ORIGINAL RESEARCH

High parasite prevalence in an ecosystem engineer correlated with both local- and landscape-level factors

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Abstract

Spatial variation in parasitic infection may have many physical and biological drivers. Uncovering these drivers may be especially important for parasites of ecosystem engineers because the engineers are foundational to their communities. Oysters are an important coastal ecosystem engineer that have declined drastically worldwide, in part due to enhanced cases of lethal oyster diseases, such as Dermo and MSX, caused by the protozoan parasites *Perkinsus marinus* and *Haplosporidium nelsoni*, respectively. Besides water quality and hydrodynamics, there is little information on how other variables influence the prevalence and intensity of these pathogens in oysters across a regional scale. To examine drivers of spatial variation in these oyster parasites—including host size, local reef properties, and landscape properties—we sampled 24 reefs systematically spread along the coast of Georgia, USA. Across sites, we found universally high prevalence of oysters with at least one of these parasites ($91.02\% \pm 8.89$, mean $\pm$ SD). Not only are high levels of parasite prevalence potentially problematic for a pivotal ecosystem engineer, but also low spatial variability may limit the explanatory power of variables across a regional scale. Our statistical models explained between 18 and 42% of the variation in spatial patterns of prevalence and intensity of these microparasites. Interestingly, landscape context was a positive predictor of *P. marinus*, but a negative predictor of *H. nelsoni*. Overall, our findings suggest that factors driving parasite prevalence and intensity operate across multiple spatial scales, and the same factor can both facilitate and hinder different parasites within the same host species.

Keywords Communities · Disease · Multiple stressors · Landscape context · Geographic variation

Introduction

Ecosystem engineers are key species that modify biotic and abiotic conditions affecting overall ecosystem function (Jones et al. 1994). Across broad spatial scales, the presence and density of autogenic ("habitat-forming") engineers varies drastically and can affect the overall engineering function of a species (Berke 2012; Lathlean and McQuaid 2017). However, the decline of these critical habitat-forming species is prominent across the globe due to a multitude of environmental stressors, including infectious disease (e.g.,

eelgrass wasting disease, chestnut blight; Burge et al. 2014; Jakobsson-Thor et al. 2020). Research demonstrates the urgent need to understand both short- and long-term effects of climate change and the impacts of parasites and infectious disease on ecosystem engineers, and subsequently the effects on healthy ecosystems (Harvell et al. 2002; Lafferty 2009; Byers 2020, 2021).

Infection by parasites can increase host mortality, as parasite or disease-induced population declines have been observed in amphibian species due to the fungal pathogen *Batrachochytrium dendrobatidis* which causes Chytridiomycosis (Scheele et al. 2019). However, effects of parasites can also be more subtle, for example by influencing how their hosts interact with the surrounding environment by modulating host behavior or physiology. For instance, the freshwater snail *Helisoma trivolvis* infected with trematode parasites consumes nearly two times as much food compared with uninfected conspecifics (Resetarits et al. 2023). These lethal and non-lethal effects of parasites on their hosts can vary across broad spatial scales due to differences in infection

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prevalence and intensity driven by a suite of physical and biological factors at both local and landscape levels. For example, Altman and Byers (2014) found that the presence of trematode parasites was directly correlated with increased anthropogenic activity, namely high contaminants, and road density at the landscape level. Therefore, understanding the spatial drivers in the variability of infection prevalence and intensity across scales is key to understanding the broader ecological impacts of parasites.

Changing abiotic conditions across large spatial scales from climate change and increased urbanization are broadly affecting species interactions and causing declines in species globally (Bellard et al. 2012). Increases in infection prevalence and intensity have been connected to increased temperatures at local scales altering optimal conditions for both host and parasites (Harvell et al 2002; Altizer et al. 2013; Ben-Horin et al. 2013; Gehman et al. 2018). At landscape scales, increased habitat fragmentation and a decline in structured habitat density have been found to correspond to increased parasite prevalence and intensity (Ulbrich and Seidelmann 2001; Albrecht et al. 2007). In addition, climate-induced changes in factors such as dissolved oxygen, salinity, as well as host and parasite distributions have also been linked to changes in infection prevalence and intensity across the globe (Byers 2021). Increases in parasite abundance and intensity with changing climate and increased human impact may be especially influential for hosts that are ecosystem engineers because infections that compromise their hosts can readily cascade to affect the entire community.

Eastern oysters (*Crassostrea virginica*) are key ecosystem engineers in temperate coastal systems. In the US, the combined effects of overharvesting, pollution, and disease have decreased oyster populations 65–85%, with populations considered functionally extinct in many areas (Beck et al. 2011; zu Ermgassen et al. 2012; Hernández et al. 2018). In addition to their extractive value for commercial fisheries, oysters provide a myriad of ecosystem services, including enhancement of water quality, removal of excess nitrogen, shoreline stabilization, and provision of essential fish habitat (Meyer et al. 1997; Lenihan et al. 2001; Grabowski et al. 2012). Therefore, oyster reef losses have reduced habitat for valuable fishes and invertebrates, increased erosion rates, and decreased water quality (Lenihan and Peterson 1998; Peterson et al. 2003; Beck et al. 2011; Grabowski et al. 2012). To mitigate the negative ecological effects of oyster declines and meet increasing demand for food resources for human populations, both habitat restoration to enhance wild fisheries and aquaculture have grown to help restore ecosystem goods and services. However, oyster diseases could compromise the success of these efforts.

Climate change has increased water temperatures and cases of oyster parasites, including the lethal Dermo caused by the protozoan parasite *Perkinsus marinus* and MSX caused by *Haplosporidium nelsoni*, which have previously caused mass mortalities of *C. virginica* (Ford and Haskin 1987; Pace et al. 2020). However, the impacts of Dermo and MSX are generally moderate, with annual oyster mortality around 30–50%, primarily affecting older oysters that had been exposed to the parasites for several years (Haskin and Ford 1982; Soniat et al. 2012). Increasing impacts of these diseases may be due to the expansion of the parasites' range and population size as temperatures warm, particularly because of rapid proliferation at temperatures > 20 °C (Cook et al. 1998; Guo and Ford 2016; Carnegie et al. 2021). Additionally, the intensity of these diseases appears to also be increasing due to changing climatic conditions (Carnegie et al. 2021).

Both these diseases have been tightly linked with increased temperature and salinity (Soniat et al. 2009; Batchelor et al. 2023) and a few studies suggest some important roles for additional factors operating at different scales, including urbanization (Gray et al. 2009), reef context (e.g., water flow, reef height, and position of an oyster of a reef) (Lenihan et al. 1999), hypoxia (Breitburg et al. 2015), tidal inundation (Malek and Byers 2017; Hanley et al. 2019), and host density (Hanley et al. 2019; Supp. Table 1). However, few studies have examined these factors in concert, let alone how these factors drive patterns in parasite prevalence and intensity across a large regional scale. Therefore, in this study, we sought to quantify the spatial patterns in the prevalence and intensity of two protozoan parasites across 24 reefs systematically spread along 150 km of coast. Then, we examined a variety of local- and landscape-level variables to reveal which were most influential in predicting the prevalence and intensity of these two parasites across a regional scale. We hypothesized that across our sampling range, temperature and salinity would exceed a critical threshold for rapid parasite proliferation, resulting in high *P. marinus* and *H. nelsoni* prevalence and intensity across the region, and that other variables may become more important in explaining variation across this spatial scale. We also predicted that parasite prevalence and intensity would increase in low oxygen (hypoxic) conditions. We expected positive associations of host size and host density with prevalence and intensity of both *P. marinus* and *H. nelsoni*, and negative associations of resident fauna density and habitat complexity with prevalence and intensity of both parasites. Lastly, we predicted that landscape-level variables, such as increased distance from roads or armored shoreline (i.e., farther from urbanization), increased distance from the nearest ocean inlet (i.e., lower recruitment potential), and more open water relative to marsh habitat (i.e., increased flow) would result in lower parasite prevalence and intensity (Supp. Table 1).

Materials and methods

Site selection

We selected 8 geographically distinct areas systematically spread across the 150 km coastline of Georgia, USA (Fig. 1). Six of these areas were in locations that Georgia Department of Natural Resources (DNR) are interested in opening for aquaculture (and therefore, there are additional water quality monitoring data near these sites). Within each of the eight areas, we identified three replicate intertidal reefs (for a total $n = 24$) based on a set of selection criteria to ensure shared broad characteristics among the sampling sites. Namely, each reef was (1) situated directly adjacent to salt marsh (< 1 m from the reef's landward edge); (2) had an intertidal area of at least 3×3 m; (3) had a density of at least 30 adult oysters m^{-2}; (4) had a reef slope between 15 and 30%; and (5) was located at least 1 km from the nearest replicate reef. To assess the local-scale predictors of parasite prevalence and intensity across a large regional scale, we sampled biological variables (oysters, resident fauna, and parasites), emergent reef properties (rugosity), and environmental conditions (temperature, salinity, and dissolved oxygen; methods described below) at each replicate reef.

Field sampling

In June 2022, during low tide, we haphazardly placed a single 0.25 m^2 quadrat along the upper edge of our designated reefs, 1 m from edge of the adjacent marsh cordgrass. Within the quadrat, we quickly excavated all oysters down to the surface of the mud placing contents into a tub to retain any resident fauna. Many oysters form clusters of two or more individuals (dead or alive) that are attached. If more than half of an individual oyster or oyster cluster was within the quadrat, then it was included in the sample. Adjacent to each quadrat, we measured habitat complexity (i.e., reef rugosity) via the chain method (Aronson and Precht 1995). Specifically, a 4-m chain was conformed to the reef topography in a straight line, and a rugosity index, Rq, was calculated as $Rq = 1 - (d/l)$, where d is the horizontal distance covered by the conformed chain and l is the length of the chain when

Fig. 1 Oyster reefs sampled across the 150 km coastline of Georgia, USA ($N = 24$). Color indicates our eight geographically distinct areas
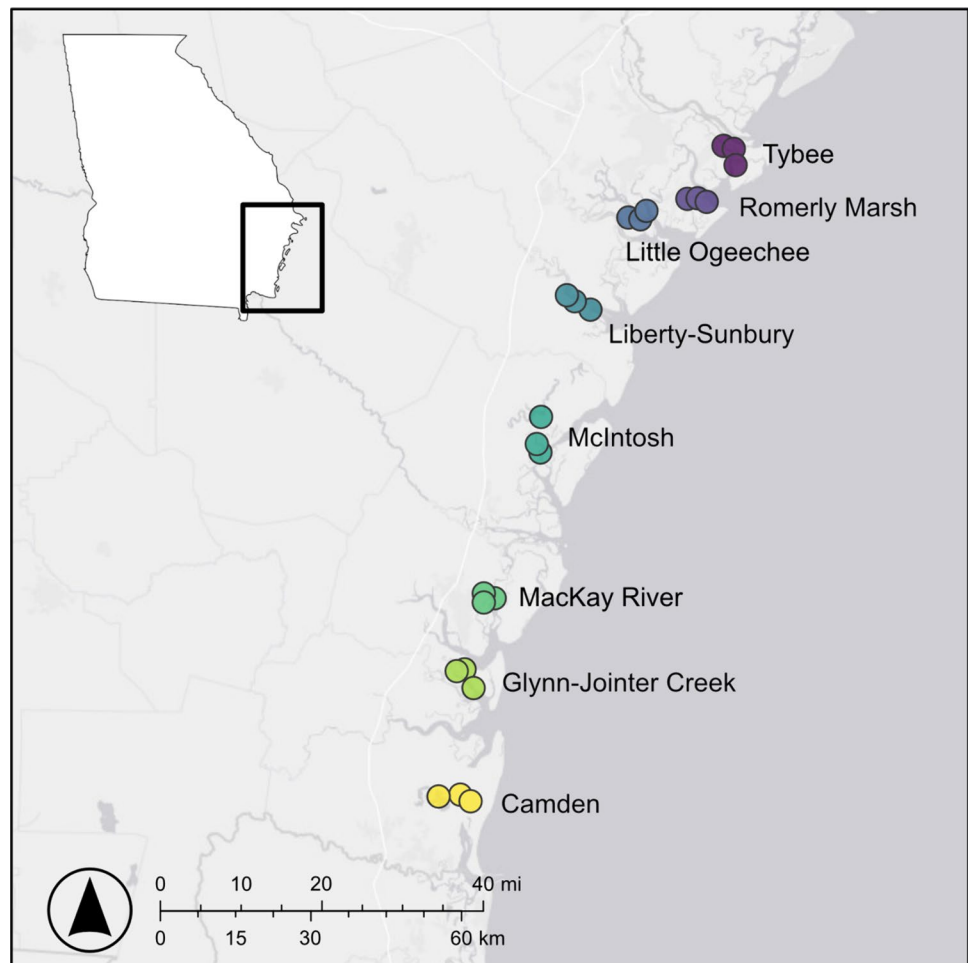
fully extended. At each reef, we recorded latitude and longitude and with a YSI meter we took point measurements of water temperature (ºC), salinity (ppt), and dissolved oxygen (DO; mg l^{-1}) 0.2 m below the surface.

Biological variables

Upon returning to shore, we rinsed single oysters and oyster clusters of mud and weighed them with a spring scale. We counted all living oysters, including spat, and measured shell height (umbo to farthest point on the shell in mm) for 100 haphazardly selected oysters. We identified all resident species down to the lowest taxonomic-level possible with particular focus on mud crabs (*Eurypanopeus depressus* and *Panopeus herbstii*) and counted and measured up to 20 individuals of each species. We also retained a subsample of juvenile and adult oysters from each reef for parasite quantification in the lab.

Physical variables

In addition to point source measures collected during sampling events, water quality data (temperature, salinity, and dissolved oxygen) were obtained from the Georgia DNR Coastal Resources Division Shellfish and Water quality team's long-term monthly sampling (2003–2022) for all reefs in the oyster growing areas ($n = 18$). The sampling of these data by Georgia DNR is not standardized by tidal cycle or time of day. For sites not located within a growing area ($n = 6$), we utilized the data from the nearest Georgia DNR water quality sampling location, which was always within 15 km. We extracted the data for five years prior to field sampling (July 2017–June 2022) and we calculated the seasonal and annual means and variance for all physical variables.

Landscape variables

To assess the landscape-level predictors of parasites for each reef, we extracted landscape variables in ArcGIS Pro 3.0.1 (ESRI 2022) with data layers downloaded from the Georgia Coastal and Marine Planner (GCAMP: https://geospatial.gatech.edu/GCAMP/) and Georgia Wetlands Restoration Access Portal (G-WRAP: https://geospatial.gatech.edu/G-WRAP/). First, we applied a 500-m radius buffer around each reef (Annis et al. 2022) and calculated the ratio of marsh habitat to open water within each buffer as a proxy for landscape context. Second, we calculated the shortest linear distance by water to the nearest oceanic inlet from each reef as a metric for recruitment potential. Finally, we calculated the distances of the reef to the nearest road, and armored shoreline to assess variation in the level of urbanization proximate to each sampled oyster reef.

Microparasites

To quantify the prevalence and intensity of *P. marinus* and *H. nelsoni* parasite loads, approximately 35 oysters (ranging from 30 to 120 mm shell height) from each reef were dissected for DNA extractions and quantitative PCR (qPCR) analysis. Each oyster was sized (shell height and length, mm) and a 20–40 mg of a combination of gill and mantle tissue was excised. DNA was extracted from tissue samples using a commercial kit (Omega Biotek E.Z.N.A. Tissue Kit, Norcross, GA, USA). All DNA samples were stored at −20 °C until tested by qPCR. Using a modified a procedure from Piesz et al. (2022) samples were analyzed using a multiplex qPCR assay modified to assess both *P. marinus* (de Faveri et al. 2009) and *H. nelsoni* (Wilbur et al. 2012) in a 1:4 Dermo:MSX ratio on Bio-Rad CFX384™ Real-Time System and Bio-Rad CFX Manager software (version 5.2). Each 10 µl reaction contained 1 µl template DNA, 2.5 µl RNAse-free water, 5 µl of the TaqMan® Multiplex Master mix, and 1.5 µl of a 1:4 (10 µm) Dermo:MSX primer–probe master mix (Piesz et al. 2022). We used gBlocks® (gene fragments containing the target region from *P. marinus* or *H. nelsoni*; Integrated DNA Technologies) to develop a standard curve to assess infection levels. All standards, samples, and controls were run in duplicate; if samples differed by > 1 Cq, they were re-run to confirm infection intensity. In this study, we considered the parasite present within the host in any sample in which parasite DNA was detected. Infection intensity in this study is defined as abundance of the parasite DNA within the host, not as a measure of severity of disease.

Data analysis

To broadly examine the spatial patterns in parasite prevalence, we calculated the prevalence of oysters infected with *P. marinus*, *H. nelsoni*, at least one of the two parasites, and both parasites (i.e., co-infection) on each of the 24 reefs systematically spread along the coast. We then only examined infected oysters from the dataset to calculate the mean parasite intensity separately for both *P. marinus* and *H. nelsoni* on each oyster reef (sensu Rózsa et al. 2000). To calculate *P. marinus* and *H. nelsoni* intensity in DNA copies per gram of tissue extracted from qPCR output (Cqs), we determined the relationship between Cq and DNA copies µl^{-1} from our standard curve with known values using a regression. We then converted all Cq values to DNA copies µl^{-1} and multiplied each value by the amount of tissue used for each extraction. To first determine if *P. marinus* and *H. nelsoni* randomly associate across our geographic range, we examined co-infection data using a Chi Square Test of Independence. For this test, we used the observed and expected number of individuals co-infected by both parasites.

Prior to analyses focused on examining the associated local and landscape variables for each parasite, we tested for collinearity among local- (physical and biological) and landscape-level variables. We examined cross-correlations using a Pearson correlation matrix. If correlation coefficients were greater than 0.7, we selected the most ecologically relevant independent variable for inclusion in subsequent statistical models. We then scaled each variable by its mean and standard deviation using the scale() function in R ([X − mean]/ SD).

To assess the relative importance of local reef-level (biological and physical) and landscape-level environmental variables on the prevalence of *P. marinus* or *H. nelsoni,* we ran a series of binomial mixed models with a logit link. To assess the relationship between the relative importance of local reef-level (biological and physical) and landscape-level environmental variables and *P. marinus* intensity or *H. nelsoni* intensity, we ran a series of generalized linear mixed effects models with a Gaussian distribution on natural log-transformed intensity values [ln(DNA copies g tissue^{-1})].

To reduce overparameterization, we independently ran models just with fixed factors for local variables (the mean and variance of temperature, salinity, and dissolved oxygen, host size, host density, resident faunal density, and habitat complexity), and then just with landscape variables (landscape/reef context, distance to nearest inlet, and distance to nearest road). From the best fit model of local variables and the best fit model of landscape variables, we extracted the fixed factors and included them in a full model with both local and landscape variables combined. For all models, we used reef as a random factor. All mixed models were run with the lme4 package in R (Bates et al. 2015). For each response variable, we identified all possible models and examined the Akaike information criterion corrected for small sample sizes (AICc). We then calculated the difference between AICc for a given model and the model with the minimum AICc (ΔAICc). For each response variable, we considered the top model (i.e., lowest AICc), as well as models with ΔAICc that were less than 2 for interpretation. All data were tested for normality with a Shapiro–Wilks test and heteroscedasticity with a Breusch–Pagan test and all statistical analyses were performed in R version 4.3.0 (R Development Core Team 2023).

Results

In total, we examined 818 oysters of which 747 had at least one microparasite species detected (either *P. marinus*, *H. nelsoni*, or both) for a reef-level mean prevalence of 91.02%. Reef-level prevalence was tightly coupled around this global average (SD = 8.89%), with the prevalence of detections of at least one parasite in oysters ranging between 69.0 and 100% (Fig. 2A). Of the 818 oysters sampled, *P. marinus* was detected in 65.6% (SD = 16.6%; Fig. 2B) and *H. nelsoni* was detected in 77.1% (SD = 15.7%; Fig. 2C). There were only three reefs with < 50% prevalence of *P. marinus* and only two reefs with < 50% prevalence for *H. nelsoni*. The lowest prevalence of each parasite did not occur on the same reefs, hence the lowest reef-level prevalence for having at least one parasite detected was 69%. The intensity of *P. marinus* and *H. nelsoni* was highly variable among individual oysters on a reef, resulting in high overall variance. The mean reef-level intensity of *P. marinus* across all reefs was 1.5×10^4 DNA copies g tissue^{-1} (SD = 4.4×10^3) and mean intensity of *H. nelsoni* was 3.1×10^{12} DNA copies g tissue^{-1} (SD = 1.7×10^{12}; Fig. 3). Co-infection data indicated no non-random association of *P. marinus* and *H. nelsoni* (i.e., independence among the parasites) ($X^2 = 56$, $df = 49$, $p = 0.22$; Fig. 4).

Collinearity and reduction of parameters

There was a strong positive correlation between latitude and the annual variance in monthly water temperature ($r = 0.89$), with increasing variance in temperature toward the northern end of our regional scale. More annual variation in temperature could affect parasite proliferation, and because water temperature is an important known predictor of oyster parasites (Burreson and Ragone Calvo 1996; Bushek et al. 2012), we removed latitude as a predictor variable in statistical models. We also found a high correlation between distance to the nearest road and distance to the nearest armored shoreline ($r = 0.81$), which are both proxies for urbanization, and therefore removed distance to the nearest armored shoreline from models.

Across all local-level models, the means and variance (annual or seasonal) in temperature and salinity from monthly DNR data performed poorly compared to point source temperature and salinity variables so were dropped from full models. Additionally, dissolved oxygen (point source, means or variance) was never included in the top-performing model for any response variable, and therefore was not considered in the full models including both local- and landscape-scale variables.

Full model results

P. marinus prevalence

Four competing models were found to explain *P. marinus* prevalence (Table 1). The conditional R^2 (R^2_c) across the model set with a random effect of reef ranged from 0.174 to 0.181 (marginal R^2 [R^2_m] = 0.096 − 0.119). The best performing model for *P. marinus* prevalence (i.e., lowest AIC$_c$) included local reef-level variables of oyster height
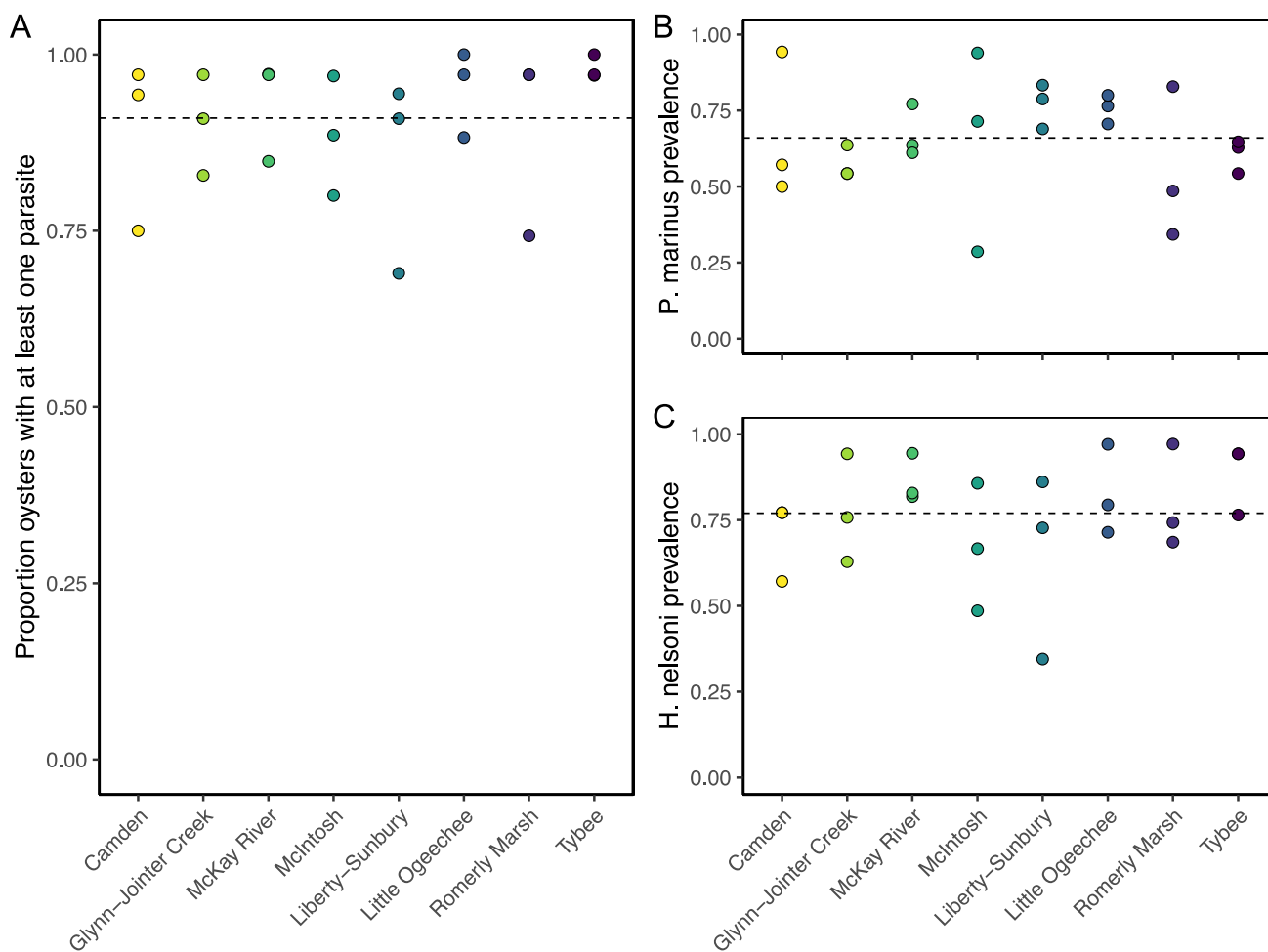
Fig. 2 The proportion of oysters with at least one parasite detected (**A**), with P. marinus detected (**B**) and *H. nelsoni* detected (**C**) at each site sampled along the GA coast (*N* = 818). Dashed lines indicated the global mean across the entire sampling area. Sites listed from south to north and color indicates broad geographic area

($\beta = 0.90$), point source temperature ($\beta = 0.42$), resident mud crab density ($\beta = 0.49$) as positive correlates of *P. marinus* presence and landscape-level marsh to open water ratio ($\beta = -0.94$) as a negative correlate of *P. marinus* presence ($R^2_c = 0.18$, $R^2_c = 0.12$; Supp. Figure S1).

P. marinus intensity

Two competing models were found to weakly explain *P. marinus* intensity across sites (Table 1). The best fit model included marsh to water ratio ($\beta = -0.17$ and point source salinity ($\beta = -0.08$) as negative predictors of *P. marinus* intensity and point source temperature ($\beta = 0.23$) as a positive predictor of *P. marinus* intensity (with a random effect of reef; $R^2_c = 0\ 0.128$; $R^2_m = 0\ 0.094$; Supp. Figure S2).

H. nelsoni prevalence

Three competing models were found to explain *H. nelsoni* prevalence (Table 1). The best fit model included positive predictors of oyster height ($\beta = 0.91$) and marsh to open water ratio ($\beta = 0.98$) and negative predictors of point source temperature ($\beta = -1.07$) and point source salinity ($\beta = -0.70$) with a random effect of reef ($R^2_c = 0.218$; $R^2_m = 0.137$; Supp. Figure S3). Mud crab density was also included in one of the top-performing models as a positive predictor ($\beta = 0.26$) of *H. nelsoni* prevalence.

H. nelsoni intensity

Two competing models were found to explain approximately 41% of the variation in *H. nelsoni* intensity (Table 1). The
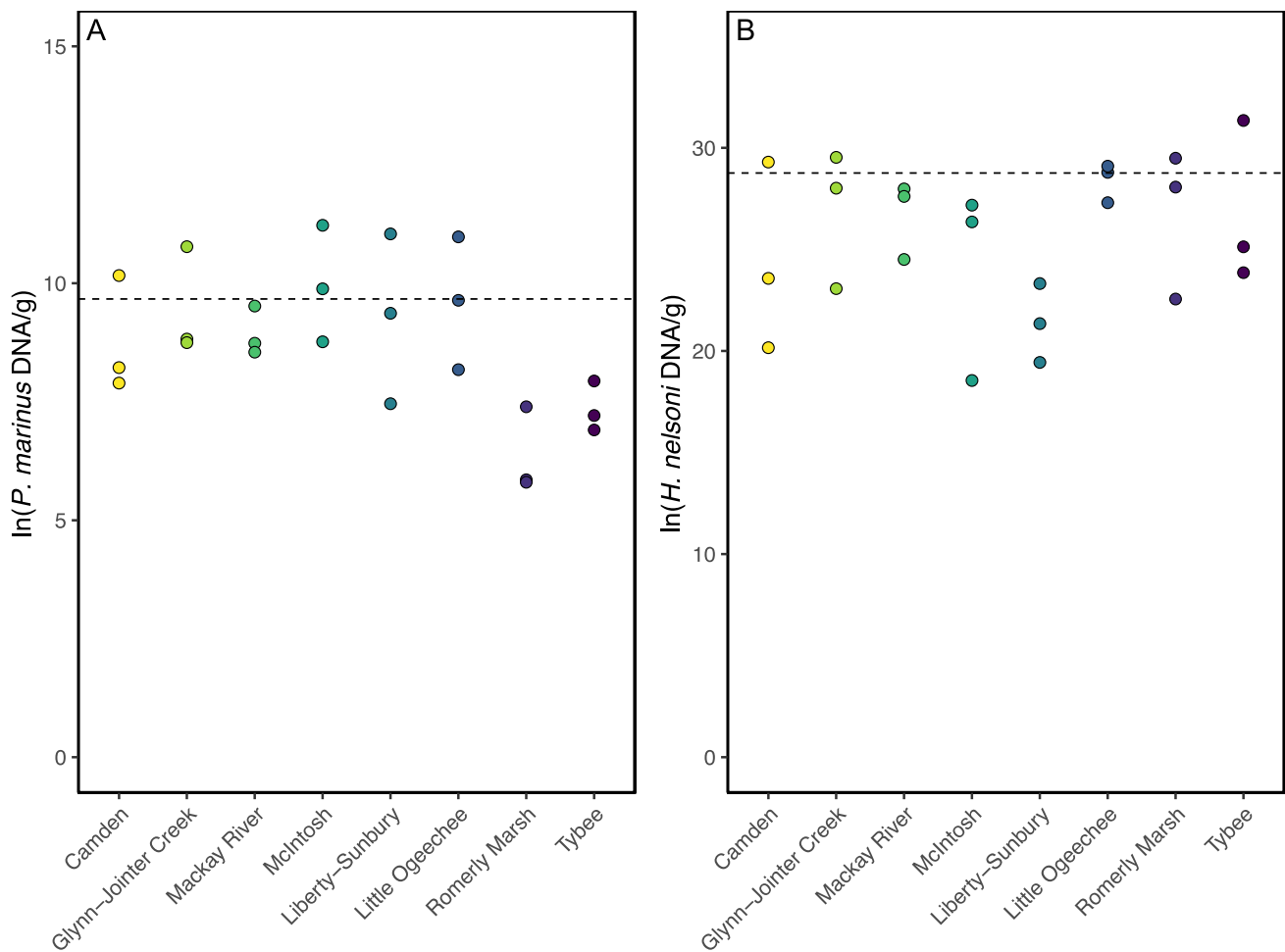
Fig. 3 The average parasite intensity (log scaled) for **A** *P. marinus* and **B** *H. nelsoni* at each reef sampled along the GA coast (*N* = 818). Dashed lines indicated the global mean across the entire sampling area. Sites listed from south to north and color indicates broad geographic area

best fit model included oyster height ($\beta = 0.59$) as a positive predictor and mud crab density ($\beta = -0.12$) and point source salinity ($\beta = -0.16$) as negative predictors of *H. nelsoni* intensity (with a random effect of reef; $R^2_c = 0.41$; $R^2_m = 0$ 0.34; Supp. Figure S4).

Discussion

Microparasite prevalence and intensity was consistently high across multiple sites over a 150 km spatial scale. The observed pattern in microparasite prevalence and intensity was striking because at large spatial scales parasites are usually highly variable due to increased heterogeneity in environmental factors (e.g., Kuris 1990; Sousa 1990; Kuris and Lafferty 1994; Galaktionov 1996; Thieltges and Reise 2007; Smith 2007; Byers et al. 2008; Falke and Preston 2022). For example, an obligate plant pathogen *Podosphaera plantaginis*, examined across 3244 populations in the Åland Islands, Finland, had high spatial variation in occurrence (~ 3–30%) driven by host population size and the proximity of both roads and coastline (Laine and Hanski 2006). In oysters themselves, in Florida across two distinct bays approximately 75 km apart, *P. marinus* prevalence ranged from 0 to 100% across multiple reefs during peak summer temperatures (Hanley et al. 2019). At times, it is possible that even at large scales, environmental conditions, resources, or biotic interactions vary less than expected because they are correlated over a large regional scale by temperature and/or differential dispersal patterns of vectors and predators (e.g., Brown et al. 1995; Holdenrieder et al. 2004; Farnsworth et al. 2006; Byers et al. 2016; Rodríguez et al. 2022). However, this explanation does not seem to apply to our study because although temperature and salinity had low variation, many of the other independent variables included in our models (e.g., oyster density, marsh to open water ratio) exhibited plenty of variation.

Fig. 4 Mean proportion of *P. marinus* detections, *H. nelsoni* detections, and co-infected oysters (*N* = 818). Error bars represent standard deviation calculated across all oysters and reefs. Solid black line represents the estimated proportion of co-infection by *P. marinus* and *H. nelsoni* if the parasites are independent or randomly associated
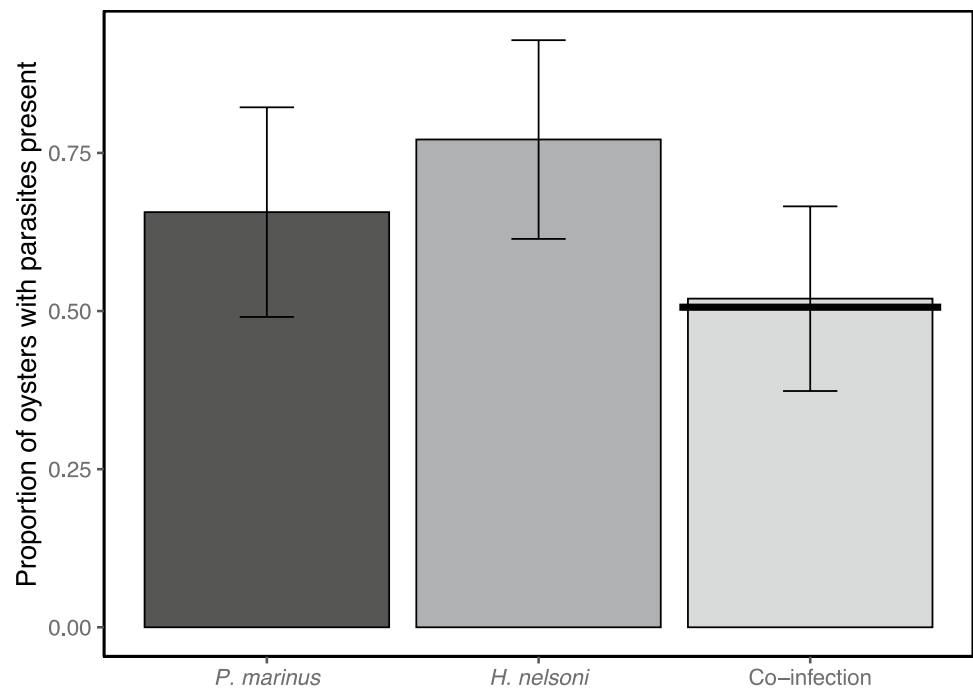
One reason parasite metrics may have been universally high despite reasonable variation in independent variables is due to certain key independent variables being above critical threshold levels needed to foster parasite transmission and growth (Artim et al. 2020). For example, previous studies have found that *P. marinus* and *H. nelsoni* rapidly proliferate above 20 °C (Guo and Ford 2016) and ~15 ppt salinity (Carnegie and Burreson 2012). All of our sites exceeded both those temperature and salinity thresholds for approximately 3 months prior to our sampling events; thus, the range of temperatures we measured across our sites (27–32 °C) may all be sufficiently high to maximally boost parasite prevalence and intensity throughout our sampling domain. Additionally, hosts experiencing high levels of physiological stress have been shown to correspond to higher levels of parasite infection (Esch et al. 1975; Martínez-Mota et al 2017). We sampled at the high end of the oyster distribution in the intertidal zone where physical factors are more extreme and stressful for oyster hosts, potentially resulting in high parasite prevalence across our regional scale (Lenihan et al. 1999; Malek and Breitburg 2016).

Importantly, one implication of the parasite metrics being saturated at high levels with low variance (SD < 17% for all parasite response variables) is that there is less parasite variability to be explained with a predictive model. However, although there was little spatial variation in prevalence of parasites across sites, host size was consistently a positive predictor of parasite metrics. This pattern commonly found with parasites often results when larger individuals are older and, therefore, have been exposed longer to contract infections (e.g., Poulin and George-Nascimento 2007; Byers

et al. 2008; Hechinger 2013). Interestingly, previous studies suggest that *H. nelsoni* is more likely to infect juvenile oysters (Ford et al. 2018) compared to *P. marinus,* which could account for the strong positive relationship we found between *H. nelsoni* intensity and oyster size, as these individuals may have had more time for the parasite to accrue in larger oysters. Interestingly, P. *marinus* intensity did not correlate with host size suggesting that even though larger oysters are more likely to be infected with *P. marinus* they may be more tolerant to more intense infections.

Previous in situ work on parasites in coastal systems has found that local physical and chemical variables can help to explain patterns of prevalence (Altman and Byers 2014). In addition to host size, we also found that local physical factors, specifically temperature and salinity, tended to be important indicators of parasite prevalence and intensity in oysters across our reefs. Both *H. nelsoni* and *P. marinus* prevalence and intensity are known to correlate with salinity and temperature (Barber et al. 1997; Bushek et al. 2012; Malek and Byers 2018). As expected, we found a positive relationship between temperature and both *P. marinus* intensity and prevalence. In contrast, our results suggest a negative relationship between temperature and salinity on *H. nelsoni* prevalence and intensity across our sites contrary to previous studies (e.g., Haskin and Ford 1982). A recent study found that sites with intermediate salinity as well as with the highest variance in salinity tended to have the highest prevalence of *H. nelsoni* (Batchelor et al. 2023). Since our salinity and temperature measurements had low variation (all high values) and were taken at only a single point in time, we may not have sufficiently captured the temporal

Table 1 Models explaining the influence of environmental variables on four parasite response variables from oysters sampled across 24 reefs along the coast of Georgia. Explanatory variables from the full models include local variables of oyster height (mm), mud crab density (no. 0.25 m^{-2}), reef rugosity, total oyster density (no./0.25 m^{-2}), point source temperature (°C), and point source salinity, and landscape variables of the proportion of marsh to open water ratio within a 500 m radius buffer surrounding each site, distance to the nearest inlet (km), and distance to the nearest road (km)

Response variable	Model rank	Local						Landscape			df	Log likelihood	AICc	ΔAICc	R^2m	R^2c
		Oyster height	Mud crab density	Reef rugosity	Total oyster density	Temperature	Salinity	Marsh:Water	Nearest inlet	Nearest road						
P. marinus prevalence	1	0.90	0.49			0.42		−0.94			6	−484.75	981.6	0.00	0.119	0.181
	2	0.90	0.43					−0.90			5	−485.87	981.8	0.22	0.110	0.181
	3	0.92						−0.89			4	−486.92	981.9	0.29	0.096	0.175
	4	0.92				0.35		−0.92			5	−486.21	982.5	0.89	0.101	0.174
P. marinus intensity	1					0.233	−0.08	−0.17			6	−1416.25	2844.7	0	0.094	0.128
	2					0.236		−0.16			5	−1417.29	2844.7	0.05	0.087	0.128
H. nelsoni prevalence	1	0.91				−1.07	−0.70	0.98			6	−395.93	804	0	0.137	0.218
	2	0.91				−1.08		1.08			5	−397.55	805.2	1.22	0.121	0.221
	3	0.90	0.26			−1.04	−0.68	0.99			7	−395.67	805.5	1.52	0.141	0.218
H. nelsoni intensity	1	0.59	−0.12				−0.16				6	−2074.41	4161	0	0.337	0.413
	2	0.59					−0.16				5	−2075.99	4162.1	1.14	0.333	0.421

The best fitting models (ΔAICc value <2) are shown for each response variable. The standardized beta coefficients associated with each independent variable are shown for each model. For each model, degrees of freedom (*df*), log likelihood, AICc, ΔAICc, marginal R^2 (R^2_m), and conditional R^2 (R^2_c) are shown

variation in these water quality parameters to fully disentangle this relationship, potentially resulting in their low predictive power within our statistical models. However, because temperature is both spatially and temporally autocorrelated (Di Cecco and Gouhier 2018), sites with warmer point source measurements may also have higher winter and spring temperature important for parasite proliferation. Further, we did examine the seasonal means and variance from monthly water quality data; however, these variables did not emerge in any of the best fit models perhaps due to being poorly representative, as a result of a lack of standardization for tidal cycle or time of day when they were collected. Overall, the effects of salinity and temperature that we measured were relatively weak. This is most likely because those factors had low variability across our sites during summer and because of the aforementioned low variability in parasites to be explained.

Interestingly, we found a few non-host-related variables that correlated with parasite prevalence and intensity at both local and landscape levels. Specifically, resident mud crab densities negatively correlated with *H. nelsoni* intensity and positively correlated with *P. marinus* and *H. nelsoni* prevalence. The positive relationship between resident crab species and parasite metrics may be a result of the crabs responding to influential landscape or other habitat features, or they may be exerting their own biological influence on the oyster parasites, for example by affecting the oysters' susceptibility to infection or differentially preying on uninfected oysters. Across multiple models, we also found the landscape-level variable of reef context (marsh to open water ratio) to correlate with parasite prevalence and intensity. Specifically, our results indicate that areas with greater amounts of marsh habitat surrounding the reef relative to open water had reduced *P. marinus* prevalence and intensity but increased *H. nelsoni* prevalence. These results suggest that landscape aspects may both facilitate and hinder parasites. Previous studies have found landscape context to be an important factor in oyster reef quality (Grabowski et al. 2005; Ziegler et al. 2018) and parasite dynamics on reefs (Lenihan et al. 1999) and across a variety of host parasite systems (De la Mora et al. 2015; Ancillotto et al. 2018). For instance, a recent study found that landscape variables such as forest edge density and percentage of conserved habitat were important predictors of gastrointestinal nematode parasites across 32 different taxa (Solórzano-García et al. 2023). However, other studies have found the opposite or no effect of landscape scale parameters on parasites (Martínez-Mota et al. 2017). Our results suggest that the importance of the landscape-level factors on host–parasite dynamics may be parasite specific even within the same host species (potentially due to differences in transmission). Distinguishing the causality and the mechanisms behind these associations will require further investigation.

Overall, our results indicate universally high prevalence of oyster parasites across a relatively large spatial scale, and patterns in parasite prevalence and intensity were driven by a combination of factors at both local and landscape levels. During summer months, it appears that Georgia's estuaries are consistently warm, and disease is high across all reefs indicating there is little refuge from disease in this area. Although there was high parasite prevalence and intensity which could cause mortality of older and, thus, larger in the oyster population, the reefs across our sampling locations appeared to be in good condition (high oyster density and complex reef rugosity). There are a few non-mutually exclusive possibilities as to why the high levels of parasites are not compromising the structural integrity of the biogenic reef habitat: (1) the oysters across this geographic range may be resistant or more resilient to mortality from these protozoan parasites and their associated diseases (Brown et al. 2005; Powell et al. 2011); (2) the parasites infecting oysters across this range may be less virulent or lethal phenotypes (Carnegie et al. 2021); (3) parasite intensities measured here in DNA copies per gram of tissue may not reflect lethal levels of disease, or (4) high recruitment and rapid growth of oysters across this range (Byers et al. 2015) overrides the effects of high disease-related mortality. It is also important to note that qPCR amplification of parasite DNA within a host does not directly correspond to disease progression and future research will benefit from pairing qPCR and histological assays to assess disease dynamics more fully.

Ultimately, relatively high oyster density and high reef structural complexity (measured via rugosity) across all the sampled reefs suggests that even if individual oysters are affected by these parasites, the integrity of the reef structure remains intact, which is important for all the species in the estuarine community that depend on the reefs for habitat. Even with intact structure, there may still be consequences of these parasites on other ecosystem engineering functions provisioned by oysters as previous work has shown parasites to correspond to reduced body condition (Hanley et al. 2019; Batchelor et al. 2023). In addition to physical structure, oysters improve water quality through their filter feeding behavior which may be altered by the presence and intensity of parasites. Parasites are known to alter feeding behavior of host species (McLaughlin et al. 2020) and may influence the ability of an engineer to maintain top-down control on lower trophic levels. Previous work has shown freshwater mussels infected with a trematode parasite have reduce feeding rates, altering filtration capacity having large consequences for water quality (Brian et al. 2022). With changing climatic conditions and expanding parasite ranges, it will be important to understand not only the local- and landscape-level variables associated with spatial patterns in parasite prevalence and intensity in ecosystem engineers, but also how parasites affect engineering and ecosystem functions.

Declarations

Conflict of interest The authors declare that they have no conflict of interest.

Ethical approval All applicable institutional and/or national guidelines for the care and use of animals were followed. Field collections were conducted under GA DNR research collection permit #1001527755.

Consent to participate Not applicable.

Consent for publication Not applicable.

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