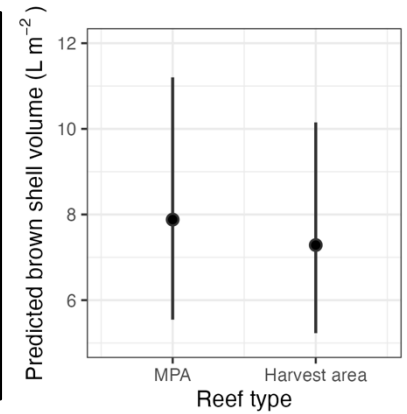
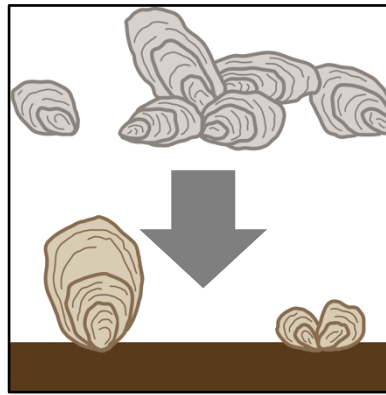
RESULTS

Our results demonstrate that the combination of shell replenishment, harvest area rotation, and marine protected areas enhance oyster reefs and the oyster fishery in the Rappahannock River.

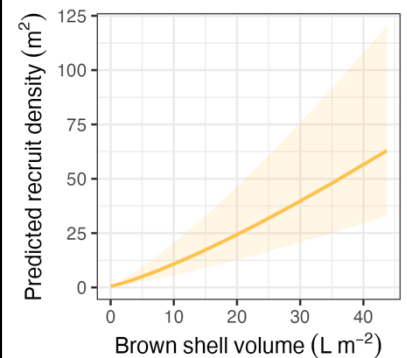
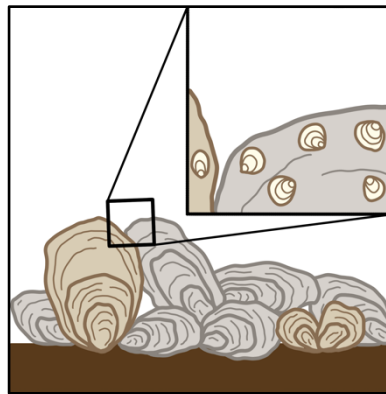
Specifically, regular **shell replenishment maintains the underlying reef structure** and reduces shell loss. Marine protected areas and harvest areas have comparable brown shell volume. **Spat density increased immediately after shell replenishment** was applied, suggesting that shell replenishment is providing additional habitat for young oysters. **Market oyster density peaked 3 years after shell replenishment** was applied. The current 3-year harvest area rotation allows oyster spat to grow to market size and is an optimal rotation interval in the Rappahannock. Additionally, harvest areas and marine protected areas had comparable reef structure (as brown shell volume, $L\ m^{-2}$), but marine protected areas had higher market oyster density on average. Marine protected areas offer protection to larger oysters, which may serve as valuable spawning stock. **Management practices directly enhanced harvester efficiency** (meeting the daily bushel limit or not), particularly in harvest areas with poor oyster reef condition. Low levels of shell replenishment (~ 1000 bushels $acre^{-1}$ on individual reefs with ~ 200 - 300 bushels suitable $acre^{-1}$ across a harvest area) provide benefits to oyster reefs and the oyster fishery. One challenge with this analysis is that harvest records are collected for harvest areas and not for individual reefs. The analysis cannot examine how the input of shell on an individual reef influences commercial harvest. Future efforts to collect harvest data at a finer spatial scale (e.g. individual reefs) would help optimize replenishment efforts and better understand the benefits (or drawbacks) to the oyster fishery.

Since shell replenishment and rotational harvest areas were implemented, oyster reefs have improved throughout the Rappahannock. Brown shell volume has steadily increased over time. Oyster spat density, though highly variable, was highest in recent years coinciding with higher brown shell volumes. Market oyster density has increased substantially since 2018. Oyster harvest has steadily increased as oyster reefs have improved in the Rappahannock.

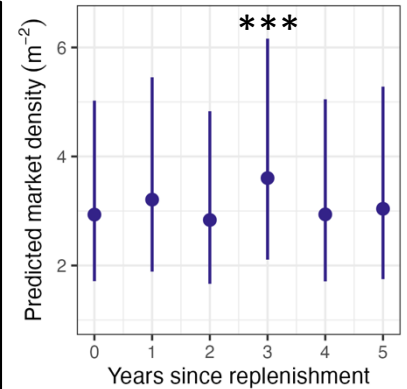
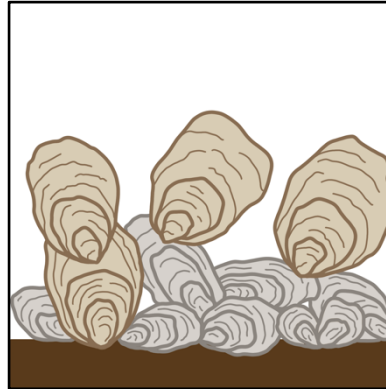
Shell replenishment maintains reef structure and habitat



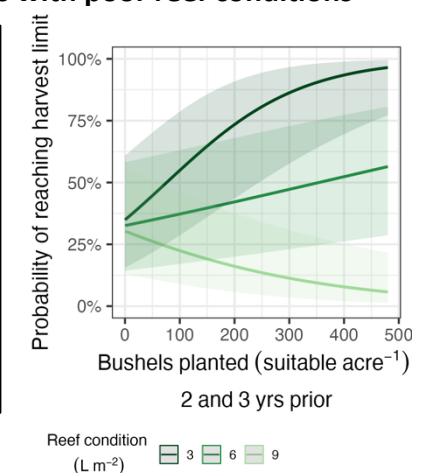
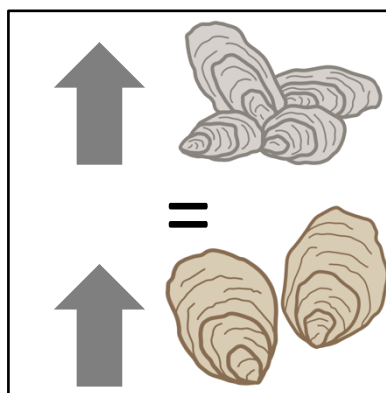
Increased habitat improves spat density



Market oyster density is enhanced with a 3-yr rotation



Replenishment improves harvester success, especially in harvest areas with poor reef conditions





Research article

Oyster reef recovery: Impacts of rotational management and restoration efforts on public fishing grounds

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ABSTRACT

Coastal ecosystems are degraded worldwide and oyster reefs are among the most threatened coastal habitats. Oysters are a critical ecosystem engineer and valuable fishery species, thus effective management strategies must balance tradeoffs between protecting reef ecosystems and continued human use. Management practices for oysters commonly incorporate shell replenishment (provisioning hard substrates to increase reef relief) and spatial management (rotational harvest areas or sanctuaries); however, the impact of these practices on reef dynamics and fisheries outcomes are poorly understood, particularly on harvested reefs. This project examines the efficacy of shell replenishment and spatial management practices on public fishing grounds by analyzing long term datasets available for the Rappahannock River in the Chesapeake Bay, USA. Using generalized linear mixed effects models, we examine how oyster reef metrics (brown shell substrate $L\ m^{-2}$, recruit density m^{-2} , market density m^{-2}) and fisheries efficiency (meeting daily bushel harvest limit or not) respond to management actions. Our results indicate that a 3 y rotation maintains the underlying reef structure, enhances recruitment, and increases market sized oyster density by 1.23 oysters m^{-2} on average. Sanctuaries and harvested reefs had comparable brown shell and recruit density; however, sanctuaries had higher market oyster density on average. Shell replenishment practices directly enhanced harvester efficiency, particularly in harvest areas with poor reef condition. Our results indicate that low levels of replenishment (~ 1000 bushels $acre^{-1}$) provide substantial benefits to oyster reefs and the fishery. This study is the first to evaluate the marginal benefits of replenishment activities for biological and fisheries outcomes, and a novel, real world assessment for oyster restoration practices on public fishing grounds. Cumulatively, our findings show that spatial management and replenishment practices enhance oyster reefs in temperate estuaries and offers a framework applicable to other degraded ecosystems worldwide.

1. Introduction

Effective natural resources management must balance tradeoffs between protecting ecosystems and continued human use. Human population density is nearly 3 times the global average in coastal regions (Small and Nicholls, 2003; Kummu et al., 2016). Coastal ecosystems face diverse pressures from human activities across global, regional, and local spatial scales, such as human induced climate change, ocean acidification, pollution, eutrophication, development and habitat loss, nonindigenous species introduction, and overexploitation (Jackson, 2001; Jackson et al., 2001; Thompson et al., 2002; Lotze, 2006; Halpern et al., 2008; Crain et al., 2009; Geist and Hawkins, 2016). No marine

areas are unaffected by human impacts and, in most countries, the majority of coastal regions are degraded (Halpern et al., 2008, 2019; Williams et al., 2022). Coastal regions support ecological processes and biodiversity, and provision critical ecosystem services that benefit humans and support livelihoods (Barbier et al., 2011; Scheld et al., 2024). Due to degradation, there is increasing effort to restore marine and coastal systems to enhance ecosystem services; however, restoration to an “original state” is not always possible and restoration targets may be in conflict with other uses (Mann and Powell, 2007; Crain et al., 2009; Geist and Hawkins, 2016). Restoration, in these cases, serves as mitigation, remediation, or rehabilitation. Managers may need to consider multiple objectives (e.g. fishery extraction, habitat maintenance) and

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spatial planning to reduce impacts to user groups and the environment.

The Chesapeake Bay is a large, biologically diverse estuary with a large watershed ($\sim 166,000 \text{ km}^2$) and extensive tidal shoreline ($\sim 18,800 \text{ km}$), which, similar to many estuaries around the world, has a history of anthropogenic modification and degradation. Indigenous peoples have lived in the Chesapeake Bay region for at least 13,000 y (late Pleistocene); however, major modification to the watershed occurred after European colonization (Miller, 2003; Kirby, 2004; Kirby and Miller, 2005; Rick et al., 2016). Historically the watershed was covered in temperate forests bordered by wetlands; however, after European colonization, land was progressively cleared for agriculture until the mid-1800s, at which time approximately half the Chesapeake Bay drainage basin was cleared (Brush et al., 1980; Brush, 1986; Kemp et al., 2005). Human populations have increased exponentially in the Chesapeake Bay region since colonial times and anthropogenic activities have negatively impacted water quality and overall ecosystem health (Cooper and Brush, 1991; Kemp et al., 2005; Bhatt et al., 2023). Excess nutrients and sedimentation over decades have led to organic enrichment, increased phytoplankton, and severe, recurring hypoxia events that negatively impact living resources, such as fish and invertebrates (Kemp et al., 2005; Ludsins et al., 2009; Seitz et al., 2009). Further, advances in technology allowed for increasingly efficient overexploitation of fish and invertebrate species (Cronin, 1986; Jackson et al., 2001). Consequently, the Chesapeake Bay experienced substantial declines in a keystone species, the eastern oyster (*Crassostrea virginica* Gmelin, 1791).

Oysters are an ecosystem engineer and valuable fishery species in temperate, boreal, and subtropical estuaries; however, oyster populations have declined globally (Kirby, 2004; Beck et al., 2011). Oysters provide critical ecosystem services that enhance estuarine health, including stabilizing shorelines, reducing eutrophication by filter feeding, carbon sequestration, and providing complex reef habitat, among others (Peterson et al., 2003; Newell, 2004; Coen et al., 2007; Grabowski et al., 2012). Estuaries typically have high sediment loads and limited available hard substrates (Thrush et al., 2004). Oyster reefs create niche space and provide nursery habitat for fishes and invertebrates (Coen et al., 1999; Harding and Mann, 1999, 2001; Karp et al., 2018), serving comparable functions as tropical coral reefs (Moberg and Folke, 1999; Woodhead et al., 2019). In the Chesapeake Bay, eastern oysters declined due to the combination of intensive overfishing and disease epizootics (*Perkinsus marinus*, “Dermo” and *Haplosporidium nelsonii*, “MSX”), which decreased oyster abundance and individual longevity (Haskins and Andrews, 1988; Rothschild et al., 1994; Andrews, 1996; Kirby, 2004). Oysters have a biphasic life cycle, where pelagic larvae develop in the water column prior to settling, metamorphosing, and adopting a sessile lifestyle. Oyster larvae preferentially settle on adult oyster shell, thereby forming complex reefs; however, reefs only persist if the accretion rate of shell material is higher than losses (Galtsoff, 1964; Tamburri et al., 1996; Mann and Powell, 2007). Oysters were a highly accessible, common pool resource in the Chesapeake Bay, which made them susceptible to overexploitation. The Virginia Marine Resources Commission (VMRC) manages the public oyster fishery and coordinates oyster restoration efforts in the Virginia portion of the Chesapeake Bay. Oyster harvest removes larger individuals, which, if left in the environment, would grow, die, and contribute to the reef structure. Thus, managers need to consider two reference points for oysters: biological production (i.e. adult spawning biomass) and maintenance of the underlying reef structure (i.e. brown shell substrate, defined as shell material above the sediment-water interface) (Powell and Klinck, 2007; Powell et al., 2012; Hemeon et al., 2020; Solinger et al., 2022). A common restoration practice for oyster reefs is shell replenishment. Replenishment involves adding material (e.g. shell from commercial shucking houses, fossil shell, juvenile oysters attached to shell, and/or granite) to increase reef relief and provide settlement habitat for juvenile oysters. Further, managers may employ rotational harvest, where public fishing grounds are open to harvest and then closed for multiple years to allow oyster reefs to

recover (Kjelland et al., 2015; Kennon et al., 2023; Steyn et al., 2023). Management actions are intended to maintain or recover oyster populations, reef habitat, and their ecosystem benefits, while continuing to support commercial use and local economies. Though shell replenishment and rotational management are common management interventions, their impact on oyster reef dynamics and fisheries outcomes are poorly understood and rarely assessed in real world scenarios.

The Rappahannock River provides a unique opportunity to assess spatial management and replenishment practices on public fishing grounds. The Rappahannock is a microtidal, partially-mixed sub estuary of the Chesapeake Bay (Pierce and Nichols, 1986) and a major producer for market sized oysters (Haven and Whitcomb, 1986; Whitcomb and Haven, 1989), with approximately 22% of the bottom either containing oysters or suitable habitat. The oyster fishery in the Rappahannock is relatively self-contained, where the majority of oysters harvested are landed in the Rappahannock. The VMRC defined 9 harvest areas in the Rappahannock and, in 2007, adopted a rotational management strategy for the 6 downriver harvest areas (areas 1–6, Fig. 1). Generally, two of these downriver harvest areas are open to harvest in a given year. Since 2000, oyster reefs in the Rappahannock have regularly received shell replenishment. Fisheries independent oyster population monitoring has occurred in the Rappahannock for over 20 years. The Rappahannock typifies a highly productive, microtidal, temperate estuary and conclusions from this system are broadly applicable to oyster management in other temperate estuaries.

The project objective is to examine the efficacy of spatial management (harvest area rotation and sanctuaries) and shell replenishment practices on public oyster fishing grounds by leveraging long term datasets available for the Rappahannock River. Specifically, we examine how management actions (replenishment volume, replenishment and rotation interval, sanctuaries) impact oyster reef metrics (brown shell substrate L m^{-2} , recruit density m^{-2} , market density m^{-2}) and fisheries efficiency (meeting daily bushel limit or not). Our findings indicate that current spatial management and shell replenishment practices are supporting both oyster reef dynamics and positive fishery outcomes. We explore how these strategies can optimize oyster reef recovery, offering a framework applicable to other degraded ecosystem worldwide.

2. Materials and methods

To examine the efficacy of spatial management and replenishment practices on public oyster fishing grounds, we integrated long term data sources from the Rappahannock River in the Chesapeake Bay, USA.

2.1. Data sources

2.1.1. Oyster population data

Annual fisheries independent patent tong surveys for oysters started in 1993 in the western tributaries of the Chesapeake Bay, as well as Tangier and Pocomoke sounds (Mann and Wesson, 1994, 1997). Early surveys did not include all currently surveyed reefs in the Rappahannock and the reef boundaries changed over time; however, 26 downriver reefs in the Rappahannock were standardized and annual data collection started in 2000, with additional reefs added in subsequent years. During the fall months, a patent tong is used to sample multiple, random 1 m^2 of bottom reef habitat on 59 oyster reefs in the Rappahannock (Table S1). Each reef has a unique reef identification number. Five reefs were excluded from all analyses due to being recently built in 2018 (1 reef), falling outside of any managed harvest areas (3 reefs) or undergoing frequent changes in regulatory status (1 reef). Oysters collected in the patent tong are measured from umbo to ventral margin (length). Since 2003, oyster length has been measured to the nearest millimeter (Southworth et al., 2010). Oysters reach commercial market size at 76 mm in length. Oysters are qualitatively assessed, based on their growth margins as either recent recruits or adult oysters. Oyster density is estimated for each reef, which may be enumerated as recruit,

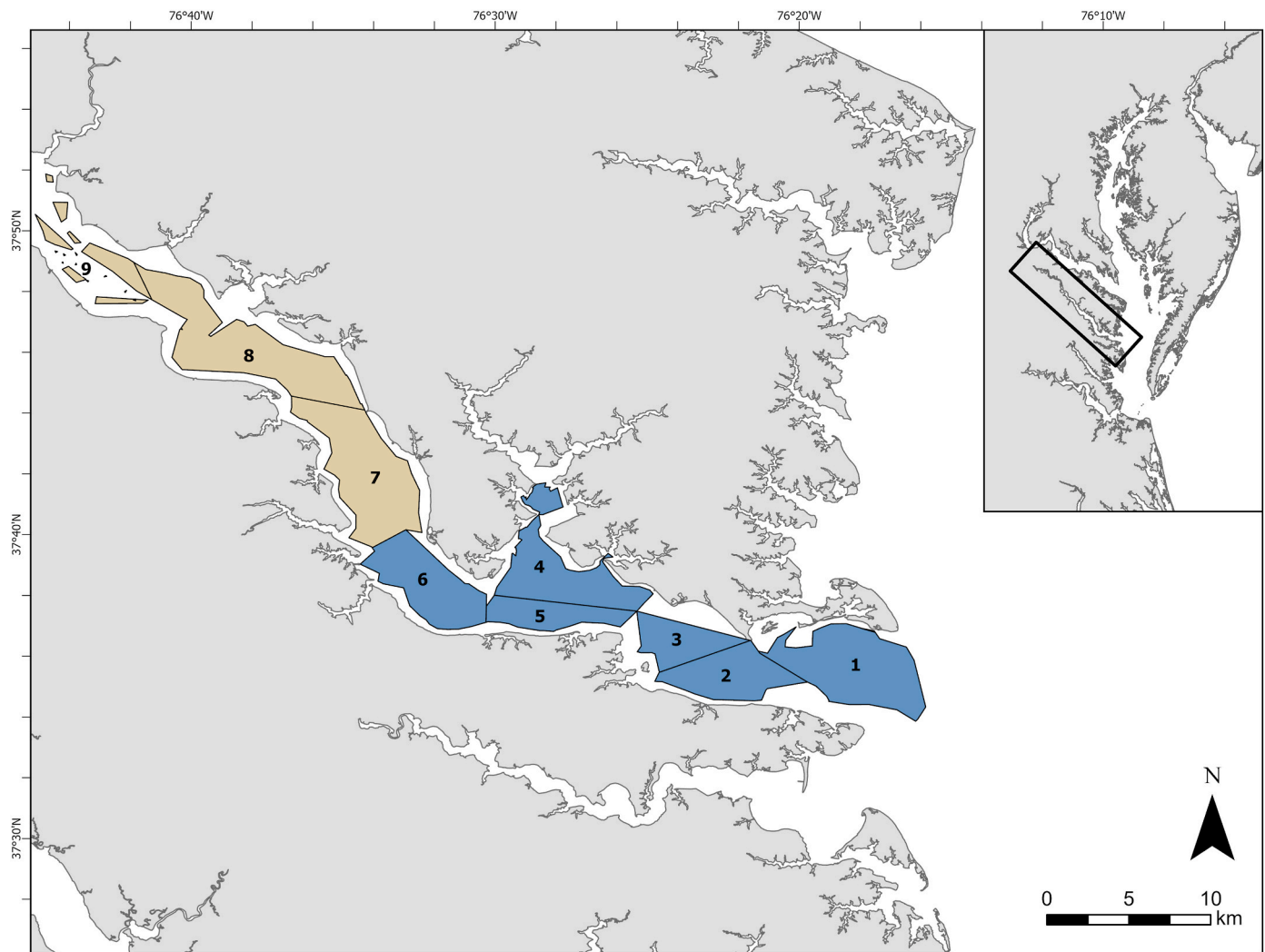


Fig. 1. Harvest areas in the Rappahannock River. VMRC uses rotational management practices in harvest areas 1–6 (blue). Harvest areas 7–9 (tan) do not experience rotational management and are open to harvest regularly.

submarket, or market sized oyster density (m^{-2}). The volume of brown shell substrate (L m^{-2}) above the water-sediment interface and depth (ft) is recorded for each sample. Long term monitoring data allows us to examine how the reef structure (Fig. 2A), recruitment (Fig. 2B), and market oyster density (Fig. 2C) vary over space and time. The patent tong methods are described more thoroughly in Mann et al. (2009a,b), Southworth et al. (2010), and Harding et al. (2010).

Using the patent tong survey data, we created biological covariates for individual reefs and harvest areas from 2003 to 2021. For each reef and year combination, we calculated the mean brown shell substrate (L m^{-2}), mean submarket oyster density (m^{-2}), and mean oyster density (submarket and market oysters m^{-2}) in the prior year. For each harvest area and year combination, we calculated a weighted mean market oyster density (m^{-2}) and weighted mean brown shell substrate (L m^{-2}) averaged across 2 and 3 year lags. We weighted these covariate estimates by reef size, such that reefs with a larger spatial footprint had a greater contribution to the harvest area wide estimate for the biological state of the resources.

2.1.2. Harvest data

In 2007 VMRC began requiring mandatory harvester reports from commercial fishers, instead of buyer reports, to monitor oyster harvest. Commercial fishers in Virginia's oyster fishery are required to submit monthly reports which detail their daily harvest, including gear used,

tributary fished, amount harvested (bushels; 1 bushel = 49.2 L in Virginia), pounds harvested, water body code (differentiates sections of the river which comprise multiple harvest areas), and, for harvest records from 2016 to present, the harvest area. Registered commercial buyers are surveyed quarterly to determine harvest value (USD). Harvest is generally open from October to March, and includes separate subseasons for fall and spring harvest.

We requested oyster harvest records from the Rappahannock River from VMRC spanning the 2007–2008 to 2020–2021 harvest seasons. VMRC provided a total of 50,250 harvest records from this time frame. We error checked the harvest records to ensure that both the harvest area and gear types matched annual oyster harvest regulations set by VMRC. For records prior to 2016, we used the reported water body code and annual VMRC regulations to identify the harvest area for each record. If two harvest areas were open in a water body code at one time, we coded them as a mixed harvest area and created weighted biological metrics using observations from both harvest areas. We excluded 3,140 harvest records due to either irreconcilable errors (e.g. reports when no areas were open to harvest) or being unable to identify the harvest area; however, we successfully error checked and validated 47,032 harvest records comprising 532,566 bushels (3,621,341 pounds or 1,642,613 kg) of oysters worth over \$24 million (2023 USD) in dockside value (Fig. 3A). For the validated harvest records, we assessed if each harvest record had met the daily bushel limit. Daily harvester bushel limits were

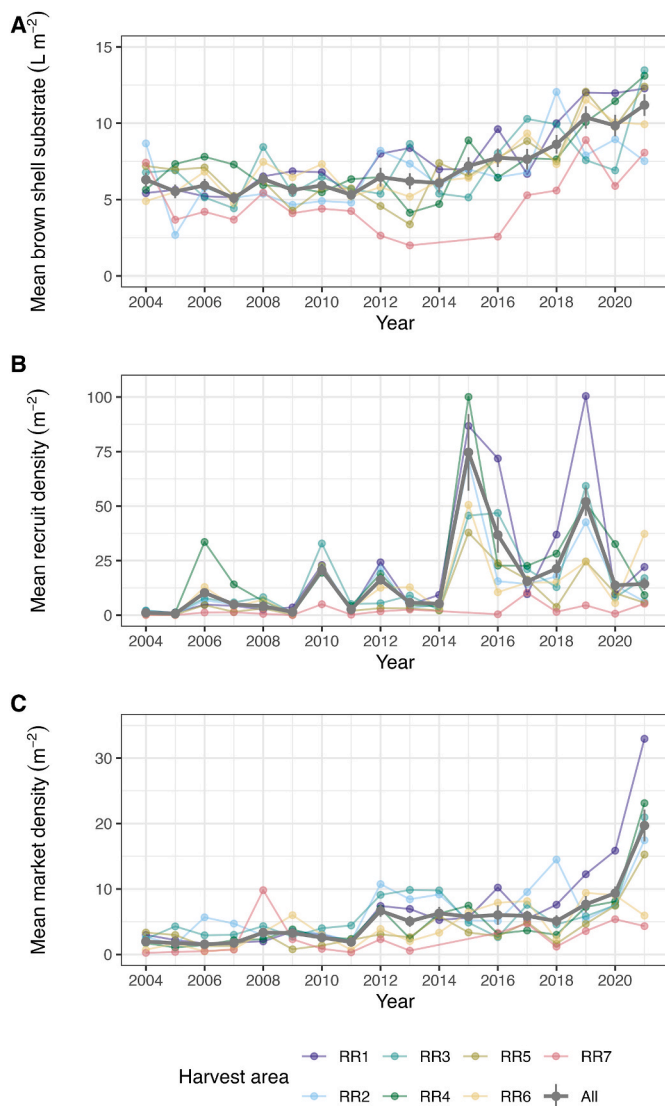


Fig. 2. Mean brown shell substrate (A), recruit density (B), and market oyster density (C) across surveyed reefs in the 7 lower harvest areas in the Rappahannock River. Data is from the annual fisheries independent patent tong survey. Colored lines and points are the average response for each harvest area. Grey line and points show the average across all harvest areas with the bars indicating SE.

either 8 or 10 bushels per harvester per day. Vessel limits were initiated in the 2011–2012 harvest season, which limited the number of harvesters to 3 (2011–2012 to 2016–2017 season) or 2 (2017–2018 to 2020–2021 season) license holders per vessel.

2.1.3. Replenishment data

VMRC coordinates shell replenishment in the western tributaries of the Chesapeake Bay. VMRC maintains records of replenishment efforts, which include the year applied (2000–2021), location (tributary and reef id), volume of material planted (in bushels or tons), type of material planted (e.g. shell, fossil, seed, granite) and costs for planting (USD). Oyster seed plantings are often sourced from other tributaries; however, the origin of seed was not recorded for all seed transfers. Between 2000 and 2021, the Rappahannock received 310 replenishment events, the majority of which were shell based (98%, 305 of 310 records). On average, reefs received 1090 bushels acre^{-1} (± 828 SD; range 28.7 to 9,940 bushels acre^{-1}) in shell based replenishment across the time series. In the Rappahannock River, fishing is generally not permitted on reefs for 2–3 years following replenishment efforts. Since 2000, VMRC

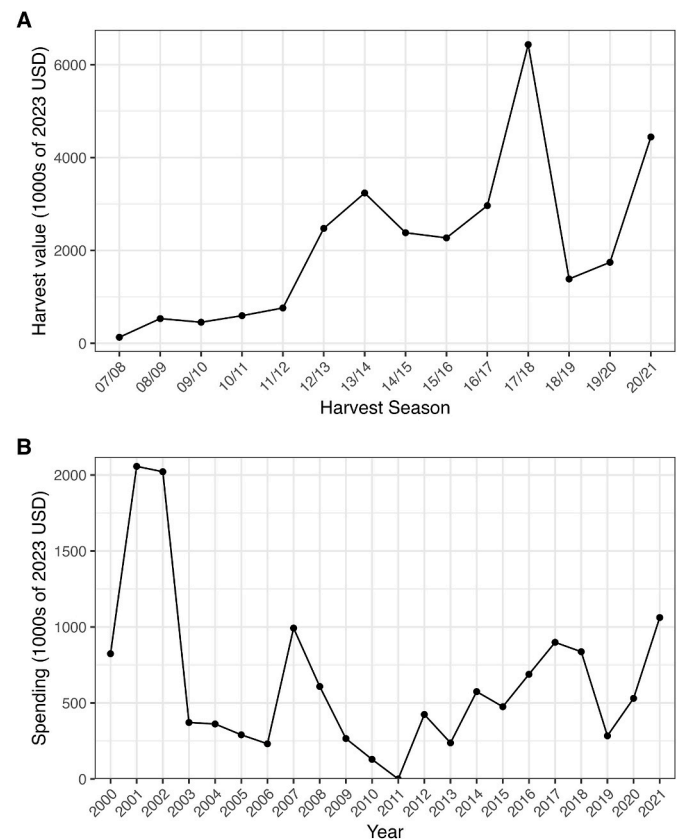


Fig. 3. Dockside value for oyster harvest (A) and amount spent on replenishment efforts (B) in the Rappahannock River over time.

has invested over \$14 million (2023 USD) towards replenishment in the Rappahannock (Fig. 3B).

To assess the impact of shell replenishment on biological oyster metrics and fisheries efficiency we focused on shell based materials (shell from commercial shucking houses, fossil shell, or seed). Biological oyster metrics are at the reef level, so we standardized bushels of replenishment applied each year by the acreage (1 acre = 4,046.9 m^2) of the reef (bushels acre^{-1}) and determined the number of years since replenishment was applied for each reef. We subset the biological data to only include observations which received replenishment within 5 years to coincide with the typical lifespan of oysters in the Chesapeake Bay (Harding et al., 2013; Mann et al., 2014). Harvester efficiency is at the harvest area level, so replenishment applied each year was aggregated to the harvest area (total replenishment applied to reefs in a harvest area) and standardized by the area of suitable bottom in the harvest area (bushels suitable acre^{-1}). We calculated the total acres of suitable oyster bottom on public oyster grounds in each harvest area based on Mann et al. (2021) (<https://cmap2.vims.edu/OysterInfoToolVa/>).

2.2. Statistical approach

To investigate the impacts of shell replenishment on biological oyster metrics and fisheries efficiency, we used generalized linear mixed effects models (GLMMs). GLMMs are flexible, and can accommodate nested data structures and a wide range of response distributions (Zuur et al., 2009). GLMMs use the general form:

$$y = Xb + Zu + e$$

$$u \sim N(0, \sigma_u^2)$$

$$e \sim N(0, \sigma_e^2 I)$$

where, \mathbf{y} is a vector of observations, \mathbf{b} is a vector of fixed effects, \mathbf{u} is a vector of random effects, \mathbf{X} and \mathbf{Z} are design matrices for the fixed and random effects, respectively, \mathbf{e} vector of the residual error, and \mathbf{I} is the identity matrix. Fixed effects are defined as variables where the specific effects of levels are of interest, whereas random effects are variables where interest is in the variability among levels (Bolker et al., 2009).

All analyses were completed in the glmmTMB package, which estimates p-values using a Wald Z-statistic (Brooks et al., 2017). For each response variable, we determined the best fitting random effects structure using the full additive model, and then refined the fixed effect structure. We identified the best fitting model using a combination of diagnostic plots, information criterion (AICc, BIC; Sakamoto et al., 1986; Burnham and Anderson, 2004), and likelihood ratio tests. Models within two ΔAICc were considered strongly supported. If multiple models were strongly supported, we used ΔBIC to identify the most parsimonious model. Diagnostic plots were created using the DHARMA package (Hartig, 2022), which uses estimated residuals from 1,000 simulations. We used a Durbin-Watson test on scaled residuals for each year to assess for temporal autocorrelation. If present, we included an $\text{ar}(1)$ on the best fitting model and used a likelihood ratio test to determine if the fit was substantially improved.

2.2.1. Biological metrics response to replenishment

We examined three separate biological response variables, which included brown shell substrate (L m^{-2}), oyster recruit density (m^{-2}), and market oyster density (m^{-2}). For the biological models, we considered GLMMs with random intercepts for year, year and reef id, and the interaction between year and reef id. For all response variables, a random intercept for the interaction between year and reef id was the best fit. We focused the analyses on reefs in harvest areas 1–7 (Fig. 1) and years 2004–2021. We used a Tweedie GLMM to assess how brown shell substrate (L m^{-2}) varied in response to reef type (harvested or sanctuary), number of years since replenishment was applied, bushels of replenishment acre^{-1} , depth, and the mean brown shell substrate m^{-2} in the prior year. We used a negative binomial GLMM to assess how oyster recruit density (m^{-2}) varied in response to reef type (harvested or sanctuary), number of years since replenishment was applied, bushels of replenishment acre^{-1} , depth, and the natural log of brown shell substrate (L m^{-2}). We used a negative binomial GLMM to assess how market oyster density (m^{-2}) varied in response to reef type (harvested or sanctuary), number of years since replenishment was applied, bushels of replenishment acre^{-1} , depth, the natural log of brown shell substrate m^{-2} , and mean number of juvenile oysters in the prior year m^{-2} . Baseline conditions from the prior year were included to tease out marginal increases from replenishment.

2.2.2. Fisheries efficiency response to replenishment

We examined one fisheries response variable, fisheries efficiency. We defined fisheries efficiency as if a harvester had met the daily bushel limit or not. For the efficiency model, we considered GLMMs with random intercepts for harvest season, harvest season and subseason, the interaction between harvest season and subseason, and harvest area and the interaction between harvest season and subseason. We focused the analyses on harvest areas 1–7 (Fig. 1) and harvest seasons 2007/2008 to 2020/2021. We used a binomial GLMM to assess how harvester efficiency varied in response to weighted mean market oyster density m^{-2} in a harvest area at the time of harvest, bushels of replenishment suitable acre^{-1} applied 2 and 3 years prior in the harvest area, and weighted mean brown shell substrate in a harvest area (L m^{-2}) when replenishment was applied.

To estimate the impact of replenishment on the commercial fishery, we examined how predicted harvester efficiency with replenishment compared to a scenario with no replenishment. We then calculated the difference in efficiency for each harvest record to quantify how replenishment practices influence the probability a harvester reaches

the limit and change in bushels of oysters harvested.

3. Results

Our best fitting models (Tables 1 and 2) indicate that replenishment practices enhance brown shell substrate (L m^{-2}), recruit density (m^{-2}), market density (m^{-2}) and fisheries efficiency in the Rappahannock River; though the benefits occur through different mechanisms.

3.1. Brown shell substrate model

We observed similar brown shell substrate between harvested and sanctuary reefs ($\beta = -0.08$, $z = -0.99$, $p = 0.32$) suggesting that current management practices are successfully maintaining the underlying reef structure. Compared to when replenishment was applied (year 0), we observed a slow decline in brown shell substrate over time (Fig. 4A). Years 0 and 1 had equivalent brown shell substrate on average ($\beta_{\text{yr}1} = -0.088$, $z = -1.47$, $p = 0.14$). In years 2 and 3, we observed a marginally significant reduction in brown shell substrate on average ($\beta_{\text{yr}2} = -0.11$, $z = -1.79$, $p = 0.07$; $\beta_{\text{yr}3} = -0.12$, $z = -1.79$, $p = 0.07$). In years 4 and 5, we observed a significant reduction in brown shell substrate ($\beta_{\text{yr}4} = -0.18$, $z = -2.55$, $p = 0.01$; $\beta_{\text{yr}5} = -0.31$, $z = -3.90$, $p < 0.001$). Brown shell substrate did not change in response to bushels applied per acre as replenishment on average ($\beta = 0.00002$, $z = 0.65$, $p = 0.52$), which may be due to the relatively low replenishment levels over a small spatial footprint or a mismatch between survey (fall) and replenishment (summer) timing that does not capture the decrease in shell volume directly after harvest. Mean brown shell substrate in the prior year had a positive relationship with brown shell substrate ($\beta = 0.039$, $z = 6.10$, $p < 0.001$; Fig. 4B). Reefs with higher brown shell substrate in the prior year were associated with higher brown shell substrate on average; however, there is shell loss between years.

3.2. Recruit density model

We observed similar recruit density between harvested and sanctuary reefs ($\beta = -0.33$, $z = -1.52$, $p = 0.13$). Compared to when replenishment was applied (year 0), recruit density was similar across the years (1–5) on average ($p \geq 0.1$); however, there was weak evidence for a small decrease in spat density two years after replenishment is applied ($\beta_{\text{yr}2} = -0.19$, $z = -1.65$, $p = 0.1$). We found weak evidence that recruit density increases as the number of bushels planted acre^{-1} increases. ($\beta = 0.00012$, $z = 1.76$, $p = 0.096$; Fig. 5A). Recruit density decreased with depth on average ($\beta = -0.03$, $z = -3.24$, $p = 0.001$; Fig. 5B). On average, recruit density increased as the natural log of brown shell substrate increased ($\beta = 1.26$, $z = 65.84$, $p < 0.001$; Fig. 5C).

3.3. Market density model

On average, market oyster density was significantly higher at sanctuary reefs than harvested reefs ($\beta = -0.38$, $z = -3.88$, $p < 0.001$; Fig. 6A). Compared to when replenishment is applied (year 0), we observed an increase in market oyster density in year 3 ($\beta_{\text{yr}3} = 0.21$, $z = 2.10$, $p < 0.05$; Fig. 6B), which corresponds to the time it takes an oyster to grow to market size in the Rappahannock River (Mann et al. Unpub data; Santopietro et al., 2009; Mann et al., 2022). The increase is equivalent to approximately 1.23 oysters m^{-2} on average or nearly 5,000 market sized oysters acre^{-1} . In years 1, 2, 4, and 5, market density did not differ from year 0 ($p > 0.1$). Market oyster density m^{-2} did not change in response to the volume of bushels applied acre^{-1} to the reef as replenishment ($\beta = 0.0005$, $z = 0.09$, $p = 0.92$). Market density increased with depth on average ($\beta = 0.02$, $z = 3.17$, $p = 0.002$; Fig. 6C). On average, market density increased as the natural log of brown shell substrate increased ($\beta = 1.17$, $z = 56.21$, $p < 0.001$; Fig. 6D). Mean submarket density in the prior year had a positive relationship with market density ($\beta = 0.007$, $z = 4.84$, $p < 0.001$; Fig. 6E).

Table 1

Model selection results from GLMMs for brown shell substrate ($L\ m^{-2}$), oyster recruit density (m^{-2}) and market oyster density (m^{-2}). For each model, the number of fixed effects (k), Akaike's information criterion corrected for small sample sizes (AICc), change in AICc relative to the top-ranked model ($\Delta AICc$), Bayesian information criterion (BIC), change in BIC relative to the top-ranked model (ΔBIC). Shaded rows indicate the best fitting model for a given response variable. Harvest: if reef is in a harvest area; repyrs: number of years since replenishment was applied (0–5); bushels_std: bushels of replenishment applied $acre^{-1}$; brownshell: brown shell substrate ($L\ m^{-2}$); mbss1: mean brown shell substrate in the prior year ($L\ m^{-2}$); moys1: mean oyster density in the prior year (m^{-2}); msma1: mean submarket oyster density in the prior year (m^{-2}); depth: depth for each sample (ft).

Parameters	k	AIC	$\Delta AICc$	BIC	ΔBIC
Brown shell substrate model					
harvest + repyrs + bushels_std + mbss1 + ar(1)	16	27438.4	0	27541.5	-1.8
harvest + repyrs + bushels_std + depth + mbss1	15	27449.3	-10.9	27546.0	-6.3
harvest + repyrs + bushels_std + mbss1	14	27449.5	-11.1	27539.7	0
harvest + repyrs + bushels_std	13	27494.1	-55.6	27577.8	-38.1
Oyster recruit model					
harvest + repyrs + bushels_std + moys1 + log(brownshell) + depth	14	24858.7	0	24948.9	0
harvest + repyrs + bushels_std + moys1 + log(brownshell)	13	24867.4	-8.6	24951.1	-2.2
harvest + repyrs + bushels_std + moys1 + brownshell + l(brownshell^2) + depth	15	25512.3	-635.5	25608.9	-660.0
harvest + repyrs + bushels_std + moys1 + brownshell + depth	14	26063.0	-1204.3	26200.3	-1251.3
Market oyster model					
harvest + repyrs + bushels_std + msma1 + log(brownshell) + depth + ar(1)	17	19740.1	0	19849.6	-8.3
harvest + repyrs + bushels_std + msma1 + log(brownshell) + depth	15	19744.7	-4.6	19841.3	0
harvest + repyrs + bushels_std + msma1 + log(brownshell)	14	19752.9	-12.8	19843.1	-1.8
harvest + repyrs + bushels_std + msma1 + brownshell + l(brownshell^2) + depth	16	19993.9	-253.9	20097.0	-255.7
harvest + repyrs + bushels_std + msma1 + brownshell + depth	15	20548.9	-808.9	20645.6	-804.3

Table 2

Model selection results from GLMM for efficiency. For each model, the number of fixed effects (k), Akaike's information criterion corrected for small sample sizes (AICc), change in AICc relative to the top-ranked model ($\Delta AICc$), Bayesian information criterion (BIC), change in BIC relative to the top-ranked model (ΔBIC). Shaded row indicates the best fitting model. Harvest: if reef is in a harvest area; bushels23_std: bushels of replenishment applied suitable $acre^{-1}$ 2 and 3 years prior; wmmar: weighted mean market oyster density in the harvest area (m^{-2}); wmbss23: weighted mean brown shell substrate ($L\ m^{-2}$) in the harvest area when shell replenishment was applied.

Efficiency Model	k	AIC	$\Delta AICc$	BIC	ΔBIC
wmmar + bushels23_std*wmbss23 + ar(1)	11	51124.9	0	51220.7	-15.6
wmmar + bushels23_std*wmbss23	9	51126.8	-1.8	51205.2	0
wmmar + bushels23_std + wmbss23	8	51145.6	-18.7	51213.3	-8.2
wmmar + bushels23_std	7	51150.7	-25.8	51211.7	-6.5

3.4. Fisheries efficiency model

On average, the probability a harvester met the daily harvest limit increased as the weighted mean market oyster density increased in a harvest area ($\beta = 0.08$, $z = 9.22$, $p < 0.001$; Fig. 7A). The bushels of replenishment suitable $acre^{-1}$ applied 2 and 3 years prior in the harvest area influenced the probability a harvester met the daily harvest limit; however, the effect depended on the condition of the reef at the time replenishment was applied (Fig. 7B). Replenishment applied in harvest areas with worse reef condition, defined as having lower weighted mean brown shell substrate, received a greater benefit to harvester efficiency ($\beta_{bushels} = 0.014$, $z = 4.10$, $p < 0.001$; $\beta_{reefcondition} = -0.03$, $z = -1.65$, $p = 0.10$; $\beta_{bushels*reefcondition} = -0.002$, $z = -4.03$, $p < 0.001$).

Across the time series, replenishment practices were associated with a 1% ($\pm 2\%$ SD, range -5 to 9%) increase in harvester efficiency; however, the difference in efficiency, and thus impacts of replenishment,

was variable (Fig. 8). When the effect of replenishment was positive, harvesters had a 2% increase in the probability of reaching the harvest limit on average (range 0.05–9%). When the effect of replenishment was negative, harvesters had a 1% decrease in the probability of reaching the harvest limit on average (range -0.02 to -5%). Further, replenishment was more effective at improving fisheries outcomes earlier in the time series when harvest areas in the Rappahannock had lower reef condition and harvester efficiency was substantially lower (Figs. 8 and 9).

3.5. Cumulative results and implications

Our results demonstrate that spatial management practices enhance biological oyster metrics. Specifically, a 3 year rotation supports oyster reef dynamics across the life history. Regular shell replenishment maintains the underlying reef structure (brown shell substrate; Fig. 4A), and reduces shell loss from the combination of fisheries extraction and

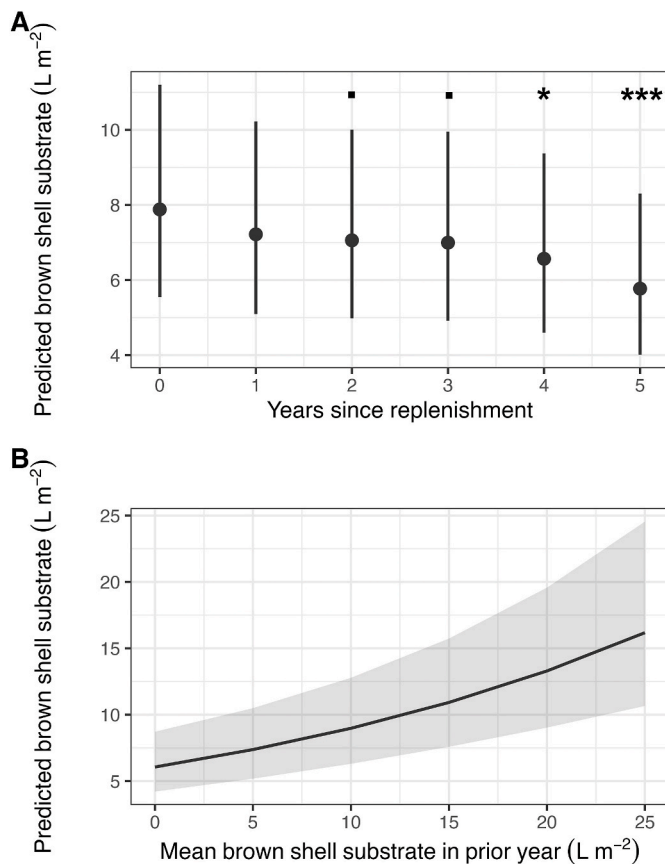


Fig. 4. Marginal effect plots displaying the effect of (A) years since replenishment was applied and (B) mean brown shell substrate in the prior year on brown shell substrate. Lines (A) and shading (B) represent 95% confidence intervals. In panel A, significance level relative to year 0 is denoted (* $p < 0.1$; * $p < 0.05$; *** $p < 0.001$).

taphonomic losses from breakage, bioerosion, and dissolution. We observed an increase in oyster recruitment immediately after replenishment was applied, indicating that the enhancement to the underlying reef structure successfully increased reef surface area. Reef surface area is critical for successful oyster recruitment to the population (Hemeon et al., 2020; Solinger et al., 2022) and we observed higher oyster recruitment with increases in brown shell substrate (Fig. 5C). Market oyster density increased 3 years after replenishment was applied (Fig. 6B), indicating that a 3 year harvest area closure enabled the newly recruited oysters to grow to market size without disturbance prior to the next harvest season. Further, oyster sanctuaries and harvest areas had comparable brown shell substrate and recruitment density; however, sanctuaries maintained higher market sized oyster density (Fig. 6A). Thus, sanctuaries offer protection to larger oysters, which may serve as important spawning stock. Comparable brown shell substrate between sanctuaries and harvested reefs provides evidence that current management practices are successfully maintaining the underlying reef structure.

Our results demonstrate that shell replenishment practices directly enhance harvester efficiency, particularly in harvest areas with poor reef condition. We observed diminishing returns with increases in the bushels of shell planted suitable acre⁻¹ (Fig. 7B) and the benefits from replenishment were variable over time (Fig. 8). Our results indicate that low levels of replenishment (~1000 bushels acre⁻¹ on individual reefs with ~200–300 bushels suitable acre⁻¹ across a harvest area) provide benefits to oyster reefs and the oyster fishery. Optimizing plantings can support positive fisheries outcomes and reduce the costs associated with oyster reef maintenance on public fishing grounds.

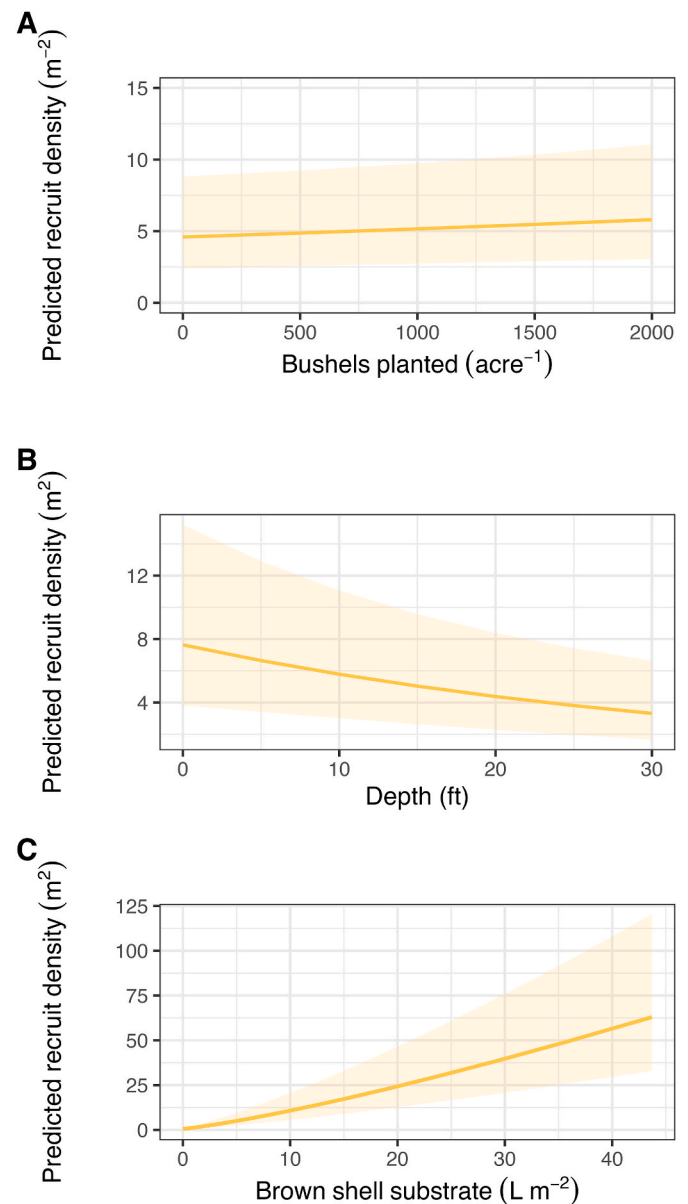


Fig. 5. Marginal effect plots displaying the effect of (A) bushels planted, (B) depth, and (C) brown shell substrate on oyster recruit density. Shading represents 95% confidence intervals.

Since shell replenishment and rotational harvest areas were implemented, oyster reefs have improved throughout the Rappahannock. Brown shell substrate has been steadily increasing over time (Fig. 2A). Recruitment, though highly variable, was highest in recent years coinciding with higher brown shell substrate across the harvest areas (Fig. 2B). Market oyster density was relatively stable across the harvest areas; however, mean market density has increased substantially since 2018 (Fig. 2C). Cumulatively, our findings indicate that spatial management and shell replenishment practices enhance oyster reefs in temperate estuaries, and offer a framework applicable to other degraded ecosystem worldwide.

4. Discussion

Broadly, this study examines how management and restoration strategies impact competing management goals (e.g. commercial harvest of an ecosystem engineer, maintaining biogenic habitat) in a coastal ecosystem. The project objective is to examine the efficacy of spatial

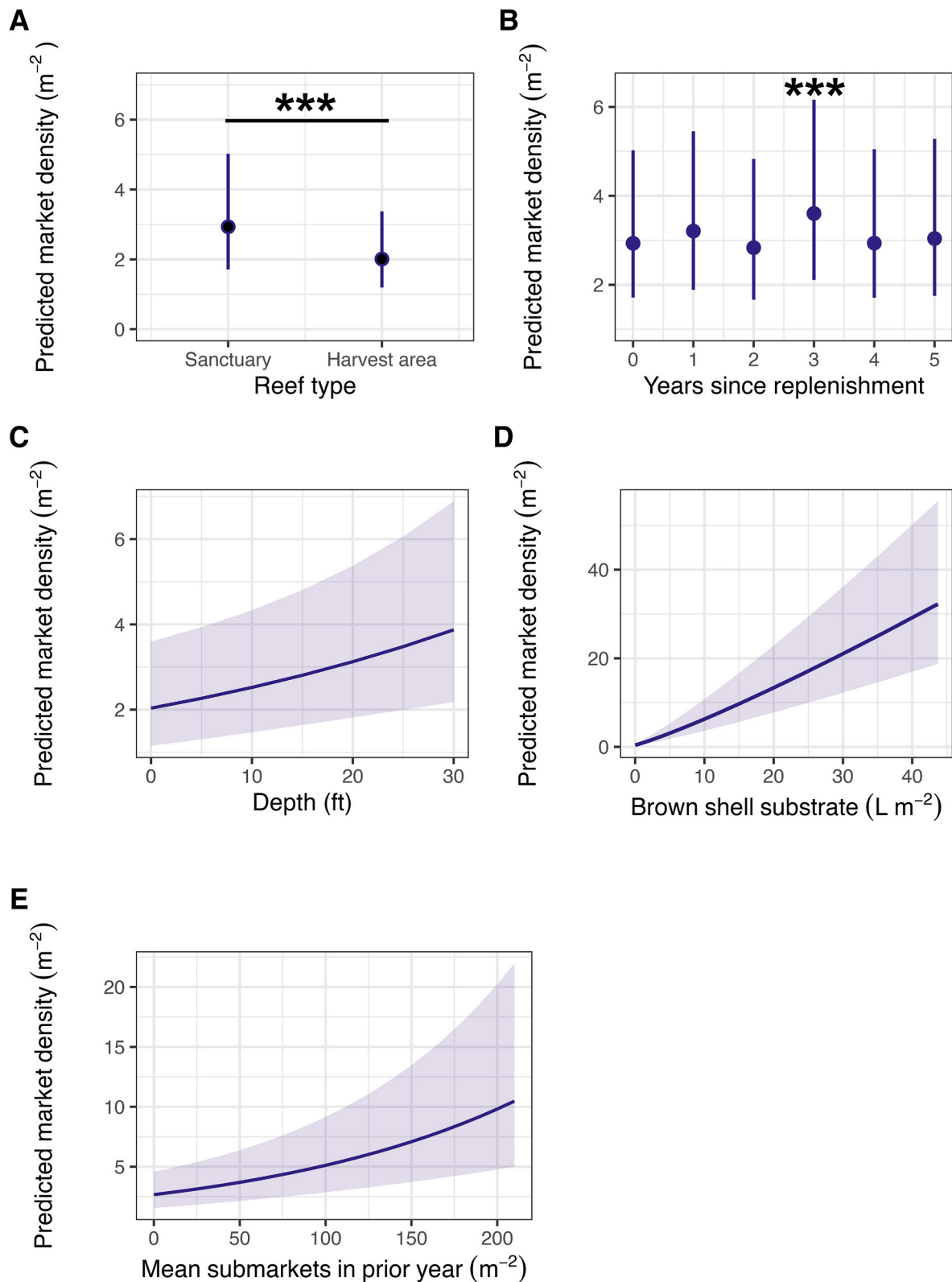


Fig. 6. Marginal effect plots displaying the effect of (A) reef type, (B) years since replenishment, (C) depth, (D) brown shell substrate, and (E) mean submarket density in the prior year on market oyster density. Lines (A, B) and shading (C, D, E) represent 95% confidence intervals. In panel A and B, significance is denoted ($p < 0.1$; $*p < 0.05$; $***p < 0.001$).

management (harvest area rotation and sanctuaries) and shell replenishment practices on public fishing grounds. Using long term data from the Rappahannock River, we evaluate how management actions impact oyster reef metrics (brown shell substrate L m^{-2} , recruit density m^{-2} ,

market density m^{-2}) and fisheries efficiency (meeting daily bushel limit or not). Our results demonstrate that the combination of harvest area rotation and replenishment support oyster reef dynamics and enhance fisheries outcomes. Replenishment supplements the reef structure after

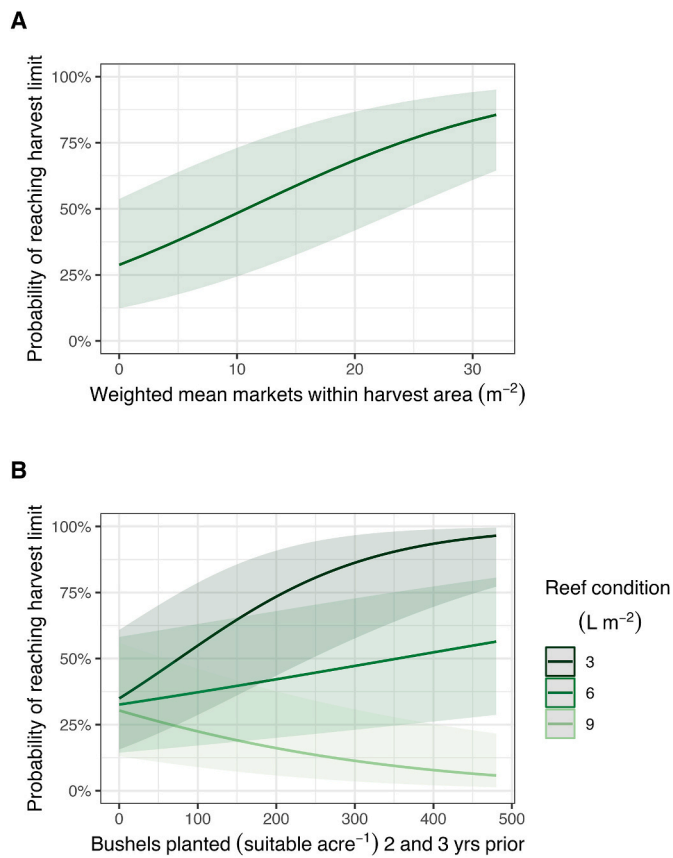


Fig. 7. Marginal effect plots displaying the effect of (A) weighted mean markets in a harvest area, and (B) bushels planted across reef condition (weighted mean brown shell substrate) at the time of planting on the probability a harvester reaches the harvest limit. Shading represents 95% confidence intervals.

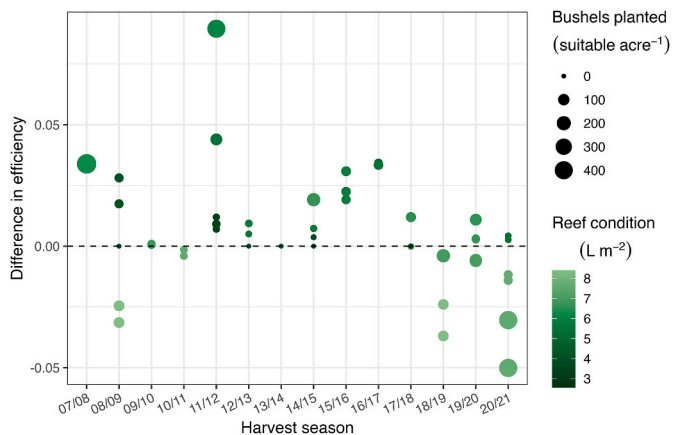


Fig. 8. Predicted difference in efficiency for harvesters in response to shell replenishment inputs from the 2007/2008 to 2020/2021 harvest season. Point size indicates the number of bushels of replenishment suitable $acre^{-1}$ applied 2 and 3 years prior to harvest. Color indicates the reef condition, as weighted mean brown shell substrate ($L m^{-2}$), when replenishment was applied.

harvest and provides additional settlement substrate for juveniles, while harvest area rotation gives oysters adequate time to reach market size for the next harvest season without disturbance. Current management strategies directly enhance harvester efficiency, particularly in harvest areas with poor reef condition. We provide the first estimates for how the quantity of replenishment material applied per unit area impacts biological and fisheries outcomes, and the marginal benefits from

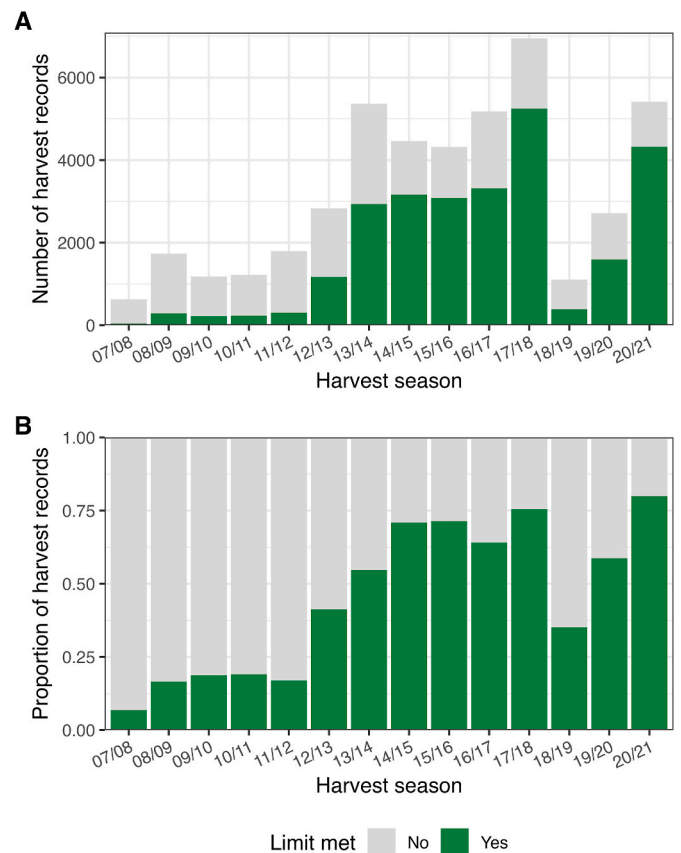


Fig. 9. Summary of harvest records from the Rappahannock River from the 2007/2008 to 2020/2021 harvest seasons. (A) Number of harvest records, and (B) proportion of harvest records that met the daily bushel limit.

replenishment. Cumulatively, our findings provide a novel, real world assessment for oyster restoration practices on public fishing grounds and key information necessary to recover coastal habitats.

4.1. Oyster reef recovery

Oyster reef persistence is governed by shell budgets. Shell accretion rates must be equal to or greater than losses from fisheries extraction and taphonomy for reef maintenance (Mann and Powell, 2007; Soniat et al., 2014). Traditional fisheries management goals focus on achieving maximum sustainable yield (MSY), where the biomass (B_{MSY}) and fisheries mortality rate (F_{MSY}) maximizes surplus production (Hilborn and Walters, 1992). Though these stock-wide reference points are commonly used to manage commercial fisheries, they are not generally applied to oyster fisheries due to the interdependence between living oyster biomass and the reef substrate (Powell et al., 2012; Hemeon et al., 2020; Solinger et al., 2022), and complex interactions with local conditions across estuaries, such as variable mortality due to disease (Andrews, 1988; Haskins and Andrews, 1988; Burreson and Calvo, 1996; Carnegie and Burreson, 2011), predator distribution (Garton and Stickle, 1980; Brown et al., 2008; Johnson and Smee, 2014; Tedford and Castorani, 2022), and salinity (Shumway, 1996; La Peyre et al., 2009; Pourmozaffar et al., 2020). Thus, oyster management and restoration efforts are, by necessity, area based.

Restoration efforts for oysters are accelerating in the United States and continue to focus on supplementing the shell base (La Peyre et al., 2014a; Berszo Hernández et al., 2018). Oyster shell (recycled or fossil) is used for the majority of restoration efforts in the Chesapeake Bay; however, oyster shell is a limited, costly resource which degrades rapidly in the environment (Berszo Hernández et al., 2018; Pace et al.,

2020). Due to this, there is increasing interest in alternative substrates for oyster restoration. Alternative substrates may include porcelain, mixed shell (e.g. combining oyster and shell from other species), concrete (e.g. oyster castles, ReefBalls), mixed concrete (e.g. concrete mixed with other materials, such as limestone, crab traps, or shell), or stone, such as limestone or granite (Bersoza Hernández et al., 2018; Goelz et al., 2020). Many alternative substrates, especially larger concrete structures, are not a suitable management intervention on actively fished reefs, as they negatively interact with fishing gear. In a few cases, granite and concrete substrates were used for replenishment in the Rappahannock; however, due to their limited usage, we are unable to assess their efficacy for restoring oyster populations on public fishing grounds.

Given that shell has rapid turnover and alternative substrates are not always suitable for public fishing grounds, optimizing shell replenishment, both the interval between applications and volume of material, is critical for effective reef maintenance. Our results indicate that applying shell every 3 years mitigates fisheries extraction on public oyster grounds and taphonomic losses in the Rappahannock by supplementing the underlying reef structure. Sanctuary and harvested reefs had comparable reef structure, as brown shell substrate ($L\ m^{-2}$). Prior work on shell taphonomy documented oyster shell half-life ranging from 2 to 6 y (Pace et al., 2020), which aligns with a 3 year rotation to mitigate shell loss on a reef. Further, our results suggest there is only a marginal increase in recruitment with increasing bushels planted $acre^{-1}$ on oyster reefs in the Rappahannock (Fig. 5A). Recruitment benefits associated with the volume (bushels $acre^{-1}$) of replenishment may be underestimated, due to the application process. Replenishment is applied to subtidal oyster reefs from a floating barge and, thus, is not evenly distributed across the entire reef surface area. The fisheries independent oyster patent tong survey samples multiple, random $1\ m^2$ of reef bottom, which may miss the areas where replenishment was applied. Further, replenishment is loose shell, which can be dislodged or moved by tidal forces in the tributary. Reefs received on average 1090 bushels $acre^{-1}$, which is equivalent to $13.3\ L\ m^{-2}$. At a larger spatial scale, increasing the replenishment volume on harvest areas shows diminishing returns for the commercial fishery beyond 200–300 bushels planted suitable $acre^{-1}$ (Fig. 7B), which is equivalent to 2.4 – $3.7\ L\ m^{-2}$. Oyster reefs that received similar low level (3.0 – $21.7\ L\ m^{-2}$) alternative shell plants, using cured Atlantic surf clam (*S. solidissima*) and ocean quahog (*Arctica islandica*), were shown to outperform unreplenished reefs in recruitment and survival during the first 4 years after planting (Ashton-Alcox et al., 2021). Repeated shell plantings may enhance reef performance even when replenishment levels are low. Maintaining high brown shell substrate is a critical metric for management that provides benefits for recruitment and market oyster density (Figs. 5C and 6D). Shell plantings provide additional reef surface area, which is known to be a critical component for successful oyster recruitment to the population (Hemeon et al., 2020; Solinger et al., 2022); however, how standardized volumes of replenishment impact biological outcomes has little information available. Our findings suggest that low level replenishment (~ 1000 bushels $acre^{-1}$ on individuals reefs with ~ 200 – 300 bushels suitable $acre^{-1}$ across a harvest area) provides optimal ecological and economic outcomes. Implementing this rate across public fishing grounds could reduce costs while maintaining reef structure.

Throughout the Chesapeake Bay, oyster reefs have continued to improve across sanctuaries and public fishing grounds in recent years (Tracy et al., 2023; Southworth and Mann, 2024; this work). Tracy et al. (2023) conducted remote rapid assessment methods to survey oyster reefs in 12 Chesapeake Bay tributaries. Restored and unharvested reefs had higher estimated percent oyster cover and vertical relief than harvested reefs. Repeated surveys (2017, 2019, and 2021) at reefs in two Maryland tributaries showed increasing habitat quality for all reefs over time; however, harvested reefs showed more variability in reef habitat quality (Tracy et al., 2023), which may be caused by fishing gear removing or breaking up the uppermost reef surface. Similarly, we

documented increasing reef habitat (brown shell substrate, $L\ m^{-2}$), across all harvest areas in recent years (Fig. 2A) and higher market oyster density in sanctuary (unfished) reefs compared to harvested reefs (Fig. 6A) in the Rappahannock. We observed comparable brown shell substrate ($L\ m^{-2}$) and recruit density (m^{-2}) between sanctuary and harvested reefs. Harvested oyster reefs may maintain high oyster density, but have less vertical structure and habitat complexity than sanctuary reefs (Lenihan and Peterson, 2004; Heggie and Ogburn, 2021; Tracy et al., 2023).

Improvements in oyster populations in recent years may be partially due to changes in disease dynamics (Carnegie and Bureson, 2011; Carnegie et al., 2021; Carnegie, 2022). MSX (*H. nelsonii*) was introduced to the Chesapeake Bay in 1959 and was a dominant pathogen responsible for major oyster mortalities in the 1960s and 1970s (Andrews, 1996). Dermo (*P. marinus*) is a native pathogen to the Chesapeake Bay, which caused annual mortalities up to 30% in primarily older individuals (Andrews, 1988); however, a hypervirulent Dermo phenotype emerged between 1983 and 1990, resulting in major, rapid oyster mortalities up to 70% (Carnegie et al., 2021). Eastern oysters were historically long lived (10–20 y), but modern populations are age-truncated and rarely live >5 y (Mann et al., 2009b). Recent oyster population surveys in the Virginia portion of the Chesapeake Bay show increasingly larger maximum sizes (Mann et al. Unpub data), suggesting oysters may be increasingly resistant or tolerant to oyster pathogens, experiencing decreased disease mortality, and living longer, which supports positive outcomes from oyster reef restoration efforts throughout the Chesapeake Bay.

4.2. Spatial management in coastal systems

Rotational harvesting is a common management strategy in terrestrial systems. Crop rotation has been used by humans for centuries and aims to maximize production of a resource while minimizing negative environmental impacts. In terrestrial agriculture, rotation increases production while enhancing soil structure and nutrient content, carbon sequestration, sustainability, and benefits to pollinators and other wildlife (Perlut and Strong, 2011; Farruggia et al., 2012; Vadeboncoeur et al., 2014; Carlisle et al., 2023). Though less commonly applied to aquatic systems, rotational harvest can be an effective tool to manage benthic or sessile marine organisms.

Benefits from rotational management may apply broadly to marine benthic organisms. Atlantic sea scallops (*Placopecten magellanicus*) were severely overfished in the United States Mid-Atlantic Bight region from the 1960s–1990s (Hart and Rago, 2006). In response to depleted populations, new management measures were implemented to reduce effort and rotationally close harvest areas (Hart and Rago, 2006). Since implementation of rotational closures in 1998, sea scallop populations have rebounded and the fishery is now one of the most valuable in the United States (Hart and Rago, 2006; NOAA, 2024). Atlantic sea scallop recovery is primarily attributed to rotational closures, which increase biomass within the closure by allowing scallops to grow, provide substantial spillover effects that enhance recruitment in down-current harvest areas, and increase fisheries yield (Hart and Rago, 2006; Hart et al., 2020). Similarly, Australia's Great Barrier Reef supports a multispecies sea cucumber fishery which showed evidence of serial depletion and overexploitation of high value species (Eriksson and Byrne, 2015; Plagányi et al., 2015; Wolfe and Byrne, 2022). Due to management concerns about overexploitation, fishers designed and implemented 156 rotational zones, which are only fished once every 3 years (Lowden, 2005). Rotational harvest reduces the local depletion risk and increases fisheries yield for the multispecies sea cucumber fishery; however, a 3 year rotation may not be adequate for all species, which may have different growth rates and life histories (Skewes et al., 2014; Plagányi et al., 2015). Identifying the best rotation interval requires understanding species specific life history traits and local environmental conditions.

Rotational harvest is a successful management and restoration tool for oyster fisheries. European flat oysters (*Ostrea edulis*) have declined throughout their range and intact reef habitat is rare (Korringa, 1946; Beck et al., 2011; Pogoda, 2019). The only remaining wild oyster fishery in Scotland is the Loch Ryan fishery (Eagling et al., 2015). This fishery, which has been privately owned and managed since 1701 by the Wallace family, employs harvest area rotation. Oyster grounds are split into 6 plots and each plot is harvested every 6 years, which allows oysters to grow to harvestable size, enhances reef condition (as shell density and percent cover), and provisions habitat for diverse macrofauna (Eagling et al., 2015; Kennon et al., 2023). Cape rock oysters (*Striostrea margaritacea*) are found throughout the coast of southeastern Africa and are the most economically valuable oyster in the region (Haupt et al., 2010). The KwaZulu-Natal province has supported oyster harvest for over a century and rotational harvest was implemented sometime in the mid-1950s (Thompson, 1913; de Bruyn et al., 2009). The North Coast and South Coast regions each have 5 fishing zones, with 1 zone open to commercial harvest in each region per year. For each zone, recreational harvest is permitted for 1 year, followed by 1 year of commercial harvest, and then the zone is closed to all fishing for 3 years. Thus, each zone is harvested for two out of every five years (de Bruyn et al., 2009). Oyster harvest targets larger individuals, thus, fishing reduces the mean shell size. During the 3 year fallow period, oyster populations show rapid recovery in biomass and increases in mean oyster size to the level prior to harvest (de Bruyn et al., 2009; Steyn et al., 2023). Eastern oysters (*C. virginica*) are on a 3 year rotation in the Rappahannock River. Reefs in a harvest area receive replenishment and then generally fishing is not permitted for 3 years. We observed an increase in market oyster density 3 years after replenishment was applied and a marked decrease in the reef structure (as brown shell substrate) in year 4 when fishing occurred. A 3-year interval between harvest corresponds with the time necessary for an oyster to grow to market size in the Rappahannock (Santopietro et al., 2009; Mann et al., 2022; Mann et al. Unpub data).

Marine protected areas (MPAs) are a form of spatial management in coastal and marine systems. MPAs are portions of the ocean where anthropogenic impacts, such as commercial fishing, are highly regulated or banned to protect biodiversity, increase ecosystem resiliency, and benefit fisheries management (Hilborn et al., 2004). MPAs may also be called marine reserves or sanctuaries. Within MPAs, commercially harvested species recover density, biomass, and size when well enforced (Halpern, 2003; Aburto-Oropeza et al., 2011); however, the direct benefit to commercial fisheries is achieved through spillover effects (Jennings, 2000; Burgess et al., 2014; Di Lorenzo et al., 2016). Ecological spillover is the net export of larvae, juvenile, and adult biomass from an MPA into surrounding areas, whereas fishery spillover is the portion of exported biomass available to a fishery and is dependent upon fishing regulations (Di Lorenzo et al., 2016). The effectiveness of MPAs to support fisheries is highly dependent on species life history traits and appropriate siting, with placement in upstream, “source” locations (Crowder et al., 2000; Hilborn et al., 2004; Munroe et al., 2014; Hart et al., 2020). Sessile invertebrates disperse as larvae, so understanding local hydrodynamics and larval transport is critical. Oyster reef sanctuaries in the Rappahannock had higher market oyster density than harvested reefs. Market-sized oysters are larger (>76 mm) and more fecund (Galtsoff, 1930; Cox and Mann, 1992; Mroch et al., 2012; Mann et al., 2014). Well placed sanctuaries may enhance larval supply due to the presence of larger individuals on the reefs; however, reducing fishery pressure alone is not enough to increase oyster density and reef habitat (Heggie and Ogburn, 2021; Tracy et al., 2023), as many areas in the Chesapeake Bay are substrate limited.

Cumulatively, harvest area rotation and sanctuaries can be valuable tools to manage coastal and marine species. Area based management is low cost and easy to implement (Myers et al., 2000); however, success depends heavily on the species life history, length of closures, fishing intensity, and enforcement capacity (Caddy and Siejo, 1998; Cohen and Foale, 2013; Plagányi et al., 2015). Our results suggest that harvest area

rotation and sanctuaries, when coupled with shell replenishment, provide tangible benefits to oyster reefs on public fishing grounds.

4.3. Economic impacts

Ecosystem service valuation plays an important role in informing best management practices and policy decisions (Guerry et al., 2015). Further, ecosystem service valuation provides a mechanism to quantify the benefits and costs from restoration, which can aid in optimizing restoration interventions. Oysters provide well documented ecosystem services in estuaries (Peterson et al., 2003; Newell, 2004; Coen et al., 2007; Grabowski et al., 2012). Oyster reef ecosystem services, excluding commercial harvest, have an estimated value between \$18,162 to \$326,959 (2023 USD) $\text{acre}^{-1} \text{ year}^{-1}$ (Grabowski et al., 2012). Commercial oyster harvest value has an estimated value of \$13,615 (2023 USD) $\text{acre}^{-1} \text{ year}^{-1}$ (Grabowski et al., 2012). Published values, such as these, have been used to estimate ecosystem services for a variety of aquatic organisms and ecosystems, including oyster restoration efforts (Brander et al., 2007; Camacho-Valdez et al., 2013; Callihan et al., 2016; Bersoza Hernández et al., 2018; van der Schatte Olivier et al., 2018; Wang et al., 2021). The process of applying existing estimates from one context (e.g. original study area) to a new context (e.g. new location) is a benefit transfer approach (Spash and Vatn, 2006; Richardson et al., 2015). While these methods have the advantage of being low cost, they do not provide customized estimates for benefits in novel scenarios and are often unreliable (Spash and Vatn, 2006; Brander et al., 2007; Richardson et al., 2015).

Restoration efforts ideally should be economically viable and confer benefits that exceed their costs. Eastern oysters on the US Atlantic and Gulf coasts have received extensive restoration efforts over the last several decades (Powers et al., 2009; La Peyre et al., 2014b). Bersoza Hernández et al. (2018) used a benefit transfer method to determine the return on investment from ecosystem services gained from restoration projects, excluding fisheries enhancement. In the Chesapeake Bay, approximately 81% of restoration projects used oyster shell (Bersoza Hernández et al., 2018). Shell based projects were shown to have a higher return on investment over a 14 year time period than concrete substrates (Bersoza Hernández et al., 2018). Replenishment efforts on public fishing grounds in the Rappahannock were primarily shell based (98%, 305 of 310 records). Further, Bersoza Hernández et al. (2018) reported evidence for economies of scale, where restoration projects greater than 0.4 ha (~1 acre) yielded more positive return on investment values. All replenishment records in the Rappahannock from 2000 to 2021 meet or exceed this area threshold on public fishing grounds. On average, the reef area replenished was 5.1 ha (12.7 acres) and ranged from 0.4 to 49.1 ha (0.93–121.3 acres). A challenge with benefit transfer methods is the uncertainty regarding which value to use, as values are produced outside the system of focus. When return on investment is calculated using higher values in the range for oyster reef ecosystem services, nearly all restoration projects have a positive return on investment (Bersoza Hernández et al., 2018), which illustrates the importance in using customized, local benefit estimates whenever possible and monitoring actual restoration outcomes in the environment. Restoration projects are generally limited to 1–2 years; however, longer time frames are necessary to determine restoration success and ecosystem recovery (Bayraktarov et al., 2016).

Specifically in the Rappahannock, our findings suggest that shell replenishment has a net positive benefit on harvester efficiency; however, this effect was variable over time and depended on the reef condition when replenishment was applied (Fig. 8). Oyster harvest had a dockside value of approximately \$24 million (2023 USD) in the Rappahannock during the study period. Efficiency increased by a maximum of 9% in response to replenishment practices, which would correspond to around \$2 million (2023 USD) in added harvest value. Estimated gains in harvest value are substantially lower than replenishment investment in the Rappahannock River (\$14 million 2023 USD), which

agrees with prior work (Santopietro et al., 2009). A bioeconomic model for rotational management and replenishment in the Rappahannock determined that net revenues to harvesters could be positive under some scenarios, but net revenues to the state were always negative (Santopietro et al., 2009). While interpreting these findings, one must acknowledge this is a coarse estimate. Oyster fisheries data in Virginia is collected at the harvest area level, as opposed to the individual reef, and does not collect information on harvester effort, which could be used to explore changes in catch per unit effort over time. As with many fisheries, non-reporting or mis-reporting harvest data may be occurring, which would bias our estimated benefits from replenishment practices. For example, if a harvester who had met their bushel limit failed to report their harvest, we would underestimate the benefits from prior replenishment activities in that harvest area. We are unable to account for direct inputs (replenishment) and outputs (bushels of oysters harvested) from each reef. We observed less benefit from replenishment in recent years as reef condition improved across the harvest areas (Fig. 8) and harvester efficiency increased (Fig. 9). Harvesters preferentially choose to harvest on certain reefs over others. Harvester behavior creates differential fishing pressure across reefs in a given harvest area; however, we are unable to account for this with the current harvest reporting requirements. Further, the benefits from replenishment on public fishing grounds go beyond just harvest value. Seafood harvest, including oysters, provide economic benefits across the supply chain (e.g. harvesters, processors, distributors) and to a variety of other economic sectors (e.g. restaurants, boat building, sport and athletic goods manufacturing) in Virginia (Gonçalves et al., 2024). Thus, replenishment practices provide broad benefits to economic activity, which are substantially greater than harvest value alone. We did not account for cumulative impacts from repeated replenishment, enhanced ecosystem services from population increases, or social benefits to local communities from seasonal oyster harvest income, which could be explored in future work. Prior to the initiation of the repletion program, the oyster fishery in the Rappahannock was ostensibly closed. Replenishment provided the literal foundation for resumed fisheries activity through repeated shell replenishment over time. Today, oyster populations in the Rappahannock and elsewhere in the Chesapeake Bay are increasing.

5. Conclusion

Coastal ecosystems, including oyster reefs, are degraded worldwide; however, natural resources management must balance tradeoffs between restoration and human use. This study examines competing management goals (e.g. commercial harvest of an ecosystem engineer, maintaining biogenic habitat) for oysters on public fishing grounds in a temperate estuary. Our results show that spatial management and replenishment practices provide benefits to both oyster reefs and the fishery, and provides a framework applicable to other degraded ecosystem worldwide. To holistically understand the benefits from management and restoration actions over time, managers require high-resolution, long-term data. Our work incorporates long-term fisheries independent data and replenishment records; however, our fisheries dependent data was collected at coarse spatial scales. Managers should prioritize collecting high-resolution fisheries dependent data to inform spatial management practices, especially for marine benthic organisms. Often restoration research focuses on ecosystems in the absence of humans (e.g. sanctuaries, reserves); however, humans are intimately connected to coastal habitats and substantially alter coastal ecosystems. Therefore, it is imperative that future work examine management and restoration practices in concert with fisheries and other human impacts, and identify strategies which are adaptable to changing conditions.

CRedit authorship contribution statement

Alexandria R. Marquardt: Writing – original draft, Visualization, Methodology, Funding acquisition, Formal analysis, Conceptualization.

Melissa Southworth: Writing – review & editing, Methodology, Data curation, Conceptualization. **Andrew M. Scheld:** Writing – review & editing, Methodology, Funding acquisition, Formal analysis, Conceptualization. **Andrew Button:** Writing – review & editing, Methodology, Data curation, Conceptualization. **Roger Mann:** Writing – review & editing, Funding acquisition, Data curation, Conceptualization.

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Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.jenvman.2025.124179>.

Data availability

The raw data required to reproduce the findings are publicly requestable through the Virginia Marine Resources Commission and Virginia Institute of Marine Science.

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