Reefs in no-take reserves host more oysters, macroparasites, and macrofauna than harvested reefs across an estuarine salinity gradient

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ABSTRACT: No-take reserves and habitat restoration are important management tools for reversing the effects of fishing on coastal habitats, associated faunal assemblages, and host—parasite interactions. Populations of the eastern oyster *Crassostrea virginica* have declined by 99% in areas of Chesapeake Bay, USA, due to overharvesting, disease, and other factors, and are now the focus of extensive restoration efforts. We surveyed subtidal oyster reefs using classic quantitative approaches and emerging videography methods to contrast pairs of harvested reefs and reefs protected in subtidal no-take marine reserves (oyster sanctuaries) in the Choptank, Great Wicomico, and James River tributaries of Chesapeake Bay. Overall, sanctuary oyster reefs contained more intact habitats and communities. Relative to nearby harvested reefs, sanctuary reefs (1) contained higher densities of oysters, (2) held larger oysters of lower condition, (3) hosted stronger oyster—macroparasite (boring sponge [*Cliona* spp.] and mud blister worm [*Polydora* spp.]) interactions, (4) had more complex habitat, and (5) supported a greater richness and abundance of macrofauna. Oyster and mobile macrofauna abundance increased with salinity, whereas macroparasite prevalence peaked at mesohaline (5—20 psu) sites. Our results suggest that restored, sanctuary-protected oyster reefs are beginning to rebound from the effects of >100 yr of intensive harvest, as indicated by increased oyster density, recovery of host—parasite interactions, improved habitat characteristics, and more mobile macrofauna. Additionally, these patterns, observed across the salinity gradient in Chesapeake Bay, reflect a widespread trend in aquatic ecology: relative to fished areas, unfished areas have more complex habitats and communities, larger and higher densities of hosts, and stronger host—parasite interactions.

KEY WORDS: Biodiversity · Macroparasites · *Crassostrea virginica* · Habitat · Harvest · Oyster reef

1. INTRODUCTION

Fishing is one of the strongest and most pervasive anthropogenic disturbances influencing coastal and marine populations, community assemblages, and ecosystem functions (Jackson et al. 2001, Kirby 2004, Pauly et al. 2005, Crowder et al. 2008). Marine protected areas (MPAs), also known as no-take reserves or sanctuaries, close waters to extractive or destructive activities, and consequently have positive impacts on provisioning of habitat structure, biodiversity, and ecosystem services (Worm et al. 2006, Sala et al. 2021).

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MPAs also enhance important ecological processes such as parasitism (Wood & Lafferty 2015), which modify host populations through effects on energy reserves (Barber et al. 1988), reproduction, and survival, but also have community-wide impacts (Wood & Johnson 2015). Restoration can reverse the negative effects of overfishing (Jackson et al. 2001), but reversals do not occur post-restoration where fishing pressure remains high (Spalding & Brown 2015). Ecosystem recovery following protection and restoration can be assessed by documenting improvements in species abundance and diversity, habitat quality, ecological processes, and ecosystem services.

Comprising at least 40% of global biodiversity, parasites — enemy species that derive resources from a single living host at the host organism's expense (Dobson et al. 2008) — increase the complexity of, and often dominate, marine food webs (Lafferty et al. 2006, 2008, Lafferty 2013). Disease is a normal part of healthy ecosystems, and parasites perform the essential ecological role of energy transfer (Wood & Johnson 2015); higher parasite abundances can therefore be a sign of a healthy ecosystem with more intact host pathways (Moore et al. 2020). Global overfishing practices have resulted in 'fished down' marine food webs that lack robust higher trophic levels (Pauly et al. 1998). Because fishing selects larger hosts with a greater parasite load for extraction, and reduces the density and complexity of fish host trophic assemblages (and therefore, parasite transmissibility), these same practices have 'fished out' marine parasites (Wood et al. 2010). When the parasite's host is a foundation species that plays a strong role in physically structuring the community, extractive processes affect the diversity and abundance of marine life (Burge et al. 2014), regardless of whether the foundation species was the fishery target, bycatch, or indirectly affected (e.g. bottom trawling can disturb seagrass though it is not a target species). Unfished aquatic habitats are consistently able to support greater biodiversity, including greater abundances of parasites (Wood & Lafferty 2015). Though individual parasite species vary in response to fishing pressure (Wood et al. 2010), fishing is often a dominant force in marine host—parasite dynamics (Wood et al. 2013). Thus, host—parasite interactions can be valuable indicators for the health of ecosystems undergoing fishing pressure.

In addition to anthropogenic pressures like fishing, environmental gradients can shape the distributions and performances of species, including hosts and parasites (Rohde 2010). Identifying how such gradients influence host—parasite dynamics is particularly important when the host organism is a coastal foundation species (i.e. seagrass, coral, marsh plants, mangroves, oysters), as they form some of the most valuable but threatened biogenic habitats in the world (Rothschild et al. 1994, Peterson et al. 2003, Orth et al. 2006, Beck et al. 2011, Schulte 2017). Drivers of host—parasite dynamics vary amongst habitats. For example, in salt marshes, biotic factors (i.e. the presence of highly competent hosts gammarid shrimp and littoral snails) were more important than abiotic factors like salinity in predicting parasite diversity (Anderson & Sukhdeo 2009). Contrastingly, on intertidal oyster reefs, both tidal inundation (abiotic) and parasites (biotic) are critical drivers of oyster dynamics (Dieudonne & Carroll 2021). Coastal foundation species are frequent targets of restoration projects to mitigate the repercussions of their widespread losses. Knowing which drivers matter for a given host—parasite system and possessing the flexibility to work with the environment are, therefore, necessary for optimizing restoration plans and ensuring positive restoration outcomes.

Oysters are an important foundation species because they are both an ecologically critical ecosystem engineer (Coen et al. 2007, Walles et al. 2016) and have been a socially pivotal food source to coastal communities for millennia (Breitburg et al. 2000, Coen & Luckenbach 2000, Rick et al. 2016). Over the past 150 yr, reefs that once proliferated in temperate estuaries along the Gulf and East Coasts of North America have experienced precipitous losses in oyster habitat coverage and biomass of 64 and 88%, respectively (zu Ermgassen et al. 2012). Global oyster declines are a classic example of the consequences of overharvesting (Newell 1988, Rothschild et al. 1994, Kirby 2004), disease (e.g. due to microparasites *Perkinsus marinus* ['dermo'] and *Haplosporidium nelsoni* ['MSX']) (Lenihan et al. 1999, Wilberg et al. 2011), and habitat degradation via fishery disturbance (Lenihan & Peterson 1998, Smith et al. 2005, Mackenzie 2007, Schulte 2017). Oysters can be extracted using a variety of methods, including with patent tongs, hydraulic dredges, sail dredges, cores, and by hand/SCUBA (Schulte et al. 2018). The extraction of this group of foundation species also has rippling consequences for reef-associated macrofauna. For example, unharvested oyster reefs can support an order-of-magnitude greater macrofaunal densities compared to nearby harvested reefs (Rodney & Paynter 2006). Similarly, rugosity (a measure of oyster reef structural complexity) is positively related to macrofaunal diversity (Karp et al. 2018). In response to collapsing oyster reef populations and communities, oyster restoration rates in eastern North America have in-

creased in recent decades to ~150 ha yr^{-1} (Bersoza Hernández et al. 2018). This restoration provides novel opportunities to understand what has been lost due to historical overfishing.

Measures of the effectiveness of oyster restoration can be obvious, such as oyster abundance, habitat characteristics, and macrofauna abundance, or more subtle and sometimes unexpected, such as host—parasite interactions. Although lesser known than the microparasitic diseases dermo and MSX, endemic oyster macroparasites can be both biologically/ecologically important and economically damaging. The historical record attributes episodic oyster reef collapse to boring sponge (*Cliona* spp.) infestation (Leidy 1889), as does a robust mid-20th century record of clionid-based research in the eastern United States (Old 1941, de Laubenfels 1947, Wells 1959, 1961, Guida 1976, Pomponi & Meritt 1990). However, the oyster—sponge relationship dates back to the Paleozoic (White 1884). Therefore, despite the deleterious effects of boring sponge infestation on oyster reefs (Dunn et al. 2014, Peters et al. 2017), parasite abundance can be an indicator of trophic complexity (Moore et al. 2020). Detecting these host—macroparasite interactions may thus counterintuitively indicate an ecologically intact oyster reef. Additionally, endemic mud blister worm macroparasites *Polydora* spp. may be valuable indicators of the strength of host—parasite interactions on oyster reefs. *Polydora* spp. are also potential causal agents of oyster reef decline (Lunz 1941, Loosanoff & Engle 1943). *Polydora* blisters are unsightly, make oysters harder to shuck, and reduce the market value of the harvested product (Shinn et al. 2015). Recent field research has explored how environmental gradients like tidal elevation and salinity influence oyster host—macroparasite interactions (Hanley et al. 2019, Carroll et al. 2021, Dieudonne & Carroll 2021), but not how harvesting shapes these same dynamics. Considering the anecdotal evidence linking *Cliona* spp. and *Polydora* spp. to oyster reef decline, there is substantive motivation for investigating host—macroparasite interactions for the bioeroders across environmental gradients in the dual context of oyster harvest and restoration.

The combined effects of fishing pressure and parasites have been devastating to oyster populations in Chesapeake Bay, where abundances in the Maryland portion of the Bay are at less than 1% of 19th-century levels (Wilberg et al. 2011). In addition to habitat destruction and overfishing (Rothschild et al. 1994), MSX and dermo diseases contributed to oyster reef collapse in the Bay (Andrews 1979, Mann et al. 1991, Wilberg et al. 2011). However, there is evidence that

the overall impact of MSX is declining (Carnegie & Burreson 2011), and oysters appear to be developing microparasitic disease resistance in a lower tributary of the Bay (Lipcius et al. 2015). Chesapeake Bay's modern oyster restoration efforts commenced in 1993, and by 2018 comprised 35% of all oyster restoration in Eastern North America (Bersoza Hernández et al. 2018). Following in the spirit of plans to restore 20 tributaries in Executive Order 13508 (EPA 2010), a major goal of the 2014 Chesapeake Bay Watershed Agreement is to restore oyster habitat and populations in 10 Bay tributaries by 2025 (Chesapeake Bay Watershed Agreement 2014). To date, 10 tributaries across latitudinal and salinity gradients have been identified for restoration; over $80 million USD have been spent restoring 2 reef complexes completely and constructing/seeding 7 others (ChesapeakeProgress 2022), and restoration has been characterized as successful (Schulte et al. 2009, ChesapeakeProgress 2022). Within these reef complexes and beyond, there remain large areas suitable for restoration (Theuerkauf & Lipcius 2016); of those that are already restored, some areas are open to oyster harvest, and others are oyster sanctuaries, which prohibit oyster extraction but are open to fishing for other species (e.g. finfish, crabs). The increased virulence of the parasites MSX and dermo at higher salinities influenced the siting of these restored Chesapeake Bay oyster reefs (Maryland Interagency Oyster Restoration Workgroup 2013). However, to our knowledge, macroparasite—oyster interactions have not been included formally in Chesapeake Bay oyster restoration plans prior to this study.

Our objective was to determine the contribution of fishing pressure and abiotic factors to the health of restored oyster populations and host—parasite interactions by contrasting several characteristics of sanctuary and harvested subtidal oyster reef pairs across the salinity gradient of the Choptank, Great Wicomico, and James River tributaries in Chesapeake Bay. Target characteristics included: (1) oyster population metrics, including densities and size; (2) oyster-bioeroder macroparasite compositions; (3) habitat structure; and (4) oyster-associated macrofaunal communities. We hypothesized that, relative to sanctuary reefs, harvested reefs would have lower oyster densities, smaller oysters, and therefore lower qualitative habitat scores. Further, we hypothesized that more macrofaunal organisms would use the sanctuary reef habitat, and bioeroder load (e.g. *Cliona* spp. and *Polydora* spp. macroparasites) would be greater in oyster hosts collected from sanctuary reefs.

2. MATERIALS AND METHODS

2.1. Tributary and site characteristics

At 11 601 km^2 in size, Chesapeake Bay (Fig. 1A) is one of the largest and most productive estuaries in the world. Its broad, shallow (<10 m) areas flank a narrow, deep (20–30 m) central channel (Kemp et al. 2005). The Susquehanna River at the head of the Bay provides more than half of the freshwater volume input (Schubel & Pritchard 1986), resulting in vertical stratification and longitudinal salinity gradients, though strong winds cause infrequent destratification (Goodrich et al. 1987). To understand how tributary and oyster harvest influences oyster reef communities across a salinity gradient, we sampled eastern oysters *Crassostrea virginica* on subtidal oyster reefs at 1 harvested site and 1 nearby sanctuary site in 3 Chesapeake Bay tributaries during the summer of 2019 (Choptank in June, Great Wicomico in August, and James in July) (see Fig. 1A).

2.1.1. Choptank

The Choptank is in Maryland on the eastern side of Chesapeake Bay; it was the northernmost tributary we sampled for this study. Planning and siting of the Harris Creek oyster sanctuary started in 2011 and the restoration of its 348 acres (1.41 km^2) finished
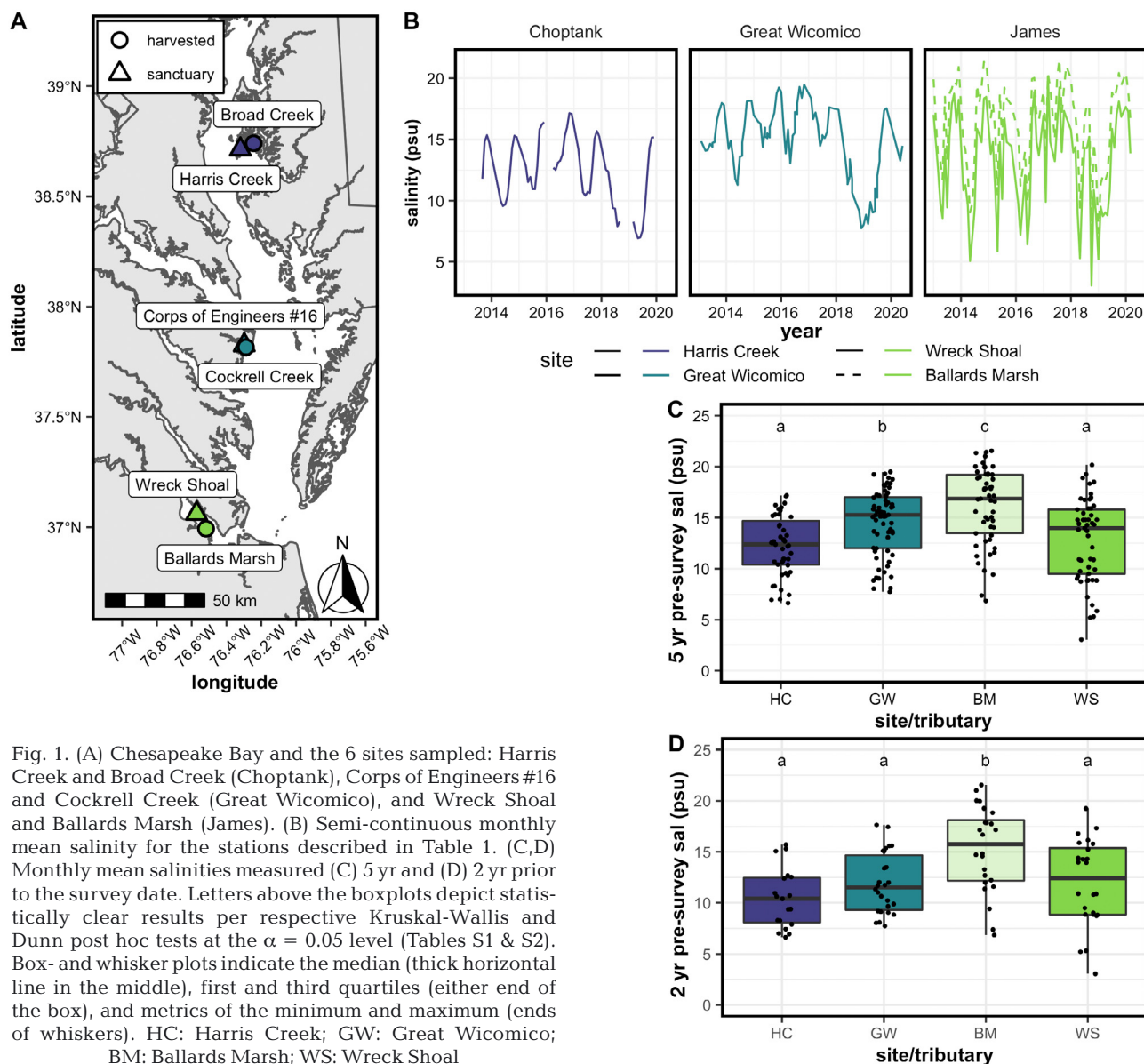

Fig. 1. (A) Chesapeake Bay and the 6 sites sampled: Harris Creek and Broad Creek (Choptank), Corps of Engineers #16 and Cockrell Creek (Great Wicomico), and Wreck Shoal and Ballards Marsh (James). (B) Semi-continuous monthly mean salinity for the stations described in Table 1. (C,D) Monthly mean salinities measured (C) 5 yr and (D) 2 yr prior to the survey date. Letters above the boxplots depict statistically clear results per respective Kruskal-Wallis and Dunn post hoc tests at the α = 0.05 level (Tables S1 & S2). Box- and whisker plots indicate the median (thick horizontal line in the middle), first and third quartiles (either end of the box), and metrics of the minimum and maximum (ends of whiskers). HC: Harris Creek; GW: Great Wicomico; BM: Ballards Marsh; WS: Wreck Shoal

in 2015. Rather than scatter-planting young oysters, the construction coalition focused on planting many juveniles in concentrated areas. Some areas in Harris Creek used substrate and seed oysters, but the area we sampled was a 'seed only' area (Table 1). In the harvested tributary, Broad Creek, all major gear types are used, but the particular site is harvested with hand tongs for market-size oysters. Every year since 2013, Broad Creek has been open to harvest and managers have also annually supplemented the reef with spat on shell (Table 2).

2.1.2. Great Wicomico

The Great Wicomico discharges water from Virginia into the western side of Chesapeake Bay. Restoration practitioners first constructed the sanctuary site we sampled in the Great Wicomico (Corps of Engineers [COE] #16) in 2004 as a high-relief reef (Schulte et al. 2009), and it is now 7.26 acres (0.029 km^2) in size. This site has been closed to harvest since its construction, and reef managers have not added more seeded shells to the reef since the construction (Table 1). The harvested site, Cockrell Creek, has been open to hand-scrape market oyster harvest since 2009; however, it was closed to harvest in 2018. Managers added seeded oyster shells to the site in 2009, 2010, and 2013 (Table 2).

2.1.3. James

Following the mid-20th century's functional extinction of all natural 3-dimensional oyster reefs in James River, Virginia (Woods et al. 2005), the tributary became an area of concentrated oyster restoration efforts. This tributary was the southernmost sampled for this study and is also on the western side of the Chesapeake Bay. The sanctuary site, Wreck Shoal, was the largest of the 6 we sampled at 585 acres (2.37 km^2). Managers designated the majority of this area

as a sanctuary in 2010 and added seeded shell to it in 2012. From 1999 to 2010, the area was open for market oyster and seed harvest with hand tongs, but it has been closed ever since (Table 1). Ballards Marsh is 78 acres (0.32 km^2) in area and has been open to hand scrape harvest since 2006; managers added seeded shells to the site in 2014 and 2015 (Table 2).

2.1.4. Salinity

An abundance of salinity data exist for the Chesapeake Bay in publicly available databases like the Chesapeake Bay Foundation's DataHub and Maryland Department of Natural Resources' Eyes on the Bay (Chesapeake Bay Program 2021, Maryland Department of Natural Resources 2021). The Chesapeake Bay Program's data management document describes the standard water quality methods for both databases (Chesapeake Bay Program 2018). We found long-term salinity data collected within or near each of the 3 tributaries we sampled at fixed stations (Table 3), but the specific temporal and spatial resolutions of salinity profiles amongst the paired sanctuary-harvested sites vary. In the Choptank, there are multiple water quality stations and continuous monitoring assets within Harris Creek (from which we chose the water quality station closest to our sampling site), but none for Broad Creek. Conversely, the Great Wicomico's water quality station is located between the harvested and sanctuary sites. For the James River, we have site-specific data because there are water quality stations close to each of our respective harvested and sanctuary sites (Table 3). Because we lacked highly resolved site-

Table 1. Sanctuary site characteristics. COE: Corps of Engineers; NA: not applicable

Tributary	Site	Substrate	Year established	Shell plant 1	Shell plant 2
Choptank	Harris Creek	Spat on shell	2012	2012	2017
Great Wicomico	COE #16	Shell	2004	2004	NA
James	Wreck Shoal	Spat on shell	2010	2012	NA

Table 2. Harvest schedule from 2015–2019, or the 5 yr preceding the survey, for the 3 harvested sites. O: open; C: closed; S: spat on shell added to reef. Major gear types include hand tongs, patent tongs, diver, power dredge, and sail dredge

Tributary	Site	Gear type	2013	2014	2015	2016	2017	2018	2019
Choptank	Broad Creek	All major	O/S	O/S	O/S	O/S	O/S	O/S	O/S
Great Wicomico	Cockrell Creek	Hand scrape	O/S	O	O	O	O	C	O
James	Ballards Marsh	Hand scrape	O	O/S	O	O	O	O	O

Table 3. Salinity data stations and sources for each of the 6 sites sampled. COE: Corps of Engineers

Tributary	Site	Salinity zone	Site type	Station ID	Data source
Choptank	Harris Creek	Mesohaline	Sanctuary	HC Downstream XFG2810	Chesapeake Bay Program (2021)
Choptank	Broad Creek	Mesohaline	Harvested	HC Downstream XFG2810[a]	Chesapeake Bay Program (2021)
Great Wicomico	COE #16	Mesohaline	Sanctuary	Great Wicomico (CB5.4W)[a]	Maryland Department of Natural Resources (2021)
Great Wicomico	Cockrell Creek	Mesohaline	Harvested	Great Wicomico (CB5.4W)[a]	Maryland Department of Natural Resources (2021)
James	Wreck Shoal	Mesohaline—polyhaline	Sanctuary	Buoy #9 Hampton Rds (LE5.3)	Chesapeake Bay Program (2021)
James	Ballards Marsh	Mesohaline—polyhaline	Harvested	Buoy #C12-13 (LE5.2)	Chesapeake Bay Program (2021)

[a]Station is not directly adjacent or within the boundaries of the site area, and rather represents a proxy salinity profile

specific salinity data for all 6 sites, we used our salinity profiles to (1) establish that we sampled along a salinity gradient and (2) inform our understanding of the recent natural histories of the tributaries (and, where relevant, specific sites). We did not use salinity as a specific quantitative predictor of oyster population or community structure.

2.2. Habitat quality

To measure oyster reef habitat characteristics, we followed the qualitative methods detailed in Heggie & Ogburn (2021). Briefly, we randomly selected 10 points within a GIS polygon of reef site footprints, which we acquired from state governments. At each of those 10 points within the site, we recorded 2 simultaneous 2—3 min (the approximate amount of time it takes to obtain at least 1 min of video after any disturbed sediment settled) GoPro videos of the benthos,

with the cameras positioned about 10 cm above the sediment and aimed horizontally in opposite directions. From the 20 videos, we selected the clearest still image and assessed reef percent cover and qualitative habitat score in ImageJ (Schindelin et al. 2012; 0: sand or mud only; 1: sand or mud with <50% structured bottom cover; 2: habitat structure covering >50% but less than the shell height of an adult oyster [~75 mm; Fig. 2A]; 3: habitat structure covering >50% and is greater than the shell height of an adult oyster). We captured GoPro footage on the same day as the summer oyster density and demography surveys (see Section 2.3), but the water was too turbid to evaluate habitat characteristics from the June 2019 Choptank footage. We returned in October 2019 to collect new videography footage when water clarity was improved to repeat the video methods at the Harris Creek and Broad Creek sites. Examples of video stills are included in the Supplement (Fig. S1) at www.int-res.com/articles/suppl/m739p065_supp.pdf.
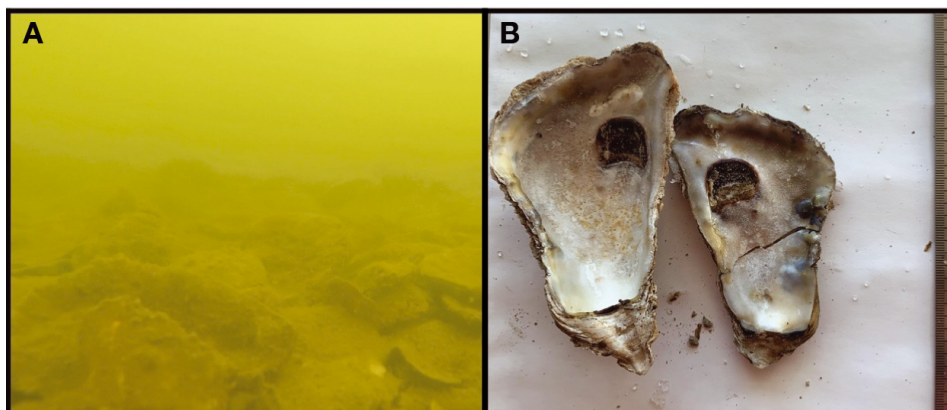

Fig. 2. (A) A screen grab from a GoPro video taken at Harris Creek shows a habitat score of 2. (B) Oyster shell remains of an adult oyster collected from Harris Creek, the sanctuary reef site we sampled in the Choptank River. Sponge perforated through to the mantle of the shell on the left, and the shell on the right has blisters formed by *Polydora* spp.

2.3. Oyster density and demography

We assessed oyster density and demography using quantitative excavation surveys. Within each of our 6 sites, we selected the excavation points from the GoPro videos, returning to the first 3 points where oysters appeared in the footage. Divers scooped all oyster and shell material into mesh sacks by hand within three 0.25 m^2 quadrats per site to hand-depth to estimate live oyster densities. In addition to comparing the total oyster densities amongst the sites, we also separated the oysters into 3 size classes to compare size distributions across sites: spat (<30 mm), sublegal (30−75 mm), and legal (>75 mm). For each oyster, we collected the following information: left valve length (LVL; mm), whole wet weight (g), whole volume and shell volume (ml; using an apparatus described in Coleman 2014), and dry tissue weight (g). From these values, we calculated the oyster's condition index (Hopkins 1949), a unitless metric:

$$\text{Condition index} = \frac{\text{Dry tissue weight}}{\text{Whole volume} - \text{Shell volume}} \times 100 \quad (1)$$

2.4. Macroparasites

2.4.1. Boring sponges

Clionid sponges bioerode, or excavate galleries (Neumann 1966), into the calcium carbonate shells of oysters, exacerbating stress (Guida 1976): bioerosion forces oysters to divert energy from growth and reproduction to shell maintenance (Pomponi & Meritt 1990), which depletes their condition (Watts et al. 2018, Carroll et al. 2021) and survival (Carroll et al. 2015). Boring sponges also deter larval oyster recruitment (Barnes et al. 2010). Population distributions are tightly correlated to salinity (Old 1941, Hopkins 1962), with abundances declining substantially below salinities of 10−15 psu (Wells 1961). Both *Cliona celata* and non-*celata Cliona* spp. are tolerant of higher salinities, whereas non-*celata Cliona* spp. extend into lower-salinity areas (Wells 1961). Non-*celata Cliona* can regress into gemmules, a life history stage that facilitates asexual dispersal and survival during adverse freshet conditions, which may help them to survive at lower salinities (Wells et al. 1964). *C. celata* forms larger (>1 mm) perforations than non-*celata* clionids (<0.5 mm) and excavates larger galleries, and thus *C. celata* is often considered to be more destructive (Guida 1976).

Because the sponge parasite protrudes from the external surface of the shell, we began processing each individual oyster by noting the presence or absence of *C. celata* (large, ~1 mm perforations) and non-*celata* clionid (small, <1 mm perforations) bioerosion. If perforations were present, we measured the maximum distance that the perforations extended up the left valve from the umbo (mm), as sponge infection of an oyster most often starts at the umbo and moves up the shell (Carver et al. 2010). The proportion of the LVL that is perforated is a measurement of total lifetime sponge bioerosion intensity, regardless of the status of the sponge at collection (i.e. chronic infection). Next, we noted if live sponge tissue or gemmules, a dormant sponge life stage that non-*celata Cliona* spp. form during times of environmental stress (Wells et al. 1964), were present. From that information, we assigned each oyster a sponge score to categorize acute infection status: 1 (no perforations present), 2 (perforations only, no live sponge or gemmules), 3 (gemmules, or dormant and therefore stressed sponge state), 4 (gemmules and live sponge tissue, or sponge regressing into or progressing out of a stressed state), or 5 (live sponge tissue only).

2.4.2. Mud blister worms

Like clionid sponges, endemic mud blister worm macroparasites *Polydora* spp. may be valuable indicators of the strength of host—parasite interactions on oyster reefs. *Polydora* spp. are abundant within a salinity range from 10 to 25 psu (Loosanoff & Engle 1943, Wells 1961). To quantify *Polydora* spp. infection, we counted the number of blisters on the interior surface of both valves and calculated the proportion of the total internal shell surface area blistered (Fig. 2B). We used Fiji/ImageJ (Schindelin et al. 2012) to measure the surface area of the oyster shell and the total area of the blisters. For the oysters that did not have relatively flat shell surfaces, we captured several images of the shell from different angles, measured the blisters from the photo where each blister and the underlying shell area looked most flat, and carefully compiled total blister and shell surface area values from the photo series to avoid double-counting areas of overlap.

2.5. Macrofaunal community

We analyzed the GoPro video footage to assess the macrofaunal community, again in ImageJ. For each

video, we recorded the number and type of fish and crustaceans observed, identifying each down to the most specific taxonomic level possible. To standardize macrofaunal observations as MeanCount, we divided the number of observations by the number of frames underwater during which the view was clear in a ~2 min video (Campbell et al. 2015). The data were Poisson-distributed after accounting for number of frames, but were no longer integers, and the values were too small (0—2) to reliably round to the nearest integer without creating artificial zeroes. Therefore, we scaled up all the values from approximately 2 min videos to calculate the abundance and richness expected in 10 min of video. Specifically, we calculated the number of observations per frame (Mean-Count), multiplied that value by 10 min worth of frames at 60 frames s^{-1} (i.e. 36 000), and then rounded to the nearest integer. This step allowed us to round to the nearest integer without compromising the data, and then run the appropriate Poisson-family statistical analyses. Because MeanCount estimates are linear at low abundances (Schobernd et al. 2014), the scaling of our values to 10 min is reasonable.

2.6. Statistical analyses

Performing all analyses in R (version 4.0.3; R Core Team 2020), we used the package 'stats' to compare the average monthly salinity profiles of the tributaries/sites for the entire 2 and 5 yr preceding the survey date using 2 separate Kruskal-Wallis (i.e. non-parametric ANOVA, because the data were neither normally distributed nor homoscedastic) and Dunn post hoc tests (see Fig. 1C,D, Table S1). To compare the condition indices of the oysters across all the site types and tributaries (a proxy for salinity), we again used a Kruskal-Wallis and a Dunn post hoc test for non-parametric data (Table S2).

We calculated and compared the maximum habitat scores for each of the 10 video pairs. Using a multinomial logistic regression (package 'nnet'; Venables & Ripley 2002), we determined if site type (harvested or sanctuary), site, tributary, or salinity zone were important predictors of the observed habitat structure. We used a habitat score of 3 as the reference level in the multinomial logistic regressions because there were so few observations of scores of 0.

Beta regressions model response variables bound between 0 and 1, like proportional data, and, therefore, are appropriate approaches for the macroparasite prevalence data. Because there were a number of oysters whose shells were either not in-

fected with sponge at all, or had sponge covering the entire length of the left valve, we used a zero-and-one-inflated beta regression with a logit link (package 'brms'; Bürkner et al. 2021) to determine if tributary and site type are interactive predictors of the observed sponge infection intensity (measured by the proportion of the LVL perforated). We used an ordinal logistic regression to model sponge score as a function of site type and tributary (package 'ordinal'; Christensen 2019), satisfying the proportional odds assumption (Brandt's test, $p < 0.001$).

A number of oysters had no *Polydora* spp. blisters, and there were no oysters whose shell interior was completely blistered. Therefore, we used a zero-inflated beta regression (package 'brms'; Bürkner et al. 2021) to evaluate tributary and site type as interactive predictors of observed *Polydora* spp. infection levels in the oysters. Finally, we used Poisson-distributed generalized linear models (package 'stats') to determine if our observed patterns in diversity (number of species) and abundance (individual count) were functions of site type or tributary or a combination of the two (i.e. site). We checked for over-parameterization and over-dispersion in diagnostic plots and AIC values, from which we determined best model fit.

3. RESULTS

3.1. Site salinity profiles

The paired harvested and sanctuary oyster reef sites we sampled in the Choptank, Great Wicomico, and James tributaries of Chesapeake Bay spanned mesohaline and low polyhaline (i.e. ~5—22 psu) salinity zones (Fig. 1A,B). Monthly salinities exhibited a seasonal pattern from 2013—2017, with lower salinities in spring and higher salinities in summer and fall. The entire bay experienced an extended freshwater pulse through late 2019, the year we conducted our surveys (Fig. 1B). Sites experienced lower median salinities in the 2 yr preceding the survey compared to the 5 yr preceding collection (Fig. 1C,D). The Choptank had the lowest recorded salinities, followed by Great Wicomico and James ($p < 0.001$ and $p < 0.001$, respectively; Table S1). Of the 3 pairs, the James sites were farthest apart, but both had adjacent long-term salinity monitoring assets. Ballards Marsh, the site closest to the mouth of the Bay, was the most saline (median salinities of 16.9 and 15.7 psu for the 5 and 2 yr pre-survey profiles, respectively). Ballards Marsh was ~3 psu more saline than Wreck Shoal

(p < 0.001 and p = 0.021, for the 2 and 5 yr comparisons, respectively). Wreck Shoal was far enough upstream that it was substantially fresher than the Great Wicomico sites in the 5 yr preceding the survey (p = 0.039), though the 2 yr pre-survey comparison showed no clear differences between the sites because of the freshwater pulse (p = 0.882). However, the Choptank sites had a statistically similar salinity profile to the Wreck Shoal site in both the 5 and 2 yr pre-survey comparisons (p = 0.230 and p = 0.211, respectively; Fig. 1C,D, Table S2).

3.2. Habitat quality

Overall, the sanctuary reefs had higher habitat scores than harvested reefs (sanctuary: n = 26, $\bar{x}$ = 2.63, 95% confidence interval [CI]: 2.35−2.92; harvested: n = 30, $\bar{x}$ = 2.04, 95% CI: 1.71−2.37; Fig. 3A). Multinomial logistic regression model selection showed that site type — whether the oyster reef sampled was harvested or sanctuary-protected — was the most important predictor of habitat quality (AIC = 118.4; Table S3). Two-tailed z-tests comparing the specific proportions of habitat scores suggest that significant differences in the number of habitats with scores of 3 relative to the number with scores of 2 and 1 amongst the harvested and sanctuary reefs drove this observed discrepancy ($p_{1,3}$ = 0.034; $p_{2,3}$ = 0.002;

Table S4). The sanctuary sites also had significantly more maximum observed habitat scores of 3 than their respective paired harvested sites in all 3 tributaries (Fig. 3B, Table S4). In general, the proportion of score 3 habitat decreased with decreasing salinity (i.e. salinity zone was a significant predictor). Wreck Shoal had a habitat score of 3 at all sample locations. All video samples contained at least some oyster reef habitat (i.e. there were no maximum habitat scores of 0; Fig. 3B).

3.3. Oyster demography

Broadly, sanctuary sites contained more oysters than harvested sites. Sanctuary sites in all 3 tributaries had greater densities of legal-sized oysters than their paired harvest sites (Fig. 4).

In the Choptank, the sanctuary site Harris Creek had 30.7 ± 13.9 legal oysters m^{-2}, whereas Broad Creek, a reef that had recently been open to harvest (Table 1), had no legal oysters. The harvested site, Broad Creek, also had more sublegal oysters (121.3 ± 18.7 m^{-2}) and spat (6.67 ± 3.52 m^{-2}) than the Harris Creek sanctuary site (21.3 ± 10.9 sublegal oysters and 0 spat m^{-2}). In the Great Wicomico and James rivers, the pattern of oyster densities being higher in sanctuaries relative to harvested sites extended beyond legal oysters to sublegal oyster and spat densities. The
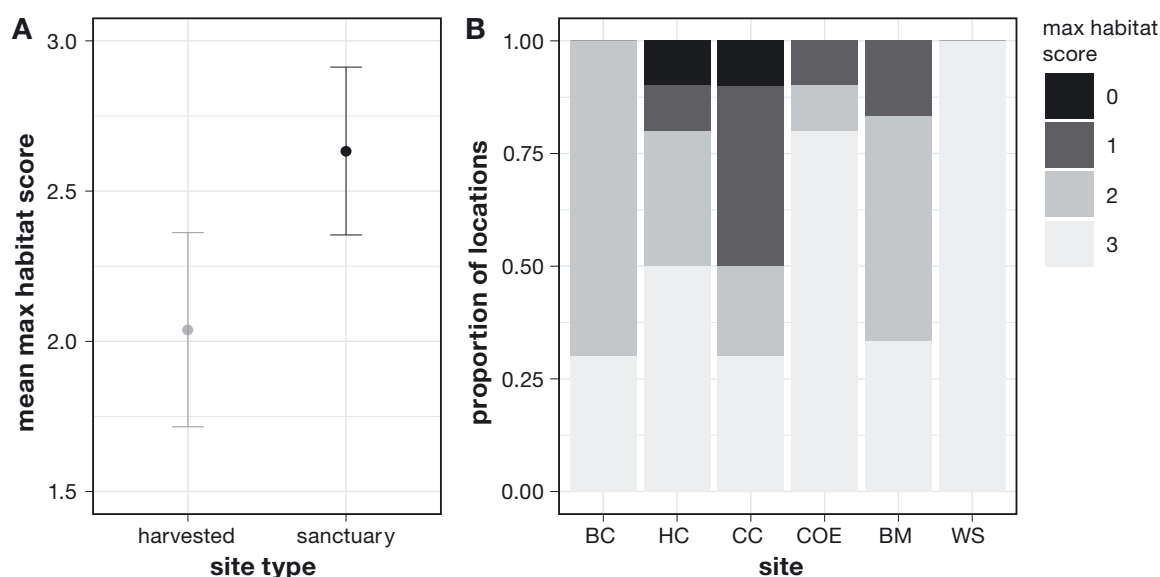

Fig. 3. (A) Mean maximum habitat scores for all pooled harvested and sanctuary GoPro image samples with 95% confidence intervals. (B) Proportion of all maximum habitat scores (0: sand or mud only; 1: sand or mud with <50% structured bottom cover; 2: habitat structure covering >50% but less than the shell height of an adult oyster [~75 mm]; 3: habitat structure covering >50% and is greater than the shell height of an adult oyster) by site. BC: Broad Creek; HC: Harris Creek; CC: Cockrell Creek; COE: Corps of Engineers #16; BM: Ballards Marsh; WS: Wreck Shoal
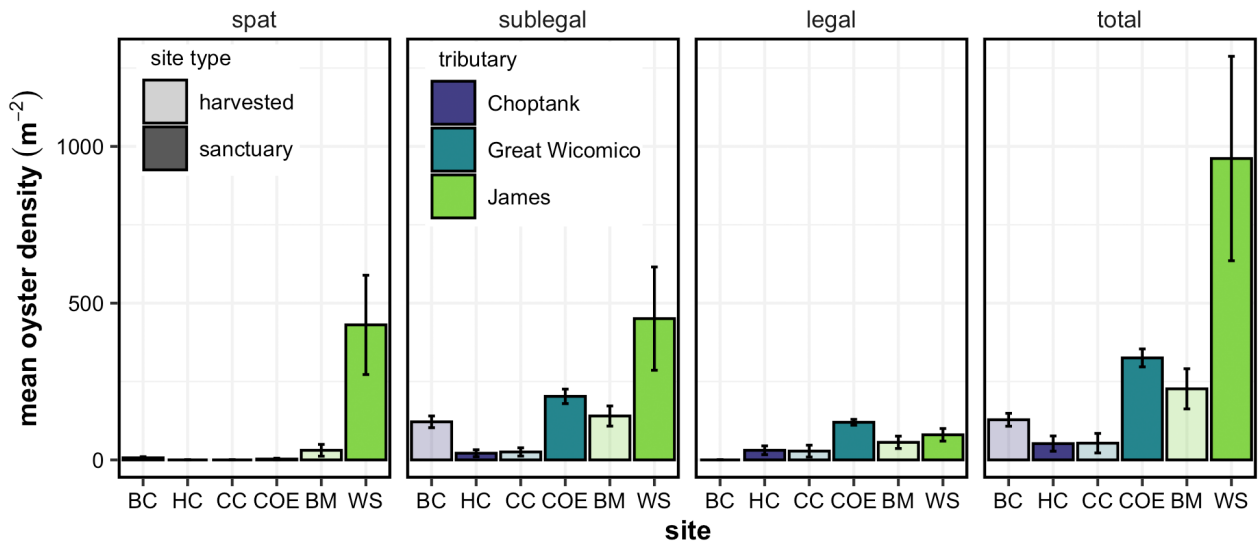
Fig. 4. Mean observed densities of 3 size classes of oysters (spat: <30 mm; sublegal: 30–75 mm; and legal: >75 mm) by site. Site abbreviations as in Fig. 3. Error bars: ±1 SE. Colors indicate sites with lighter colors for harvested sites and the corresponding darker color for the sanctuary in the same tributary

Great Wicomico sanctuary site (COE #16) had the overall greatest density of legal oysters (120 ± 9.24 m^{-2}), though the James sanctuary site (Wreck Shoal) also had relatively high densities of legal oysters (80 ± 10 m^{-2}). Across all size classes, oyster densities generally increased with increasing salinity (with the one exception of the Great Wicomico sanctuary site having the greatest density of legal oysters).

Although oyster density was generally greater in the sanctuary sites, oyster condition in the sanctuary sites was significantly lower relative to the harvested sites (Kruskal-Wallis test: p < 0.001; Table S5, Fig. 5). For example, the Great Wicomico and James sanctuary sites had median condition indices of 5.05 and 4.09, respectively, whereas their paired harvested sites had significantly greater condition indices of 6.73 (Dunn post hoc test: p = 0.003) and 6.38 (p < 0.001; Table S6, Fig. 5), respectively. The Choptank sanctuary site also had a lower median condition index (5.74) than its paired harvested site (6.76), though this difference was not statistically clear (p = 0.123). Across all the harvested sites (Broad Creek, Cockrell Creek, and Ballards Marsh), the oysters we collected all had statistically similar condition indices (Table S6); but for oysters from the sanctuary sites, condition index decreased with increasing salinity, with James sanctuary (Wreck Shoal) oysters having significantly lower condition indices than Choptank sanctuary (Harris Creek; p = 0.014) and Great Wicomico sanctuary (COE #16; p = 0.015) oysters (Table S6, Fig. 5). The Choptank sanctuary site oysters had a significantly greater internal volume
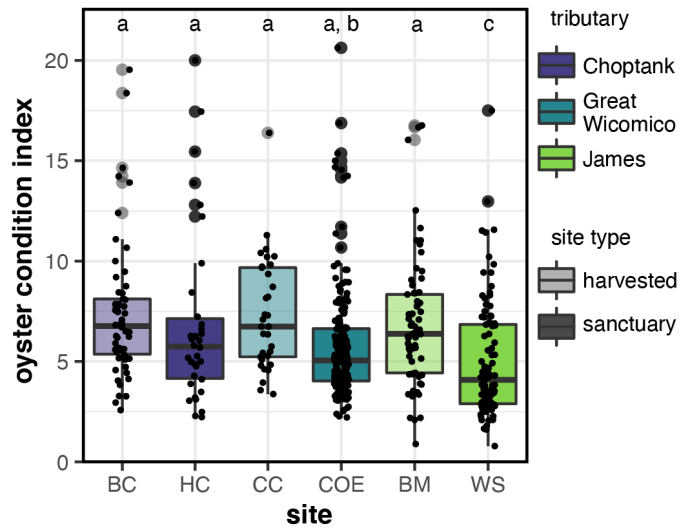

Fig. 5. Oyster condition index by site. Jittered points show the distribution of individual measurements. Letters above the boxplots depict statistically clear results per respective Kruskal-Wallis and Dunn post hoc tests at the α = 0.05 level (Tables S5 & S6). Box and whisker plot features as in Fig. 1. Site abbreviations as in Fig. 3. Colors indicate sites with lighter colors for harvested sites and the corresponding darker color for the sanctuary in the same tributary

than the Choptank harvested site (Broad Creek) oysters (p < 0.001), while the internal volumes of oysters from the Great Wicomico sanctuary and James sanctuary were lower than oysters from the respective Great Wicomico (p = 0.046) and James (p = 0.036) harvested sites (Cockrell Creek and Ballards Marsh, respectively; Table S6).

3.4. Macroparasite prevalence and intensity

Across subtidal reefs in 3 tributaries of the Chesapeake Bay, *Cliona celata* was not observed and non-*celata Cliona* spp. perforated a greater proportion of the LVL on oysters collected from sanctuary reefs compared to oysters from harvested reefs (zero-one-inflated beta regression credible interval does not contain 0: 0.06−0.98); Table S7, Fig. 6A). More specifically, oysters within the Choptank and Great Wicomico sanctuary sites both had more of their shells perforated (78.9 and 71.2% respectively) relative to oysters in their paired harvested sites (68.5 and 59.5%, respectively; Fig. 6A, Table S7). The proportions of oyster shells perforated within the James sanctuary and harvested sites did not differ. There were also differences in the proportion of oyster shell perforated on the tributary level: oysters from the Choptank and James had significantly greater proportions of their shells perforated (~75 and ~63%, respectively) compared to oysters from the Great Wicomico (~60%; credible interval is negative and does not contain 0: −0.74 to −0.03; Table S7). Sanctuary oysters also clearly had a greater proportion of their interior shell surface area

blistered by *Polydora* spp. relative to oysters from harvested reefs (Fig. 6B, Table S8). Oysters from the Great Wicomico and James had a greater proportion of shell surface area blistered relative to oysters collected within the Choptank sites. The Choptank and James sanctuary site oysters had greater proportions of their shells blistered (4.70 and 9.55%, respectively) relative to oysters collected from their harvested tributary pair (1.66 and 5.76%, respectively), but proportions amongst the Great Wicomico sanctuary and harvested oysters did not differ (10.3 and 10.0%, respectively; Fig. 6B, Table S8).

Using an ordinal scoring system to evaluate acute infection, we determined that live, non-*celata Cliona* spp. (i.e. small perforation-boring, gemmule-forming) sponge tissue was present at all 6 sites, though was most prevalent at the Great Wicomico sanctuary site (Fig. 7A). Sponge tissue was relatively evenly distributed across oysters greater than 50 mm, though the relative amount of sponge tissue varied by tributary and site type. Indeed, the best-fit ordinal logistic regression model included the fixed-effects interaction between these 2 variables (AIC = 1996; Table S9). The proportions of individual sponge scores varied across sites. Between the Choptank harvested and tributary sites, the scores were nearly identical, with a majority of sponge scores being low (1 or 2; Fig. 7B). In contrast, the Great Wicomico and James sanctuary sites had greater proportions of high sponge scores (4 and 5) and lesser proportions of the lower sponge scores (1 and 2) relative to their respective paired harvested sites. More specifically, the sanctuary James site contained only half as many sponge scores of 1 (35−48%) compared to the respective harvested site (75−88%). And while the harvested James site had almost no sponge scores of 3, 4, or 5 (i.e. evidence of live sponge or gemmules; ~0−2% each), the paired sanctuary site, Wreck Shoal, had a small, but significantly greater, proportion of these same scores (7−11, 3−7, and 5−10%, respectively). Despite having relatively little evidence of live sponge tissue or gemmules, Wreck Shoal had substantial evidence of past sponge infection (i.e. shell perforations, sponge score 2: 33−43%). Across all 3 tributaries, the Great Wicomico had the greatest non-*celata*
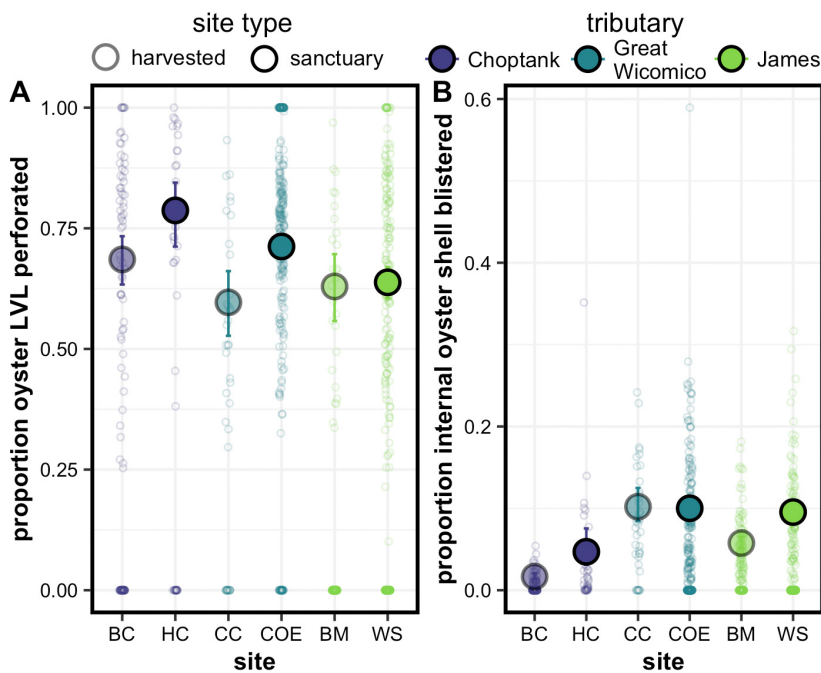

Fig. 6. (A) Zero-and-one-inflated beta regression comparing the proportion of the oyster left valve length (LVL) containing boring sponge perforations as a function of the interaction between site type and tributary. (B) Zero-inflated beta regression comparing the proportion of the internal oyster shell blistered by *Polydora* spp. as a function of the interaction between site type and tributary. Site abbreviations as in Fig. 3. Error bars: 95% credible intervals. Colors indicate sites with lighter colors for harvested sites and the corresponding darker color for the sanctuary in the same tributary
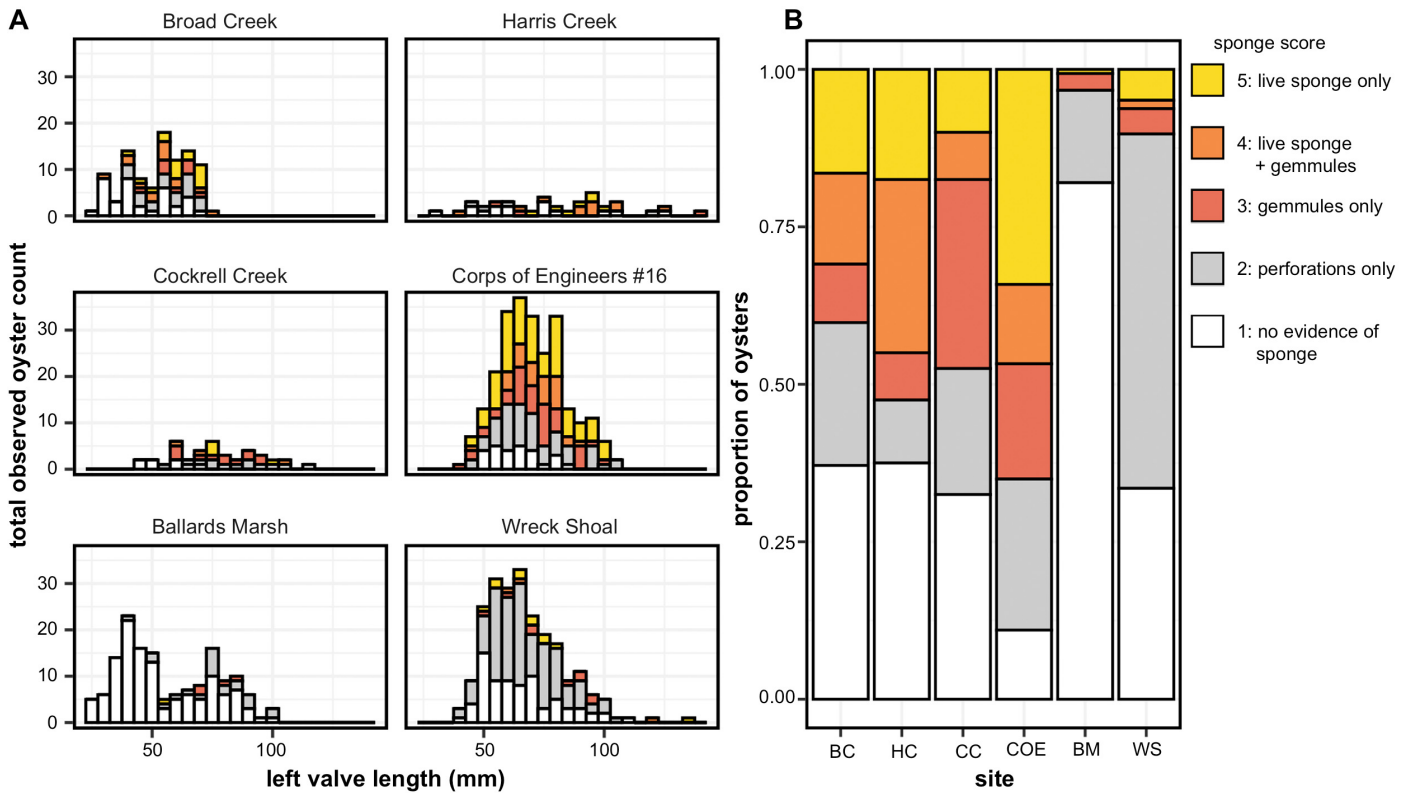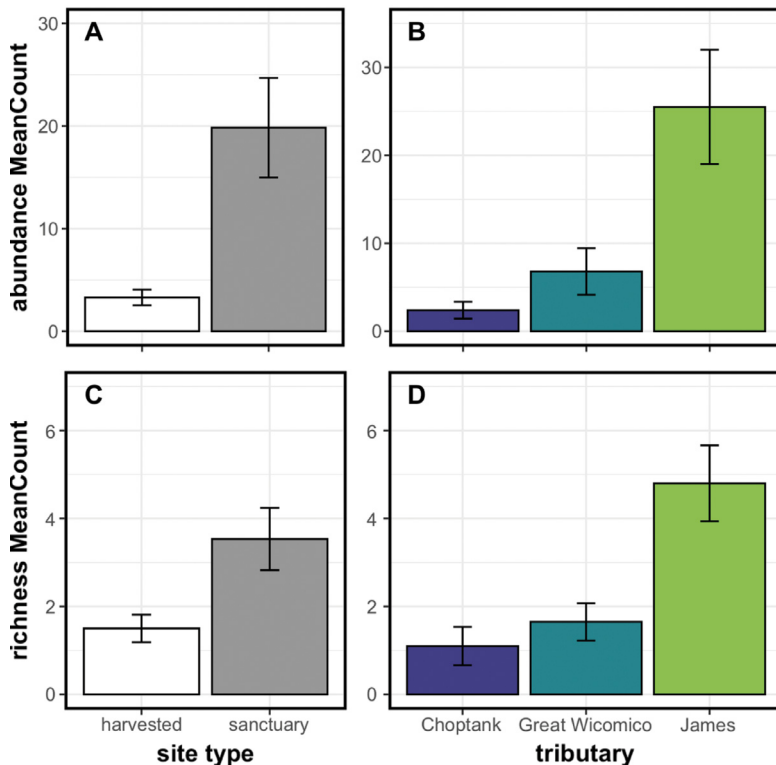
Fig. 7. (A) Total counts of oysters by sponge score, collected in 3 sample quadrats at each of our 6 sites. (B) Ordinal logistic regression-predicted proportions of sponge scores at harvested and sanctuary reefs in the Choptank, Great Wicomico, and James tributaries. Site abbreviations as in Fig. 3

Cliona spp. load, but the sanctuary site had significantly more scores of 5 (28– 40%) and fewer scores of 1 (7–13%) than the respective harvested site (5– 14% 5s and 15–40% 1s; Fig. 7B).

3.5. Macrofaunal community

From the GoPro footage, we ascertained 2 clear patterns in macrofaunal (i.e. fishes and crustaceans) use of the oyster reefs (Fig. 8): (1) abundance and richness were both greater in the

Fig. 8. MeanCount abundance (scaled to number per 10 min video) measured from GoPro footage by (A) site type and (B) tributary. MeanCount richness (scaled to number per 10 min video) measured from GoPro footage by (C) site type and (D) tributary. Error bars: ±1 SE

sanctuary reefs than the harvested reefs (Fig. 8A,C); and (2) as salinity increased, abundance and richness increased (Fig. 8B,D). The organisms we observed were black sea bass *Centropristis striata*, blenny *Chasmodes bosquianus*, blue crab *Callinectes sapidus*, grass shrimp *Palaemonetes* spp., goby *Gobiosoma* spp., northern puffer *Sphoeroides maculatus*, striped bass *Morone saxatilis*, summer flounder *Paralichthys dentatus*, and white-fingered mud crab *Rhithropanopeus harrisii*. Of the linear regression models that compared richness across sites, we found that the best-fit model included tributary and site type as predictors (AIC = 790.9; Table S10). Similarly, the linear model that best fit the abundance data included both tributary and site type predictors (AIC = 265.1; Table S11). For both sets of the richness and abundance model series, the model that included tributary and site type as interactive factors had the lowest AIC values, but based on large standard errors, they appeared to be overfit; therefore, we did not consider them to be the 'best fit' (Tables S10 & S11). The site-level richness and abundance data both showed near-identical patterns to the total oyster density and habitat score data. For example, videos of the James sanctuary site showed 47 ± 8.4 individuals comprising 8.2 ± 0.63 species using the reefs per 10 min video, whereas the paired intra-tributary harvested site only supported 3.6 ± 1.4 individuals across 1.4 ± 0.43 species. Likewise, the Great Wicomico sanctuary site had greater abundance (12 ± 4.8 individuals per 10 min video) and richness (2.4 ± 0.7 species per 10 min video) than the harvested site (1.5 ± 0.72 individuals and 0.9 ± 0.38 species per 10 min video). However, we did not observe any individuals amongst all the videos at the Choptank sanctuary site, while the harvested site supported approximately 4.8 ± 1.6 individuals and 2.2 ± 0.73 species per 10 min video (Table S12).

4. DISCUSSION

This survey of 6 subtidal oyster reefs in 3 tributaries spanning a latitudinal and biophysical gradient in Chesapeake Bay demonstrated that oyster harvest reduces: (1) oyster density and size, (2) reef habitat scores, (3) host—parasite interactions, and (4) associated reef macrofauna. Amongst the site type pairs and all dependent variables, there were a few exceptions to these overarching trends. Despite these few deviations and a relatively small sample size of paired harvest and sanctuary reefs (n = 3 pairs for n = 18 total samples across Chesapeake Bay), our findings largely support our overarching hypothesis that harvest reduces oyster density, habitat quality, and macrofaunal reef use, as well as the strength of host—parasite interactions. Below, we use our knowledge of the site salinity profiles to describe the observed site-specific distributions of the oyster host, boring sponge and mud blister worm macroparasites, and reef-associated mobile macrofauna.

Across all survey sites, both total and adult oyster densities were higher on sanctuary reefs compared to harvested reefs, and total oyster densities increased with increasing salinity. Adult oyster densities were greatest at the middle- (COE #16) and high-salinity (Wreck Shoal) sanctuary sites, suggesting that these salinities are optimal for oyster growth. Across all 3 pairs of sites, sanctuary reefs had twice as many adult oysters as harvested reefs, demonstrating how harvest targets larger oysters. It is also valuable to consider whether oyster density was above the minimum restoration threshold (15 oysters m^{-2}) or target (50 oysters m^{-2}) in at least 30% of samples (Maryland Oyster Restoration Interagency Workgroup of the Chesapeake Bay Program's Sustainable Fisheries Goal Implementation Team 2020). For at least half of the sites we sampled (COE #16, Ballards Marsh, and Wreck Shoal), adult oyster densities exceeded the total target density of 50 oysters m^{-2}. Harvest had the most obvious impact in the Choptank River. Broad Creek reefs were open to harvest <2 mo prior to our survey, and we were unable to find any legal oysters, but rather many oysters just under the 76 mm legal size limit (i.e. sublegal; Fig. S2). This is consistent with stock assessments that have indicated that oysters are overfished in Broad Creek (Maryland Department of Natural Resources 2020).

Associations between reef harvest or sanctuary status and the abundance of smaller oysters were less clear. The absence of spatfall at the Choptank and Great Wicomico sites may instead be attributed to the extended low salinities that the entire Bay, and especially the Maryland portion of the Bay, experienced from 2017—2019. In the months preceding our survey, salinities were >10 psu, the approximate minimum salinity required for oyster spawning to be successful (Loosanoff 1948, 1953, Davis 1958). Our finding that the Choptank had no spat matches the low spatfall observed in the Maryland Department of Natural Resources annual fall oyster surveys in 2018 and 2019 (Tarnowski et al. 2019, 2020). However, the Virginia fall state surveys found spatfall at the Great Wicomico site, suggesting we sampled before the first summer spat settlement (Virginia Institute of Marine Sciences 2021). The sanctuary James site, Wreck Shoal, may

have had more spatfall than the harvested site, Ballards Marsh, because it also had greater densities of sublegal and legal, and therefore potentially reproductive, oysters. Wreck Shoal is also surrounded by other oyster sanctuaries, whereas Ballards Marsh is a more isolated site, and this proximity to additional reproductive oysters could contribute to the increased spat densities we observed at Wreck Shoal.

Although the Harris Creek sanctuary reefs had lower total oyster densities than Broad Creek, sublegal oysters drove the differences. Both Choptank sites also had oyster densities above the restoration target of 50 oysters m^{-2}. Consistent with our study's findings, 98% of 6 yr old reefs in Harris Creek met minimum success criteria for oyster density (15 oysters m^{-2} in 2019 surveys) and biomass, and 56% met the higher target criteria (Maryland Oyster Restoration Interagency Workgroup of the Chesapeake Bay Program's Sustainable Fisheries Goal Implementation Team 2020).

At the reef scale, greater oyster densities coincided with higher habitat scores, which parallel findings from previous studies that have demonstrated higher relief reefs have higher densities of oysters (Schulte et al. 2009, Powers et al. 2009, Colden et al. 2017, Lipcius & Burke 2018). Oyster reef habitat existed at all 6 sites, despite lower oyster densities at the sites in the upper Bay. Therefore, the differences amongst the habitat scores were not driven by the proportion of habitat with no oyster cover (0s) and <50% cover (1s), but rather the proportions of more complex habitats, or whether the oysters were configured as a rubble-like mound (2s), or in a reef-accreting, upright position (3s). Amongst the 6 sites we sampled, the sanctuary reefs had a greater proportion of accreted (score 3) habitat compared to harvested reefs, further demonstrating that harvest reduces habitat complexity (Lenihan & Peterson 1998) and thus site type has a strong effect on the observed habitat scores. This finding also showcases the value of coupling a non-extractive and rapid habitat measurement (i.e. habitat scores collected from the GoPro videos) with an extractive and tedious measurement (i.e. quadrat excavation and subsequent oyster processing): 3 replicate quadrats at Harris Creek alone would not have completely represented the oyster habitat at that site, but the larger sample size of the GoPro videos (n = 10 per site) helped clarify our understanding of the reef structure.

We did not observe *Cliona celata* at our study sites, and non-*celata Cliona* spp. boring sponge load was greater in sanctuary sites than harvested sites. *C. celata* is found in more polyhaline (e.g. >20 psu) parts of the Chesapeake and Virginia Coastal Bays (Z. B.

Anchondo et al. unpubl. data). Boring sponges were also differentially distributed along the Chesapeake Bay's salinity gradient, peaking in the mid-salinity (Great Wicomico) sites. The Great Wicomico sanctuary reef (COE #16) contained the most oysters infested with either live sponge tissue or gemmules. The high densities of sublegal and legal oyster hosts at that site likely contributed to this trend in the sponge distribution, as increased host densities often correspond with greater parasite transmissibility (Krkosek 2010, Lafferty 2017, 2020). High oyster densities and favorable environmental conditions likely supported robust boring sponge populations at the Great Wicomico sanctuary site prior to the 2017—2019 bay-wide freshening, because after 2 yr of persistently low salinities, we observed live and healthy sponge tissue. Few oysters from the harvested and sanctuary Choptank sites contained live sponge, but many had gemmules or large proportions of their shells perforated. The historical salinity profile of the tributary can in part explain these observations: in the 2 yr prior to the 2017—2019 freshet, there was an unusual high-salinity event, during which clionid populations apparently thrived in the Choptank, but the nearly 2 yr freshet caused the sponge to regress considerably before we collected their oyster hosts in 2019 (Chesapeake Bay Program 2021, Maryland Department of Natural Resources 2021). The Harris Creek oysters also had the most evidence of chronic sponge infection because they are larger and likely older than many of the other oysters collected across the other 5 sites. The James River oysters had the least live sponge tissue, and its harvested site (Ballards Marsh) also contained little evidence of past sponge infection. We suggest that harvest reduces host density and size, and that the site may be too salty (i.e. often >20 psu) for non-*celata Cliona* spp. growth and bioerosion. Wreck Shoal, the sanctuary James site, had little live sponge but did have substantial evidence of past sponge infection (i.e. many oysters with perforations), suggesting that the site's salinity profile prior to the freshet was conducive to sponge growth. These findings demonstrate the need to understand how salinity and harvest differentially influence restoration outcomes.

Polydora spp. were distributed in a similar, though not identical, manner as the boring sponges. For instance, *Polydora* spp. infection (measured by the proportional internal shell surface area blistered) was lower in the Choptank compared to the Great Wicomico and James sites. At Broad Creek, the site where the lowest salinities were coupled with intense harvesting pressure (i.e. a removal of the largest macro-

parasite oyster hosts from the reef system), *Polydora* spp. blisters were almost completely absent. Similarly, a combination of harvesting and higher overall salinities at Ballards Marsh were conditions that facilitated lower *Polydora* loads relative to Wreck Shoal. Early documentation of *Polydora* spp. blisters showed that infection is greatest in salinity ranges of ~10−20 (Lunz 1941), and more recent work suggests that *Polydora* mortality increases at salinities <10 psu (Brown 2012). Similarly, we found that shell blistering was greatest in the Great Wicomico, suggesting that *Polydora* spp. performs better in mid-range (median ~15 psu), low-variance salinity regimes than low-range or high-variance salinity conditions. *Polydora* spp. infection intensity did not differ between individual oysters collected from the harvested and sanctuary Great Wicomico sites. However, at the reef level, because the sanctuary site contained greater densities of larger oysters than the harvested site, the total *Polydora* spp. blistering load was also significantly higher in the sanctuary (CEO #16). Overall, our research reaffirms the cross-aquatic habitat trend that parasite loads are higher in unfished areas than fished areas (Wood & Lafferty 2015) and establishes the importance of understanding the interaction between fishing pressure and environmental gradients in structuring oyster reef macroparasite communities in Chesapeake Bay.

The individual oysters comprising the sanctuary reefs were of a lower condition relative to oysters on harvested reefs within the same tributary. Though we did not directly test the relationship between oyster condition and parasites, as our focus was on the impacts of harvest on oyster reef characteristics, this finding is unsurprising — previous studies have suggested that clionid infection can lower oyster condition indices (Carroll et al. 2015, Dieudonne & Carroll 2021). In our study, the differences in the Choptank oyster conditions can be attributed to the larger lengths and internal volumes of the Harris Creek oysters, and condition naturally declines as oysters get bigger. Conversely, the internal volumes of oysters from the sanctuary Great Wicomico and James sites were lower than their respective harvested reef oysters, as were their condition indices, suggesting the internal volume did not drive the patterns we saw. Rather, we attribute lower conditions of the Great Wicomico and James sanctuary oysters primarily to oyster length, higher macroparasite loads, and the relationship between habitat structure and individual oyster morphology. Larger oysters are older, have had longer to become infected by macroparasites, and thus often carry greater bioeroder

loads. Further, we observed that the sanctuary reefs had more vertically accreting oysters in higher measured densities, resulting in more oblong (i.e. 'coon') shaped oysters that are of lower condition compared to less clumped oysters or single oysters more often found at harvested sites.

As anticipated, the more complex sanctuary oyster habitat was associated with greater macrofaunal abundance and richness compared to harvested oyster reefs, and macrofaunal abundance generally increased with increasing salinity because the lower Bay is more hospitable to mobile macrofauna (Karp et al. 2018). Overall, these findings are consistent with previous studies that showed (1) MPAs or sanctuaries consistently enhance species richness (Côté et al. 2001) and faunal abundances of rocky reef communities (Edgar & Stuart-Smith 2009) relative to fished sites, and (2) across coastal foundation species, habitat complexity predicts fish abundance and assemblages (e.g. Charbonnel 2002, Orth et al. 2006, Taylor & Bushek 2008, Hunter & Sayer 2009, Darling et al. 2017). The macrofauna species we commonly observed on sanctuary reefs included important fishery species and predators of juvenile blue crabs (Longmire et al. 2021). Notably, we observed these differences despite the continuation of harvest of macrofauna (e.g. finfish and crabs) in the oyster sanctuaries.

Perhaps the most interesting and applicable finding from this study is that in addition to reducing the density and size distributions of oysters, extractive oyster harvest also depresses habitat characteristics, macrofaunal abundance and richness, and host—parasite interactions between oysters and endemic parasites. While not a surprising result, it is nevertheless important, provided the unique dual roles that oysters serve as foundational habitat-builders and a food resource. Compared to harvested reefs, the sanctuary reefs had higher densities of oysters comprising a more complex reef structure, which in turn supported more mobile macrofauna than harvested reefs. Our findings show that mud blister *Polydora* spp. worms and non-*celata* *Cliona* spp. sponges can also co-occur with high oyster densities on subtidal sanctuary oyster reefs, suggesting they may not need to be considered in restoration planning at lower mesohaline salinities, but *C. celata* may need to be included in planning efforts at higher polyhaline salinities if it is found to play a more important role there. Though our study was limited to 6 sites, the patterns of sanctuary reefs having more oysters, complex habitat, macroparasites, and macrofauna than harvested sites were relatively clear and consistent with similar studies of oyster reefs along a dynamic estuarine

salinity gradient (Tracy et al. 2023). Therefore, this work suggests that the process of oyster restoration and protection within no-take reserves revitalizes important host—parasite interactions that are reduced by extractive harvest methods. *Cliona* spp. and *Polydora* spp. are viewed as pests in fisheries and aquaculture, but they are endemic parasites, and parasite biodiversity is experiencing its own global crisis (Carlson et al. 2017). Although these parasites negatively affect the health of individual oysters, which is problematic for harvested oysters, this study shows that infected oysters commonly occur on ecologically healthy reefs in restored sanctuaries without preventing high oyster densities and complex reef structure.

These data suggest that harvest has far-reaching consequences for oyster reef ecosystems, highlighting the value of oyster sanctuaries for restoring and protecting ecosystem functions, including the procurement of critical habitat for fisheries species and revitalizing host—parasite interactions. Our results advocate for including additional metrics beyond oyster density and size to inform oyster management decisions. Management discussions are typically centered around the length of the harvest season, harvest gear types, daily harvest limits, and other management options such as seeding programs and rotational harvest (i.e. opening areas to harvest every 3–4 yr) that are focused directly on oyster fisheries. This study demonstrates that opening oyster sanctuaries to harvest, even on a rotational basis, would result in lower oyster densities, lower percent cover and height of reef habitat, and lower abundances and richness of macrofauna. Thus, protecting investments in sanctuary reefs and the more complex oyster reef ecosystems they support should continue to be a top priority in addition to addressing methods to enhance oyster populations in areas currently open to harvest. Additionally, we show that to make informed decisions about the management of oyster reef ecosystems, scientists and managers need to collect oyster reef data beyond oyster metrics (i.e. macroparasites and macrofauna). Researchers also need to focus more attention on the ways in which harvest influences other aspects of restored oyster reef ecosystem performance, including the recovery of ecosystem services and processes.

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