








RESEARCH ARTICLE

Variation in the density and body size of a threatened foundation species across multiple spatial scales

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Population characteristics (e.g. density and body sizes) of foundation species can affect their own persistence and provisioning of ecosystem functions. Understanding the drivers of population characteristics of foundation species at multiple spatial scales is therefore critical for maximizing ecosystem functions of restored habitats. We analyzed variation in population characteristics (densities, 95th percentile, and median lengths of live oysters) of the Sydney rock oyster, *Saccostrea glomerata*, on remnant oyster reefs at regional scales (among three estuaries) along an approximately 250 km of coastline in New South Wales, Australia. We then analyzed how population characteristics were further related to spatial attributes at smaller spatial scales including within-patches (rugosity, distance to patch-edge, and elevation), whole-patches (size and shape), and among-patch (connectivity) within each estuary. The densities and body sizes of *S. glomerata* were related to spatial attributes occurring within-patch (e.g. elevation), whole-patch (e.g. shape), and landscape (i.e. connectivity) scales, but these relationships varied among estuaries. The greatest variation in oyster density and size occurred at regional scales, suggesting that processes acting at larger spatial scales (e.g. water quality and/or climate) set the context for smaller scale influences on oyster characteristics. Our results highlight the potential importance of incorporating site-specific, spatial attributes in the design of restored oyster reefs to maximize ecosystem services and functions provided by restoration efforts.

Key words: connectivity, foundation species, landscape ecology, oyster reefs, *Saccostrea glomerata*, seascape, spatial scales, structural complexity, Sydney rock oyster

Implications for Practice

- Understanding spatial variations for the population characteristics of target foundation species will maximize the ecosystem benefits provided by the restored habitats.
- The marine foundation species, the Sydney rock oyster (*Saccostrea glomerata*), varied in population characteristics (i.e. density and body size) within habitat-patches and with patch connectivity across landscapes but the largest variation occurred at regional scales (among estuaries).
- Reef restoration should avoid “one-size-fits-all” strategies and consider local ecological knowledge (e.g. size, shape, and connectivity) of the remnant foundation species or utilize pilot studies at the proposed restoration sites.

Introduction

Marine foundation species (sensu Dayton 1972) such as mangroves, seagrasses, seaweeds, and shellfish provide critical ecosystem functions and services, including habitat and food provision for fish and invertebrates, nutrient cycling, water quality improvement, and coastal protection (Ellison et al. 2005; Grabowski & Peterson 2007; Angelini et al. 2015; Bulleri et al. 2018;

Gribben et al. 2019; Lloyd et al. 2020). Despite their importance to ecosystems, foundation species have experienced staggering losses globally. For example, oyster reefs have been globally reduced by 85% (Beck et al. 2011), mangrove forests by 35% over 50 years (Polidoro et al. 2010), and seagrass meadows by up to 29% from 1880 to 1990 (Waycott et al. 2009). Because of the critical services they provide, they are a focus of global

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restoration efforts (Lindenmayer et al. 2008; Bayraktarov et al. 2016; Swan et al. 2016).

The population characteristics (e.g. density and body size distribution) of foundation species have strong consequences for their own persistence and the ecosystem functions and services they provide. For example, the density and size of marine foundation species can influence their own growth, recruitment, and survivorship (Gribben et al. 2020), the biodiversity they support (Stelling-Wood et al. 2020), hydrodynamics and wave attenuation (Salvador de Paiva

et al. 2018), and water filtration (Green et al. 2013). From a restoration perspective, population characteristics of a target species may therefore inform the persistence and magnitude of the ecological services in areas of interest, and thus may be a fundamental yet understudied component of many restoration strategies (Baggett et al. 2015; Ladd et al. 2018).

Population characteristics of foundation species can vary across multiple spatial scales (Godron & Forman 1981; Fahrig 2003). At small spatial scales, these characteristics can vary within habitat patches, although patterns are equivocal. For

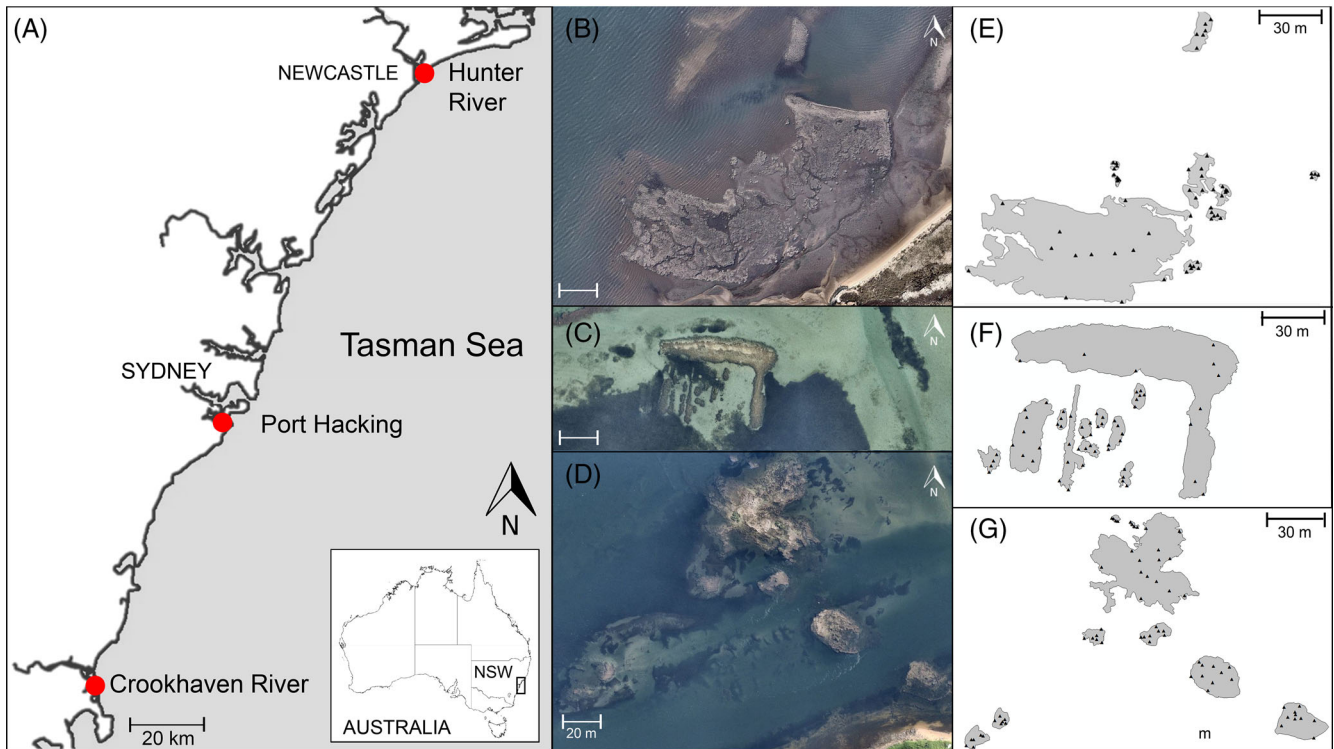


Figure 1. Locations of sampled *Saccostrea glomerata* oyster reefs (red dots) in estuaries in New South Wales (NSW), Australia (inset; A). Satellite imagery of the reefs (NearMap Ltd.) during low tide and the corresponding sample locations (see triangles) on reef contours of the selected reefs in Hunter River (B & E), Port Hacking (C & F), and Crookhaven River (D & G), respectively.

Table 1. Characteristics of estuaries where the sampled oyster reefs are located. Observed and/or calculated characteristics of each estuary were obtained from: ^aOzCoasts (2015), ^bNSW Office of Environment and Heritage (2016) for periods between 2007 and 2015, and ^cNearMap Ltd. unless specified.

Estuary Characteristics	Estuary		
	Hunter River	Port Hacking	Crookhaven River
Estuary-type classification ^a	Wave-dominated estuary	Tide-dominated estuary	Wave-dominated delta
Average annual summer temperature \pm SE ($^{\circ}$ C) ^b	24.7 \pm 0.3	25.7 \pm 0.3	24.1 \pm 0.3
Average annual turbidity \pm SE (NTU) ^b	19.1 \pm 7.2	2.4 \pm 0.6	2.3 \pm 0.2
Disturbance class ^c	High	Low	Medium
Number of reefs ^c	25	14	10
Base material of remnant reefs	Mud banks (McLeod et al. 2019)	Ballast heap (Albani & Cotis 2013)	Sand and rock boulders (R.C.L., 2018, personal observation)
Approximate distance to estuary mouth (km) ^c	6.5	4.3	2.2
Mean patch area (m ²) \pm SE ^c	237 \pm 155	112 \pm 78	355 \pm 200
Mean distance between reefs (m) \pm SE ^c	32.2 \pm 1.4	12.7 \pm 1.0	80.8 \pm 7.8

example, the population density and mean body size of foundation species can be smaller at patch edges in comparison to patch centers (Hanke et al. 2017), but the opposite pattern also occurs (Bell et al. 2001; Boström et al. 2011; Bertolini et al. 2020). Such variation may be explained by within-patch attributes (i.e. distance from patch-edge) interacting with whole-patch attributes such as patch size and shape (edge-to-area ratios), as larger patches are often associated with higher densities of foundation species and may be better at buffering abiotic and biotic stress than smaller patches (Angelini et al. 2011; Livernois et al. 2017; Crotty et al. 2018). Thus, understanding how multiple spatial scales interact to influence the population characteristics of foundation species, and potentially their function, is critical to inform the design of restored habitat patches and maximize ecosystem functions provided and restoration outcomes.

At larger scales, habitat patches can interact with each other across the landscape by altering ecological flows of resources and progeny (Brooks 2003; Ewers & Didham 2006; Zambrano et al. 2019) and ecological interactions (e.g. predation rates; Martin et al. 2018), all of which may influence the population characteristics of foundation species. Indeed, patch configuration and their connectivity can affect population characteristics in both terrestrial (e.g. Fahrig 2017; Thompson et al. 2017) and aquatic ecosystems (Angelini et al. 2011; Crotty et al. 2018). Moreover, the density and traits of foundation species can also be determined by background environmental variation (e.g. temperature) occurring at regional scales (e.g. grassland—le Roux & McGeoch 2010; macroalgal beds—Leonard 2000). Understanding the roles of landscape and regional scales on controlling population characteristics of foundation species will help identify the configuration of restored patches and site selection that maximizes their ecological functions and resilience, improving on existing restoration strategies (Angelini et al. 2011; Gilby et al. 2018).

In Australian estuaries, oysters once formed extensive reef complexes up to 10 ha in areas from the intertidal to depths of approximately 8 m (Ogburn et al. 2007). However, more than 90% of these complexes, including those of the iconic Sydney rock oyster, *Saccostrea glomerata* (Gould 1850), have been lost through overharvesting for food and lime, disease, and pollution (Ogburn et al. 2007; Gillies et al. 2018). *S. glomerata* reefs are now considered functionally extinct (Beck et al. 2011) and they are a key focus for restoration (Gillies et al. 2018). To date, global oyster restoration efforts consist mostly of substrate provision for recruitment (Westby et al. 2019). Oyster densities and size can affect their own recruitment (Knights & Walters 2010), growth (Honkoop & Bayne 2002), survival (Holliday et al. 1991; Honkoop & Bayne 2002), and filter-feeding capacity (Ozby 2006), as well as the biodiversity they host (Wilkie et al. 2012). However, few restoration projects have considered how spatial context may influence the persistence of the restored oyster populations and the ecological functions they provide (McAfee et al. 2020). This is due, in part, to a lack of understanding about how population characteristics vary with patch attributes (e.g. edge-vs.-center, size, shape, complexity) and configuration at multiple spatial scales.

In this study, we used the natural variation of patch-size, patch-shape, and connectivity in remnant oyster reefs in three estuaries in southeast Australia to determine how spatial variation from within patches to regional scales influence the population characteristics of *S. glomerata*. At each estuary,

Table 2. List of metrics used to quantify within-, whole-, and among-patch (patch-connectivity) attributes. Formulae of metrics can be found in Table S3.

Attributes	Description
Among-patch	
Nearest-neighbor distance	The shortest Euclidean and edge-to-edge distance between a focal reef and its nearest neighboring reef (McGarigal et al. 2012).
Mean nearest-neighbor distance	Average of the nearest Euclidean and edge-to-edge distances from a focal reef to all other reefs in the same landscape (McGarigal et al. 2012).
Proximity index	Index which measures the distance of a focal reef to other reefs in relation to area of the focal patch. Index for a patch is calculated by summing ratios of focal patch-area to nearest neighbor distances from focal patch to other patches (Gustafson & Parker 1992).
Isolation index	Index is a weighted sum of products between nearest neighbor distance from focal patch to other patches, and the ratios of focal patch area to the total patch area (Moilanen & Nieminen 2002).
Whole-patch	
Two-dimensional fractal dimension index	Standardized and scale-independent measure of perimeter of a patch relative to a square perimeter and patch-area (McGarigal et al. 2012).
Circularity index	Ratio between the patch-area and the smallest circumscribing circle of the patch (McGarigal et al. 2012).
Shape index	Ratio of actual patch-perimeter to hypothetical patch-perimeter as a square with the same area, characterizing total edges of patch (McGarigal et al. 2012).
Perimeter	Perimeter of each patch calculated from satellite image, reef contours.
Perimeter–area ratio	Ratio of patch-perimeter to patch-area for each patch.
Area	Area of each patch calculated from satellite image, reef contours.
Within-patch	
Distance to edge	Shortest distance of each sampled core to the nearest reef edge.
Surface elevation	Height of each sampled core above mean sea level.
Surface rugosity	Surface roughness on each sampled core and 20-cm radius surrounding each core derived from photogrammetry and digital elevation models sensu Figueira et al. (2015).

Table 3. Selected spatial attributes that relate to oyster density, 95th percentile length, and median length from “best” models obtained for Crookhaven River (CR), Hunter River (HR), and Port Hacking (PH) reefs. “+” and “-” represent positive and negative estimates, respectively, for selected attributes. White and black cells represent attributes that were not selected and not included (due to collinearity) in best models, respectively. Refer to Tables S8–S11 for detailed model outputs.

Spatial Scales and Patch Attributes		Population Characteristic and Estuaries								
		Abundance			95th Percentile Length			Median Length		
		CR	HR	PH	CR	HR	PH	CR	HR	PH
Within-patch	Surface elevation	-	-	+	-	-				
	Distance to edge									
Whole-patch	Surface rugosity		■			■			■	
	Area		-							
	Fractal dimension		-		-	■		+	-	
Among-patch	Circularity index		■		+	■		+	■	
	Isolation index	■			■			■	-	
	Proximity index	-	■			■		+	■	-

we sampled oyster densities, median, and 95th percentile body size on remnant oyster reefs at local (within- and whole-patch) and landscape (among-patch) scales and regional (among estuaries) scales. We tested the hypotheses that oyster densities and size would be correlated to (1) distance from the patch-edge within patches, (2) area and perimeter-to-area ratios as whole-patches, and (3) proximity of patches. Additionally, we hypothesized that (4) oyster sizes and densities would vary among estuaries due to differences in background environmental conditions operating at regional scales.

Methods

Sampled Estuaries Across the Regional Scale

Remnant *Saccostrea glomerata* reef complexes were sampled in three estuaries across approximately 250 km of the coastline in New South Wales (NSW) Australia; Hunter River (32°52'56.5788"S, 151°47'20.9508"E), Port Hacking (34°4'22.0404"S, 151°7'14.5956"E), and Crookhaven River (34°54'21.04"S, 150°44'48.62"E) (Fig. 1). Reef complexes in Hunter River, Port Hacking, and Crookhaven River were characterized by *S. glomerata* aggregation on mud banks, ballast heaps, and rocky boulders, respectively (Table 1). Each estuary contained different levels of anthropogenic disturbances, annual temperatures, and turbidity measurements (NSW Office of Environment and Heritage 2016; Table 1). Crookhaven River reefs possessed the largest mean patch area and spatial range of all estuaries, followed by Hunter River and Port Hacking (Table 1). Hunter River contained almost twice the number of reefs compared to Crookhaven River and Port Hacking (Table 1). In each estuary, 9–11 reefs ranging in area from 5 to 4,000 m² and consisting of different shapes (e.g. ovoid, elongate, irregular) were randomly selected for mapping and sampling (Table S1). Reef contours were mapped using satellite images from NearMap Ltd.

(<http://maps.au.nearmap.com/>). Small reefs (<5 m²) were not mapped or sampled to avoid damage to them.

Quantifying Oyster Characteristics

On each reef, we sampled oysters by taking 10 × 10 × 10-cm cores with a hammer and chisel during mean low tide (Bureau of Meteorology 2018). All cores were sampled in Austral spring (late October–early November 2018) outside of the recruitment period of *S. glomerata* (Diggles 2017) to focus on the oyster characteristics of postrecruitment individuals as these are likely providing the ecological functions on reefs. The number of cores sampled on each reef differed according to reef area (Table S2), with a minimum of four cores sampled on the smallest reefs (5–25 m²) and a maximum of 14 cores on the largest reefs (≥2,000 m²). Sampling locations were randomly selected within reef contours using function “spsample” from package “sp” (Pebesma & Bivand 2005) in R (v4.0.3, 2020; Fig. 1E–G) and were mapped with a real-time kinematic and differential global positioning system (RTK-DGPS; Leica GNSS 14, Leica Geosystems, Switzerland, vertical accuracy ±8 mm; horizontal ±13 mm).

Cores were fixed in 10% formalin mixed in seawater. Total volume of oysters in each core (hereafter biovolume) was estimated by displaced volume in water. The majority of live oysters were identified as *S. glomerata* (93.2% in Crookhaven River, 99.9% in Hunter River, and 92.1% in Port Hacking) following dissection methods in Wilkie et al. (2012), with the remaining identified as the invasive Pacific oyster (*Magallana gigas* Thunberg 1793, formerly *Crassostrea gigas*). Although competition between both species altered the density and body size of *S. glomerata* at low- and mid-intertidal heights on aquaculture farms (Krassoi et al. 2008), we assumed limited effects of competition, at the time of sampling, owing to small proportions (i.e. <8% at any sampled estuary) of *M. gigas* currently present on intact *S. glomerata* reefs.

We measured the shell length of all live oysters with Vernier calipers (±0.1 cm) along the anterior–posterior axis as this is

correlated to body size for live oysters (Gribben et al. 2020). Postmeasurement, we calculated the median (50th) and 95th length percentiles per core as proxies of “average” and “largest” oyster sizes in each core, respectively. We also counted all live oysters per core where individuals were categorized as either “juvenile” (defined as settled spat <1 cm in length and flesh attached) or “adults” (oysters ≥ 1 cm in length). Both adult and juvenile counts were highly correlated to each other (Pearson correlation coefficient, $r = +0.78$, $p < 0.001$); hence, they were combined as total densities per core for the statistical analyses.

Quantifying Within-Patch, Among-Patch, and Whole-Patch Attributes

We defined “patch attributes” as the spatial characteristics of reefs for all spatial measurements. We quantified within-patch attributes at each sampled core on each reef. These included surface elevations of the sampled cores, distance to the nearest patch-edge, and the surface complexity around the samples. Elevation relative to sea level at each coring point was measured with the RTK-DGPS unit as height above mean sea level. The distance of each core to the nearest reef edge was calculated in ArcGIS (v10.3; ESRI 2016) using the NEARDIST function with cores’ xy coordinates and reef-contour maps.

To quantify surface complexity of reefs on each core, oyster reefs were mapped during low tide via photogrammetry prior to coring (see Figueira et al. 2015 for methods). We used this method as it is more accurate (i.e. lower error and variance) than traditional methods, such as the chain method (Friedman et al. 2012). All reefs in Port Hacking and Crookhaven River were mapped but not all were mapped in Hunter River due to time constraints. Digital elevation models (DEMs) produced from mapped reefs were created in Agisoft Metashape PhotoScan (v1.1.6, 2015), trimmed to reef edges, and imported to ArcGIS (v10.3; ESRI 2016). Resulting three-dimensional models had an average mesh resolution (distance between vertices) of 8.2 mm and average model error of 4.7 mm, while DEMs had an average cell size of 2.5 mm. DEMs were imported into ArcGIS and sample points (based on xy coordinates) were buffered with a 20-cm radius circle. Surface rugosity independent of surface slope (hereafter “rugosity”) was calculated for each of these buffered areas (corresponding to the location of each sample core) with the arch-ratio rugosity index function (Du Preez 2015) in the Benthic Terrain Modeler plugin (v3.0; Walbridge et al. 2018) in ArcGIS (see Supplement S1 and Figs. S1–S2 for detailed method description). Five whole-patch attributes (Table 2) were calculated based on shape, area, and perimeter (McGarigal et al. 2012) using the function “calculate_lsm” in “landscape metrics” package in R (Hesselbarth et al. 2019).

We defined the “oyster reef landscape” as the mosaic of oyster reefs within an unstructured matrix (i.e. sandy and/or muddy bottom; Turner 1989). To quantify the connectivity within an oyster reef landscape, we used four metrics of habitat “isolation” (McGarigal et al. 2012; see Table 2) based on reef areas and inter-reef distances (Cushman & McGarigal 2002). The metrics were obtained in R using the reef-contour maps. The nearest neighbor distance was calculated using the function in “gdistance” package

(van Etten 2017). The proximity index was calculated using the function “ProxIndex” in package “spatialEco” (Evans 2015). The mean nearest neighbor distance and the isolation index were manually calculated (see Table S3 for formula for each metric).

Data Analysis

Oyster Characteristics Across the Regional Scale. Because patch attributes related to population characteristics differently within each estuary (Table 3; Figs. 3–5), we first tested for regional differences in oyster population characteristics (abundance, median length, and 95th percentile length) via the comparisons among estuaries. We tested relationships between

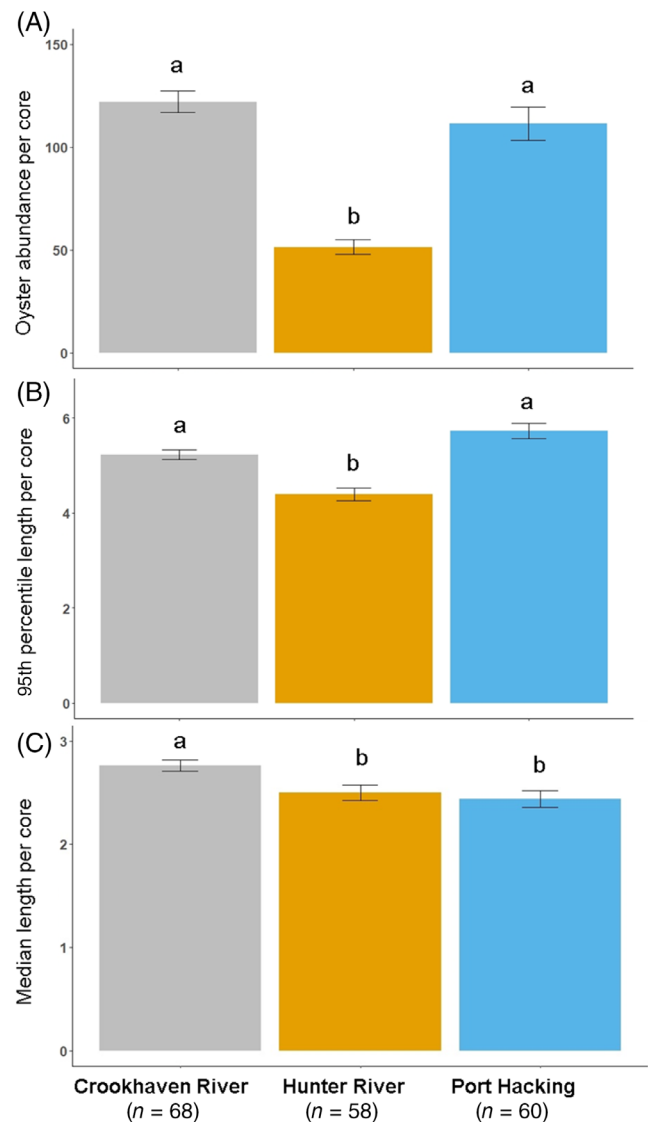


Figure 2. Mean (\pm SE) oyster abundance (A), 95th percentile length (B), and median length (C) of oysters sampled in Crookhaven River, Hunter River, and Port Hacking. Number of sampling cores per estuary is denoted as n . Different lowercase letters represent significantly different results ($p < 0.05$) from Tukey post hoc tests.

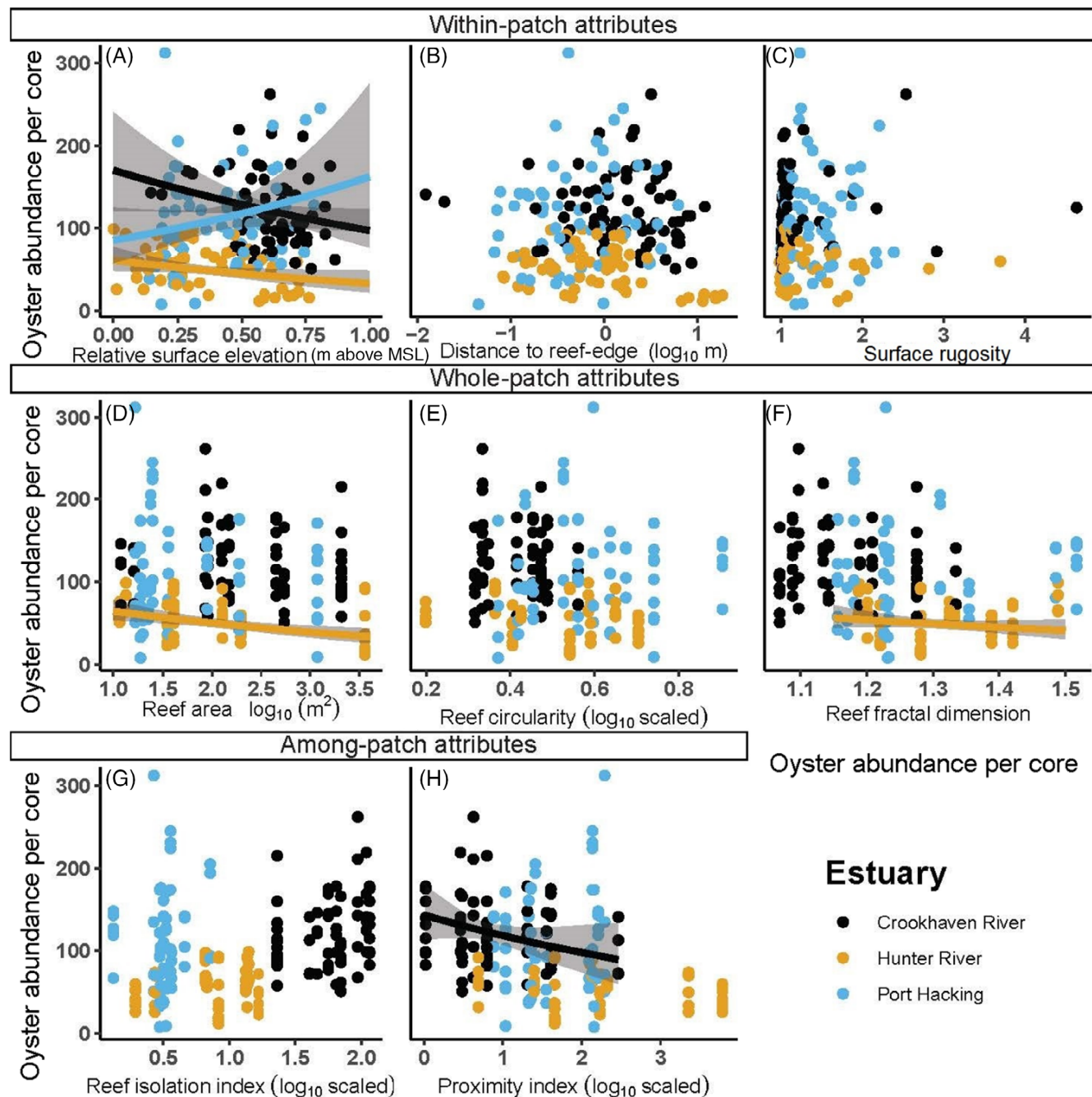


Figure 3. Relationships between oyster abundance and spatial attributes (A, elevation; B, distance to reef-edge; C, surface rugosity; D, area; E, circularity index; F, fractal dimension index; G, isolation index; H, proximity index) at sampled estuaries. Regression lines and 95% CI (shaded area) were plotted for selected spatial attributes from model selection (see “Data Analysis” section and Table 3). MSL, mean sea level.

population characteristics and patch attributes within each estuary separately (see next subsection).

We used a generalized linear mixed model (GLMM) assuming a negative binomial distribution for oyster density and linear mixed models (LMMs) for median and 95th percentile oyster lengths as response variables, with estuaries as a fixed factor. Biovolume per core (i.e. the volume of sampled structure including live oysters and dead oyster shell) was included as a

continuous covariate in each model to account for potential differences in shell matrix in each core. Reef (hereafter “reef_id”; i.e. unique reef complexes) was included as a random factor to account for potential nonindependence between samples cores from within the same patch. The GLMM was performed using “glmmTMB” package (Magnusson et al. 2020) and LMMs with the lme4 package (Bates et al. 2015). Statistical significance of estuary for each model was computed with likelihood ratio tests

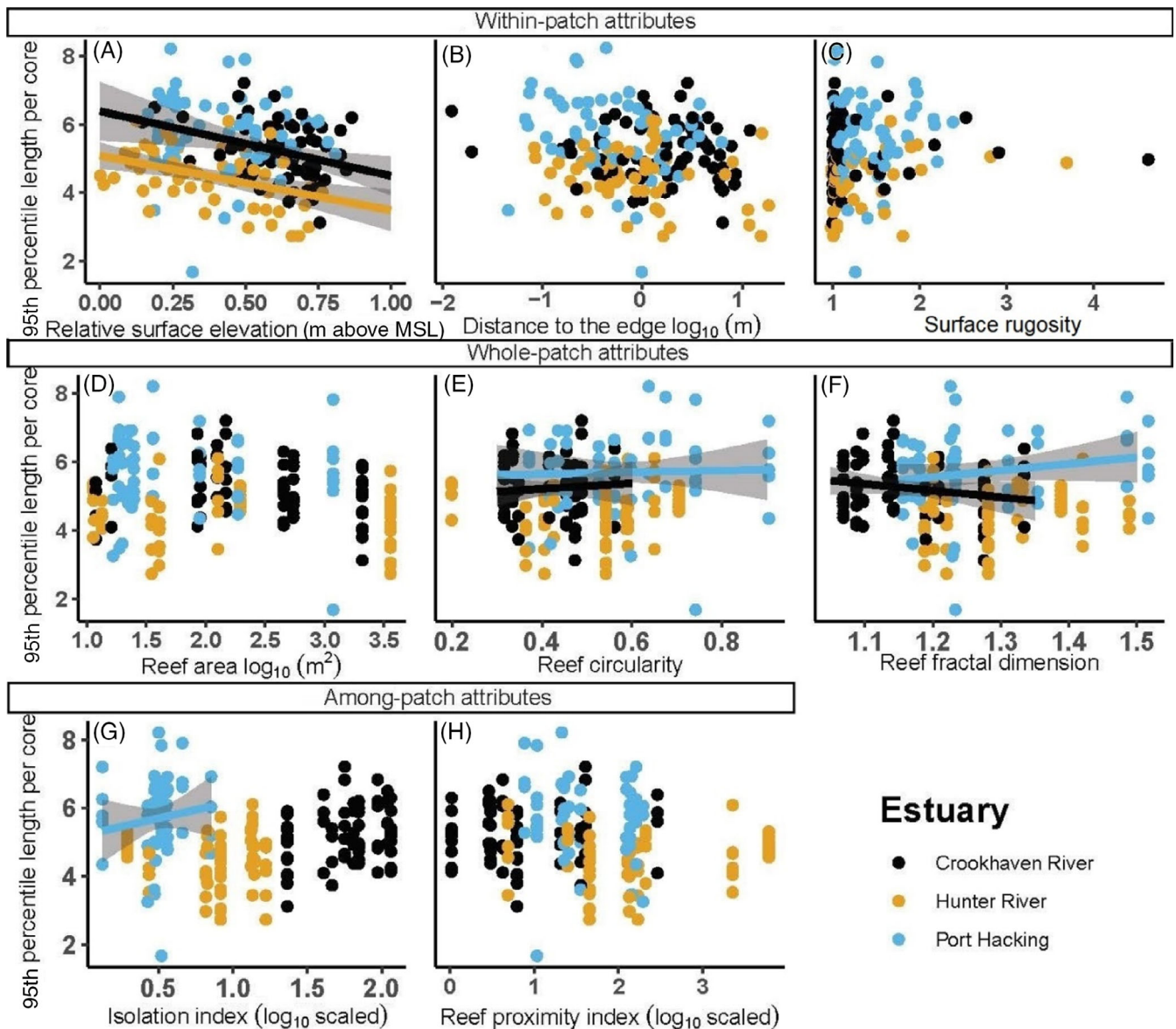


Figure 4. Relationships between largest oyster sizes and spatial attributes (A, elevation; B, distance to reef-edge; C, surface rugosity; D, area; E, circularity index; F, fractal dimension index; G, isolation index; H, proximity index) at sampled estuaries. Regression lines and 95% CI (shaded area) were plotted for selected spatial attributes from model selection (see “Data Analysis” section and Table 3). MSL, mean sea level.

(LRTs) using the “Anova” function in the “car” package (Fox et al. 2013). Post hoc tests with Tukey were performed using function “lsmeans” (Lenth 2016) in lieu of statistical significance of estuaries (see Table S6).

Oyster Characteristics Across Within-, Whole-, and Among-Patch Attributes. We tested relationships between each oyster characteristic (abundance, median length, and 95th percentile length) and patch attributes (within-, whole-, and among-patches) of the remnant reefs through model fitting and selection.

For each estuary, we first tested for collinearity of patch attributes prior to model fitting (Zuur et al. 2009); where two or more variables were correlated (Pearson’s correlation coefficient,

$r \geq \pm 0.7$), we left one of those variables in the model and excluded the remainder (see Supplement S2 for procedure to assess co-linearity between spatial attributes and Fig. S3 for correlation matrices between attributes per estuary). We then fitted each oyster characteristic as a response variable using GLMMs and LMMs where biovolume and “reef_id” were also included in each model as a continuous covariate and random factor, respectively. A total of nine models were fitted; one for each oyster characteristic (density, median length, and 95th percentile length) repeated in each of the three estuaries (see Table S7 for equation of each model fit). For each Hunter River model, rugosity was excluded as a covariate due to substantial absence of data points (refer to “Quantifying within-patch attributes” subsection) to prevent loss of precision of model estimates (Bartlett et al. 2014).

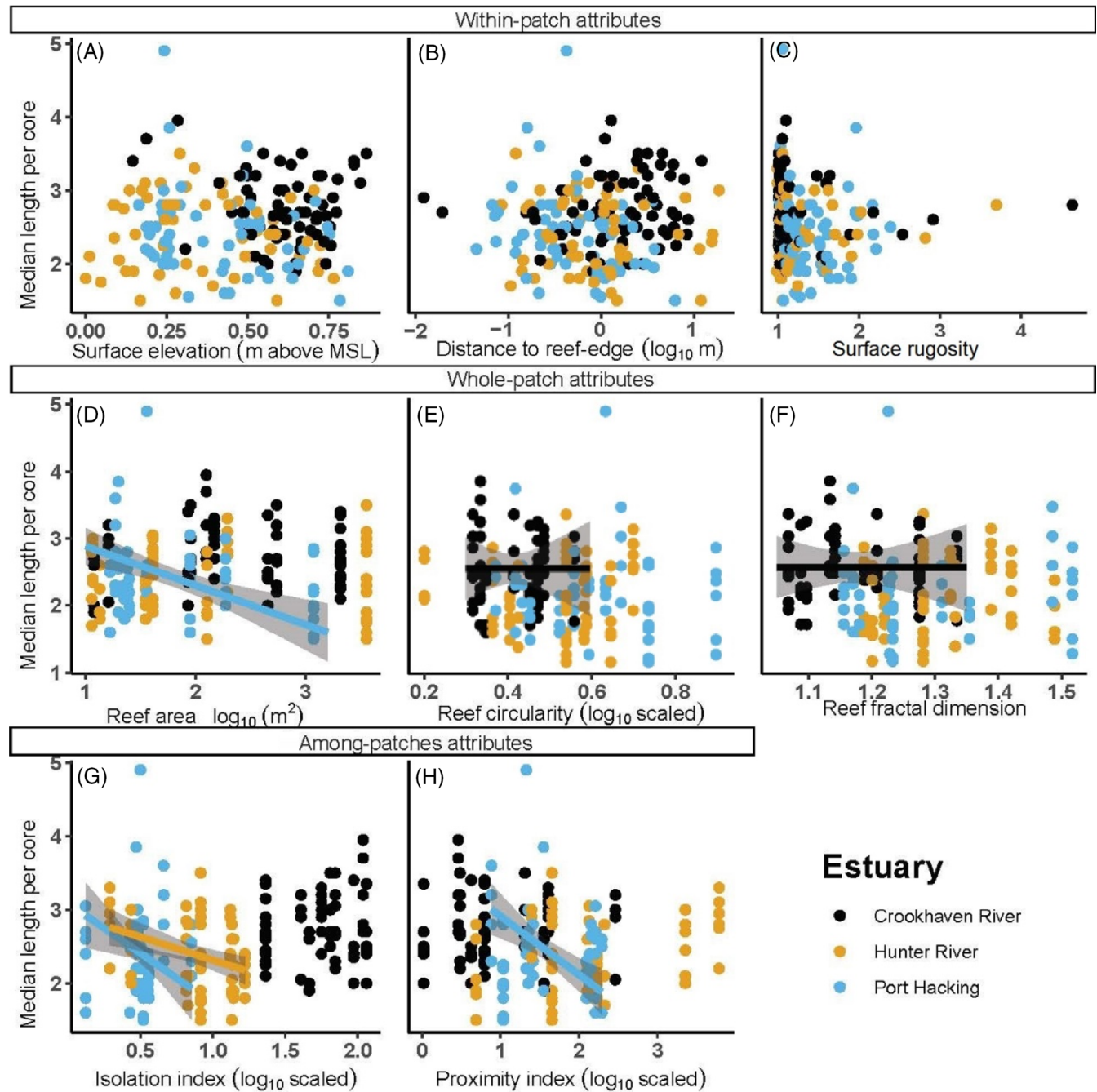


Figure 5. Relationships between median oyster lengths and spatial attributes (A, elevation; B, distance to reef-edge; C, surface rugosity; D, area; E, circularity index; F, fractal dimension index; G, isolation index; H, proximity index) at sampled estuaries. Regression lines and 95% CI (shaded area) were plotted for selected spatial attributes from model selection (see “Data Analysis” section and Table 3). MSL, mean sea level.

For each model, we conducted stepwise model regression with all possible combinations of patch attributes as predictors, using the “dredge” function in “MuMIn” package (Bartoń 2009). The most parsimonious/“best” model in each set was chosen based upon the model combination with the lowest small-sample corrected Akaike information criterion (Burnham & Anderson 2002). Selected models and their corresponding patch attributes were validated using histograms of the residuals and plots of the

residuals versus the fitted values (Zuur et al. 2009). See Tables S8–S11 for model selection outputs.

Results

Oyster Characteristics Across the Regional Scale

The abundance of oysters per core differed on a regional scale (LRT $\chi^2 = 41.7$, $df = 2$, $p < 0.001$; Table S4), with lower abun-

dances in Hunter River compared to Crookhaven River and Port Hacking (post hoc Tukey, Crookhaven River = Port Hacking > Hunter River; Fig. 2A, Table S5). Largest oysters (i.e. 95th quantile lengths per core) also differed across all estuaries (LRT $\chi^2 = 35.5$, $df = 2$, $p < 0.001$; Table S4), with shorter lengths in Hunter River compared to Crookhaven River and Port Hacking (post hoc Tukey, Crookhaven River = Port Hacking > Hunter River; Fig. 2B, Table S5).

Median oyster lengths also differed across estuaries (LRT $\chi^2 = 7.2$, $df = 2$, $p = 0.027$; Table S4); Crookhaven River had greater lengths than Port Hacking and Hunter River (post hoc Tukey, Crookhaven River > Port Hacking = Hunter River; Fig. 2C, Table S5).

Oyster Characteristics Across Within-, Whole-, and Among-Patch Attributes

Among all estuaries, oyster abundances were best explained by within-patch and whole-patch attributes, with different combinations found across estuaries (Table 3; Fig. 3). Surface elevation was the only attribute that was strongly related to oyster abundances at all estuaries (Table 3; Fig. 3A). However, the elevational trends were not the same across the estuaries; oyster abundance significantly decreased at higher reef elevations at Crookhaven River and Hunter River but increased at Port Hacking (Fig. 3A). Oyster abundance was highest for the least fractal and smaller reefs at Hunter River (Fig. 3B & 3C). Higher reef proximities were only associated with lower abundances in Crookhaven River.

The size of the “largest” oysters per core (as measured by the 95th percentile oyster lengths) was also best explained by within-patch and whole-patch attributes, with different combinations found across each estuary (Table 3; Fig. 4). Higher surface elevation of reefs was associated with smaller oysters in Crookhaven River and Hunter River (Fig. 4A). Circle and fractal dimensionality indices of reefs were associated with large oysters in Crookhaven River and Port Hacking; the former showing positive correlation with size of large oysters and the latter showing opposing relationships in both estuaries (Fig. 4E & 4F).

By contrast, median oyster lengths were associated with whole-patch and patch-connectivity attributes at two of three estuaries (Table 3; Fig. 5). None of the within-patch attributes included explained median oyster lengths. Like 95th percentile lengths, oyster median lengths were associated with decreased fractal dimensionality of reefs and increased reef circle index in Crookhaven River (Fig. 5E). At Port Hacking, median lengths were best explained by isolation index, proximity index, and reef area (Fig. 5D, 5G, & 5H) where they were negatively associated with isolation index.

Discussion

The population characteristics (e.g. densities and body size) of foundation species can mediate the functions they provide (e.g. habitat provisioning, water filtration). Thus, understanding the spatial processes that govern these may help inform the spatial design of restored oyster reefs and enhance the ecosystem

services and functions they provide. Here, we determined how the density and body size of the reef-forming Sydney rock oyster, *Saccostrea glomerata*, varied at multiple spatial scales. Our study revealed that the density and body size of *S. glomerata* were related to reef attributes at within-patch, whole-patch, and landscape scales. However, the greatest variation in both oyster density and size was observed at regional scales, suggesting that processes operating at this scale set the context for smaller scale habitat influences on oyster population characteristics.

Our results support previous studies showing that oyster characteristics can differ among estuaries (Powers et al. 2009; McAfee et al. 2016; Kimbro et al. 2020). The larger oyster sizes and densities observed in Crookhaven River and Port Hacking could be linked to better water quality and greater wave action at these sites, which can increase recruitment, food supply, and filtration rates, driving greater survival and growth (Dove & Sammut 2007; Diggles 2013; Theuerkauf et al. 2017; Vozzo et al. 2020). Hence, the potentially poorer water quality at the Hunter River, as evidenced by the greater turbidity that occurs in the river, might explain the lower densities and body sizes found at this estuary. Differences in temperature among estuaries—such as may occur with latitudinal gradients—do not explain patterns in density and shell length as there is little difference in temperature among estuaries and our warmest site is in the middle so oyster lengths are not related to any latitudinal gradient in temperature that may exist over the 250 km of coastline our estuaries span. Differences in biotic interactions could also explain patterns in body size and density among estuaries. Indeed, oyster predation in Australia is driven by fish (Anderson & Connell 1999). At the same time as this study, Erickson (2019) studied fish assemblages in Port Hacking and Crookhaven River. This study found greater fish predation at Port Hacking than Crookhaven River, which is one of the sites with high density and size of oysters. Moreover, at Hunter River, we would expect predation to be low due to high turbidity at this site as has been observed in other systems (Lunt & Smee 2014; Reustle & Smee 2020). Hence, it is unlikely that differences in rates of predation explain differences in oyster length and density among estuaries. Studies explicitly assessing how variation in water quality among estuaries influences oyster population characteristics at regional are needed to further explore these relationships.

Our models showed that factors acting at scales within estuaries also play an important role in determining oyster density and body size. Within-patch characteristics explained oyster abundances and length of the largest oysters at all estuaries, but the specific characteristics and trends varied between estuaries. For example, at Port Hacking, while densities increased with elevation, as reported in previous studies (Lenihan 1999; Schulte et al. 2009; Colden et al. 2017), the opposite trends were observed in Crookhaven River and Hunter River. Interestingly, these reefs were at higher elevation relative to sea level than Hunter River; hence, they might be at the upper limit of their optimal tidal elevation and likely affected by a reduced hydroperiod resulting in lower densities and smaller sizes at their highest points (Bartol et al. 1999; Bishop & Peterson 2006; Byers et al. 2015). Regardless, our

results support the current understanding that tidal elevation is an important environmental factor to consider when restoring oyster reefs (Wallis et al. 2016).

In terms of whole-patch attributes, our results showed that patch shape explained variation in oyster size in two out of three estuaries. Specifically, increases in circle index (i.e. narrower and elongated patches) were linked to larger oysters in Crookhaven River and Port Hacking. Meanwhile, fractal dimensionality (i.e. the geometric complexity the edge of the patch) was positively associated with large oyster sizes at Port Hacking, but negatively at Crookhaven River. These results, although variable across estuaries, suggest that patch-shape influences oyster sizes particularly at exposed sites. Reef shape at these sites might be interacting with the local hydrodynamics, with elongate and complex reef shapes providing better protection for oysters. These results indicate that oyster restoration initiatives at exposed sites might benefit from incorporating more elongate and complex shapes, while this might not be necessary for protected sites.

Patch size and edge of foundation species have well described effects on population characteristics (Godron & Forman 1981; Kennedy & Bruno 2000; Hanke et al. 2017). Moreover, surface rugosity can both influence and be influenced by the population characteristics of foundation species, as it can control larval settlement, recruitment, and postrecruitment growth by altering water flow, food supply, and predation (Scharf et al. 2006; Whitman & Reidenbach 2012; Colden et al. 2017). Somewhat surprisingly, this study found little or no relationships between population characteristics and these spatial attributes, highlighting that the spatial attributes affecting densities and size are highly variable between estuaries. Restoration projects should therefore be informed by knowledge of the ecological processes relevant to the areas targeted for restoration.

Patch-connectivity indices were related to oyster densities at Crookhaven River and oyster sizes at Port Hacking, while no effect on population characteristics was found at Hunter River. At Port Hacking, isolated patches had smaller median length of oysters, but tended to have the largest oysters. Meanwhile, at Crookhaven River, oyster abundance was greater in more isolated reefs. There is a range of factors that could be explaining these patterns. For example, these differences could be driven by the different predation pressures between isolated patches, as observed by previous studies (Harwell et al. 2011; Duncan et al. 2019). In fact, lower abundances of fish were observed in more isolated patches at Crookhaven River (Erickson 2019). Moreover, differences between patches in processes such as the timing of recruitment and growth rates can also influence oyster larval and thus reef connectivity (Theuerkauf et al. 2017). Future studies are needed to disentangle these possible explanations.

Restoration strategies for oyster reefs and, by extension, the functions they perform currently rely on build-it-and-they-will-come approaches, typically putting out substrate to encourage recruitment by increasing the availability of surfaces for settlement. These efforts usually consider the material used (e.g. oyster shells, rock, concrete; Westby et al. 2019), but they seldom consider the spatial arrangement of this material (McAfee et al. 2020; Reeves et al. 2020). Restoration programs that leverage the relationships between reef configuration and

oyster characteristics may significantly enhance their outcomes. Importantly, small-scale factors (size, shape, and connectivity) related to the reefs themselves had important implications for body size and density of oysters, so integrating these aspects into reef construction—which could be easily done—should maximize the ecosystem benefits provided. Moreover, although these reef attributes were common among estuaries, often their relationships with oyster density or body size were in opposite directions. In fact, our models suggest that the reef attributes to manipulate will be dependent on the region or environmental setting, as this was the scale at which most variation in oyster body size and density occurred. These results emphasize that a “one-size-fits-all” approach to oyster reef restoration may not be appropriate. Rather, restoration efforts need to be informed by local ecological knowledge of the remnant foundation species or pilot studies at the proposed restoration site. While this adds a level of complexity to restoration efforts, our study suggests that maximizing the benefits to oyster restoration needs to consider processes acting across multiple spatial scales.

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LITERATURE CITED

- Albani AD, Cotis G (2013) Port Hacking: past and present of an estuarine environment. Sutherland Shire Council, Sutherland, Australia
- Anderson MJ, Connell SD (1999) Predation by fish on intertidal oysters. *Marine Ecology Progress Series* 187:203–211. <https://doi.org/10.3354/meps187203>
- Angelini C, Altieri AH, Silliman BR, Bertness MD (2011) Interactions among foundation species and their consequences for community organization, biodiversity, and conservation. *Bioscience* 61:782–789. <https://doi.org/10.1525/bio.2011.61.10.8>
- Angelini C, van der Heide T, Griffin JN, Morton JP, Derksen-Hooijberg M, Lamers LPM, Smolders AJP, Silliman BR (2015) Foundation species' overlap enhances biodiversity and multifunctionality from the patch to landscape scale in southeastern United States salt marshes. *Proceedings*

- of the Royal Society B: Biological Sciences 282:20150421. <https://doi.org/10.1098/rspb.2015.0421>
- Baggett LP, Powers SP, Brumbaugh RD, Coen LD, DeAngelis BM, Greene JK, et al. (2015) Guidelines for evaluating performance of oyster habitat restoration. *Restoration Ecology* 23:737–745. <https://doi.org/10.1111/rec.12262>
- Bartlett JW, Carpenter JR, Tilling K, Vansteelandt S (2014) Improving upon the efficiency of complete case analysis when covariates are MNAR. *Biostatistics* 15:719–730. <https://doi.org/10.1093/biostatistics/kxu023>
- Bartol IK, Mann R, Luckenbach M (1999) Growth and mortality of oysters (*Crassostrea virginica*) on constructed intertidal reefs: effects of tidal height and substrate level. *Journal of Experimental Marine Biology and Ecology* 237:157–184. [https://doi.org/10.1016/S0022-0981\(98\)00175-0](https://doi.org/10.1016/S0022-0981(98)00175-0)
- Bartoň K (2009) Mu-MIn: Multi-model inference. R Package Version 0.12.2/r18. <http://R-Forge.R-project.org/projects/mumin/> (accessed 18 May 2021)
- Bates D, Mächler M, Bolker B, Walker S (2015) Fitting linear mixed-effects models using lme4. *Journal of Statistical Software* 67:1–48. <https://doi.org/10.18637/jss.v067.i01>
- Bayraktarov E, Saunders MI, Abdullah S, Mills M, Behr J, Possingham HP, Mumby PJ, Lovelock CE (2016) The cost and feasibility of marine coastal restoration. *Ecological Applications* 26:1055–1074. <https://doi.org/10.1890/15-1077>
- Beck MW, Brumbaugh RD, Airolidi L, Carranza A, Coen LD, Crawford C, et al. (2011) Oyster reefs at risk and recommendations for conservation, restoration, and management. *Bioscience* 61:107–116. <https://doi.org/10.1525/bio.2011.61.2.5>
- Bell SS, Brooks RA, Robbins BD, Fonseca MS, Hall MO (2001) Faunal response to fragmentation in seagrass habitats: implications for seagrass conservation. *Biological Conservation* 100:115–123. [https://doi.org/10.1016/S0006-3207\(00\)00212-3](https://doi.org/10.1016/S0006-3207(00)00212-3)
- Bertolini C, Capelle J, ter Veld JWD, van de Koppel J, Bouma TJ (2020) Understanding scales of density-dependence to improve the use of resources in benthic mussel aquaculture. *Aquaculture* 528:735477. <https://doi.org/10.1016/j.aquaculture.2020.735477>
- Bishop MJ, Peterson CH (2006) Direct effects of physical stress can be counteracted by indirect benefits: oyster growth on a tidal elevation gradient. *Oecologia* 147:426–433. <https://doi.org/10.1007/s00442-005-0273-3>
- Boström C, Pittman SJ, Simenstad C, Kneib RT (2011) Seascape ecology of coastal biogenic habitats: advances, gaps, and challenges. *Marine Ecology Progress Series* 427:191–217. <https://doi.org/10.3354/meps09051>
- Brooks CP (2003) A scalar analysis of landscape connectivity. *Oikos* 102:433–439. <https://doi.org/10.1034/j.1600-0579.2003.11511.x>
- Bulleri F, Eriksson BK, Queirós A, Airolidi L, Arenas F, Arvanitidis C, et al. (2018) Harnessing positive species interactions as a tool against climate-driven loss of coastal biodiversity. *PLoS Biology* 9:e2006852. <https://doi.org/10.1371/journal.pbio.2006852>
- Bureau of Meteorology (2018) New South Wales tide tables. Bureau of Meteorology, Melbourne, Australia
- Burnham K, Anderson D (2002) Model selection and multi-model inference. 2nd ed. Springer-Verlag, New York
- Byers JE, Grabowski JH, Piehler MF, Hughes AR, Weiskel HW, Malek JC, Kimbro DL (2015) Geographic variation in intertidal oyster reef properties and the influence of tidal prism. *Limnology and Oceanography* 60:1051–1063. <https://doi.org/10.1002/lno.10073>
- Colden AM, Latour RJ, Lipcius RN (2017) Reef height drives threshold dynamics of restored oyster reefs. *Marine Ecology Progress Series* 582:1–13. <https://doi.org/10.3354/meps12362>
- Crotty SM, Sharp SJ, Berszo AC, Prince KD, Cronk K, Johnson EE, Angelini C (2018) Foundation species patch configuration mediates salt marsh biodiversity, stability and multifunctionality. *Ecology Letters* 21:1681–1692. <https://doi.org/10.1111/ele.13146>
- Cushman SA, McGarigal K (2002) Hierarchical, multi-scale decomposition of species-environment relationships. *Landscape Ecology* 17:637–646. <https://doi.org/10.1023/A:1021571603605>
- Dayton PK (1972) Toward an understanding of community resilience and the potential effects of enrichments to the benthos. Pages 81–95. In: Parker BC (ed) Proceedings of the colloquium on conservation problems in Antarctica. Allen Press, Lawrence, Kansas
- Diggles BK (2013) Historical epidemiology indicates water quality decline drives loss of oyster (*Saccostrea glomerata*) reefs in Moreton Bay, Australia. *New Zealand Journal of Marine and Freshwater Research* 47:561–581. <https://doi.org/10.1080/00288330.2013.781511>
- Diggles BK (2017) Annual pattern of settlement of Sydney rock oyster (*Saccostrea glomerata*) spat in Pumicestone Passage, Moreton Bay. *Proceedings of the Royal Society of Queensland* 122:17–33
- Dove MC, Sammut J (2007) Impacts of estuarine acidification on survival and growth of Sydney rock oysters *Saccostrea glomerata* (Gould 1850). *Journal of Shellfish Research* 26:519–527. [https://doi.org/10.2983/0730-8000\(2007\)26\[519:IOEAO5\]2.0.CO;2](https://doi.org/10.2983/0730-8000(2007)26[519:IOEAO5]2.0.CO;2)
- Du Preez C (2015) A new arc–chord ratio (ACR) rugosity index for quantifying three-dimensional landscape structural complexity. *Landscape Ecology* 30:181–192. <https://doi.org/10.1007/s10980-014-0118-8>
- Duncan CK, Gilby BL, Olds AD, Connolly RM, Ortodossi NL, Henderson CJ, Schlacher TA (2019) Landscape context modifies the rate and distribution of predation around habitat restoration sites. *Biological Conservation* 237:97–104. <https://doi.org/10.1016/j.biocon.2019.06.028>
- Ellison AM, Bank MS, Clinton BD, Colburn EA, Elliott K, Ford CR, et al. (2005) Loss of foundation species: consequences for the structure and dynamics of forested ecosystems. *Frontiers in Ecology and the Environment* 3:479–486. [https://doi.org/10.1890/1540-9295\(2005\)003\[0479:LOFSCF\]2.0.CO;2](https://doi.org/10.1890/1540-9295(2005)003[0479:LOFSCF]2.0.CO;2)
- Erickson KR (2019) The effect of oyster reef size, shape, complexity, and landscape context on associated fish assemblages. Unpublished undergraduate honours thesis. University of Sydney, Sydney, Australia.
- ESRI (2016) ArcGIS desktop 10.3. Environmental Systems Resource Institute, Redlands, California
- van Etten J (2017) R package gdistance: distances and routes on geographical grids. *Journal of Statistical Software* 76:1–21. <https://doi.org/10.18637/jss.v076.i13>
- Evans JS (2015) Package “spatialEco.” Spatial Analysis and Modelling Utilities. R package 146
- Ewers RM, Didham RK (2006) Confounding factors in the detection of species responses to habitat fragmentation. *Biological Reviews of the Cambridge Philosophical Society* 81:117–142. <https://doi.org/10.1017/S1464793105006949>
- Fahrig L (2003) Effects of habitat fragmentation on biodiversity. *Annual Review of Ecology, Evolution, and Systematics* 34:487–515. <https://doi.org/10.1146/annurev.ecolsys.34.011802.132419>
- Fahrig L (2017) Ecological responses to habitat fragmentation per se. *Annual Review of Ecology, Evolution, and Systematics* 48:1–23. <https://doi.org/10.1146/annurev-ecolsys-110316-022612>
- Figueira W, Ferrari R, Weatherby E, Porter A, Hawes S, Byrne M (2015) Accuracy and precision of habitat structural complexity metrics derived from underwater photogrammetry. *Remote Sensing* 7:16883–16900. <https://doi.org/10.3390/rs71215859>
- Fox J, Friendly M, Weisberg S (2013) Hypothesis tests for multivariate linear models using the car package. *R Journal* 5:39–52. <https://doi.org/10.32614/RJ-2013-004>
- Friedman A, Pizarro O, Williams SB, Johnson-Roberson M (2012) Multi-scale measures of rugosity, slope and aspect from benthic stereo image reconstructions. *PLoS One* 7:e50440. <https://doi.org/10.1371/journal.pone.0050440>
- Gilby BL, Olds AD, Peterson CH, Connolly RM, Voss CM, Bishop MJ, Elliott M, Grabowski JH, Ortodossi NL, Schlacher TA (2018) Maximizing the benefits of oyster reef restoration for finfish and their fisheries. *Fish and Fisheries* 19:931–947. <https://doi.org/10.1111/faf.12301>
- Gillies CL, McLeod IM, Alleway HK, Cook P, Crawford C, Creighton C, et al. (2018) Australian shellfish ecosystems: past distribution, current status and future direction. *PLoS One* 13:e0190914. <https://doi.org/10.1371/journal.pone.0190914>
- Godron M, Forman RT (1981) Patches and structural components for a landscape ecology. *Bioscience* 31:733–740. <https://doi.org/10.2307/1308780>

- Grabowski JH, Peterson CH (2007) Restoring oyster reefs to recover ecosystem services. Pages 281–298. In: Cuddington K, Byers JE, Will Wilson AH (eds) *Ecosystem engineers: plants to protists*. Academic Press, San Diego, California
- Green DS, Rocha C, Crowe TP (2013) Effects of non-indigenous oysters on ecosystem processes vary with abundance and context. *Ecosystems* 16:881–893. <https://doi.org/10.1007/s10021-013-9659-y>
- Gribben PE, Angelini C, Altieri AH, Bishop MJ, Thomsen MS, Bulleri F (2019) Facilitation cascades in marine ecosystems: a synthesis and future directions. Pages 127–168. In: Hawkins SJ, Allcock AL, Bates AE, Firth LB, Smith IP, Swearer SE, Todd PA (eds) *Oceanography and marine biology: an annual review*. Vol 57. CRC Press, Taylor & Francis Group, Boca Raton, Florida
- Gribben PE, Bishop MJ, O'Connor WA, Bradley DJ, Hughes AR (2020) Intra-specific diversity in prey body size influences survivorship by conferring resistance to predation. *Ecosphere* 11:e03106. <https://doi.org/10.1002/ecs2.3106>
- Gustafson EJ, Parker GR (1992) Relationships between landcover proportion and indices of landscape spatial pattern. *Landscape Ecology* 7:101–110. <https://doi.org/10.1007/BF02418941>
- Hanke M, Posey M, Alphin T (2017) The influence of habitat characteristics on intertidal oyster *Crassostrea virginica* populations. *Marine Ecology Progress Series* 571:121–138. <https://doi.org/10.3354/meps12094>
- Harwell HD, Posey MH, Alphin TD (2011) Landscape aspects of oyster reefs: effects of fragmentation on habitat utilization. *Journal of Experimental Marine Biology and Ecology* 409:30–41. <https://doi.org/10.1016/j.jembe.2011.07.036>
- Hesselbarth MHK, Sciami M, With KA, Wiegand K, Nowosad J (2019) landscapemetrics: an open-source R tool to calculate landscape metrics. *Ecography* 42:1648–1657. <https://doi.org/10.1111/ecog.04617>
- Holliday JE, Maguire GB, Nell JA (1991) Optimum stocking density for nursery culture of Sydney rock oysters (*Saccostrea commercialis*). *Aquaculture* 96:7–16. [https://doi.org/10.1016/0044-8486\(91\)90135-T](https://doi.org/10.1016/0044-8486(91)90135-T)
- Honkoop PJC, Bayne BL (2002) Stocking density and growth of the Pacific oyster (*Crassostrea gigas*) and the Sydney rock oyster (*Saccostrea glomerata*) in Port Stephens, Australia. *Aquaculture* 213:171–186. [https://doi.org/10.1016/S0044-8486\(02\)00030-3](https://doi.org/10.1016/S0044-8486(02)00030-3)
- Kennedy CW, Bruno JF (2000) Patch-size dependent habitat modification and facilitation on New England cobble beaches by *Spartina alterniflora*. *Oecologia* 122:98–108. <https://doi.org/10.1007/PL00008841>
- Kimball DL, Scherer AE, Byers JE, Grabowski JH, Hughes AR, Piehler MF, Smee DL (2020) Environmental gradients influence biogeographic patterns of nonconsumptive predator effects on oysters. *Ecosphere* 11:e03260. <https://doi.org/10.1002/ecs2.3260>
- Knights AM, Walters K (2010) Recruit-recruit interactions, density-dependent processes and population persistence in the eastern oyster *Crassostrea virginica*. *Marine Ecology Progress Series* 404:79–90. <https://doi.org/10.3354/meps08480>
- Krassoi FR, Brown KR, Bishop MJ, Kelaher BP, Summerhayes S (2008) Condition-specific competition allows coexistence of competitively superior exotic oysters with native oysters. *Source. Journal of Animal Ecology* 77:5–15. <https://doi.org/10.1111/j.1365-2656.2007.01316.x>
- Ladd MC, Miller MW, Hunt JH, Sharp WC, Burkepile DE (2018) Harnessing ecological processes to facilitate coral restoration. *Frontiers in Ecology and the Environment* 16:239–247. <https://doi.org/10.1002/fee.1792>
- Lenihan HS (1999) Physical-biological coupling on oyster reefs: how habitat structure influences individual performance. *Ecological Monographs* 69:251–275. [https://doi.org/10.1890/0012-9615\(1999\)069\[0251:PBCOOR\]2.0.CO;2](https://doi.org/10.1890/0012-9615(1999)069[0251:PBCOOR]2.0.CO;2)
- Lenth RV (2016) Least-squares means: the R package lsmeans. *Journal of Statistical Software* 69:216–221. <https://doi.org/10.18637/jss.v069.i01>
- Leonard GH (2000) Latitudinal variation in species interactions: a test in the New England rocky intertidal zone. *Ecology* 81:1015–1030. [https://doi.org/10.1890/0012-9658\(2000\)081\[1015:LVSIA\]2.0.CO;2](https://doi.org/10.1890/0012-9658(2000)081[1015:LVSIA]2.0.CO;2)
- Lindenmayer D, Hobbs RJ, Montague-Drake R, Alexandra J, Bennett A, Burgman M, et al. (2008) A checklist for ecological management of landscapes for conservation. *Ecology Letters* 11:78–91. <https://doi.org/10.1111/j.1461-0248.2007.01114.x>
- Livorno MC, Grabowski JH, Poray AK, Gouhier TC, Hughes AR, O'Brien KF, Yeager LA, Fodrie FJ (2017) Effects of habitat fragmentation on *Zostera marina* seed distribution. *Aquatic Botany* 142:1–9. <https://doi.org/10.1016/j.aquabot.2017.05.006>
- Lloyd HB, Cruz-Motta JJ, Glasby TM, Hutchings PA, Gribben PE (2020) Unusual but consistent latitudinal patterns in macroalgal habitats and their invertebrate communities across two countries. *Diversity and Distributions* 26:912–927. <https://doi.org/10.1111/ddi.13070>
- Lunt J, Smee DL (2014) Turbidity influences trophic interactions in estuaries. *Limnology and Oceanography* 59:2002–2012. <https://doi.org/10.4319/lo.2014.59.6.2002>
- Magnusson A, Skaug H, Nielsen A, Berg C, Kristensen K, Maechler M, et al. (2020) lmmTMB: generalized linear mixed models using template model builder. Available from <https://cran.r-project.org/web/packages/glmmTMB/index.html> (accessed 9 June 2020)
- Martin TSH, Olds AD, Olalde ABH, Berkström C, Gilby BL, Schlacher TA, Butler IR, Yabsley NA, Zann M, Connolly RM (2018) Habitat proximity exerts opposing effects on key ecological functions. *Landscape Ecology* 33:1273–1286. <https://doi.org/10.1007/s10980-018-0680-6>
- McAfee D, Cole VJ, Bishop MJ (2016) Latitudinal gradients in ecosystem engineering by oysters vary across habitats. *Ecology* 97:929–939. <https://doi.org/10.1890/15-0651.1>
- McAfee D, McLeod IM, Boström-Einarsson L, Gillies CL (2020) The value and opportunity of restoring Australia's lost rock oyster reefs. *Restoration Ecology* 28:304–314. <https://doi.org/10.1111/rec.13125>
- McGarigal K, Cushman S, Ene E (2012) FRAGSTATS v4: spatial pattern analysis program for categorical and continuous maps
- McLeod IM, Boström-Einarsson L, Creighton C, D'Anastasi B, Diggles B, Dwyer PG, et al. (2019) Habitat value of Sydney rock oyster (*Saccostrea glomerata*) reefs on soft sediments. *Marine and Freshwater Research* 71:771–781. <https://doi.org/10.1071/MF18197>
- Moilanen A, Nieminen M (2002) Simple connectivity measures in spatial ecology. *Ecology* 83:1131–1145. [https://doi.org/10.1890/0012-9658\(2002\)083\[1131:SCMISE\]2.0.CO;2](https://doi.org/10.1890/0012-9658(2002)083[1131:SCMISE]2.0.CO;2)
- NSW Office of Environment and Heritage (2016) Assessing estuary ecosystem health: sampling, data analysis and reporting protocols. NSW Office of Environment and Heritage, Sydney, Australia
- Ogburn DM, White I, McPhee DP (2007) The disappearance of oyster reefs from eastern Australian estuaries—impact of colonial settlement or mudworm invasion? *Coastal Management* 35:271–287. <https://doi.org/10.1080/08920750601169618>
- Ozbay G (2006) An examination of comparative size class feeding in eastern oyster (*Crassostrea virginica*): implications for habitat restoration and conservation. *Journal of Environmental Monitoring and Restoration* 2:51–72. <https://doi.org/10.4029/2006jemrest2no16>
- OzCoasts (2015) Australian online coastal information. Geoscience Australia, Australia. <http://www.ozcoasts.gov.au/index.jspe> (accessed 07 April 2021)
- Pebesma EJ, Bivand RS (2005) Classes and methods for spatial data in R. *R News* 5:9–13
- Polidoro BA, Carpenter KE, Collins L, Duke NC, Ellison AM, Ellison JC, et al. (2010) The loss of species: mangrove extinction risk and geographic areas of global concern. *PLoS One* 5:e10095. <https://doi.org/10.1371/journal.pone.0010095>
- Powers SP, Peterson CH, Grabowski J, Lenihan HS (2009) Success of constructed oyster reefs in no-harvest sanctuaries: implications for restoration. *Marine Ecology Progress Series* 389:159–170. <https://doi.org/10.3354/meps08164>
- Reeves SE, Renzi JJ, Fobert EK, Silliman BR, Hancock B, Gillies CL (2020) Facilitating better outcomes: how positive species interactions can improve oyster reef restoration. *Frontiers in Marine Science* 7:656. <https://doi.org/10.3389/fmars.2020.00656>
- Reustle JW, Smee DL (2020) Turbidity and salinity influence trophic cascades on oyster reefs through modification of sensory performance and facilitation of

- different predator types. *Marine Ecology Progress Series* 639:127–136. <https://doi.org/10.3354/meps13283>
- le Roux PC, McGeoch MA (2010) Interaction intensity and importance along two stress gradients: adding shape to the stress-gradient hypothesis. *Oecologia* 162:733–745. <https://doi.org/10.1007/s00442-009-1484-9>
- Salvador de Paiva JN, Walles B, Ysebaert T, Bouma TJ (2018) Understanding the conditionality of ecosystem services: the effect of tidal flat morphology and oyster reef characteristics on sediment stabilization by oyster reefs. *Ecological Engineering* 112:89–95. <https://doi.org/10.1016/j.ecoleng.2017.12.020>
- Scharf FS, Manderson JP, Fabrizio MC (2006) The effects of seafloor habitat complexity on survival of juvenile fishes: species-specific interactions with structural refuge. *Journal of Experimental Marine Biology and Ecology* 335:167–176. <https://doi.org/10.1016/j.jembe.2006.03.018>
- Schulte DM, Burke RP, Lipcius RN (2009) Unprecedented restoration of a native oyster metapopulation. *Science* 325:1124–1128. <https://doi.org/10.1126/science.1176516>
- Stelling-Wood TP, Gribben PE, Poore AGB (2020) Habitat variability in an underwater forest: using a trait-based approach to predict associated communities. *Functional Ecology* 34:888–898. <https://doi.org/10.1111/1365-2435.13523>
- Swan KD, McPherson JM, Seddon PJ, Moehrenschrager A (2016) Managing marine biodiversity: the rising diversity and prevalence of marine conservation translocations. *Conservation Letters* 9:239–251. <https://doi.org/10.1111/conl.12217>
- Theuerkauf SJ, Eggleston DB, Theuerkauf KW, Puckett BJ (2017) Oyster density and demographic rates on natural intertidal reefs and hardened shoreline structures. *Journal of Shellfish Research* 36:87–100. <https://doi.org/10.2983/035.036.0111>
- Thompson PL, Rayfield B, Gonzalez A (2017) Loss of habitat and connectivity erodes species diversity, ecosystem functioning, and stability in metacommunity networks. *Ecography* 40:98–108. <https://doi.org/10.1111/ecog.02558>
- Turner MG (1989) Landscape ecology: the effect of pattern on process. *Annual Review of Ecology and Systematics* 20:171–197. <https://doi.org/10.1146/annurev.es.20.110189.001131>
- Vozzo ML, Cumbo VR, Crosswell JR, Bishop MJ (2020) Wave energy alters biodiversity by shaping intraspecific traits of a habitat-forming species. *Oikos* 130:1–14. <https://doi.org/10.1111/oik.07590>
- Walbridge S, Slocum N, Pobuda M, Wright DJ (2018) Unified geomorphological analysis workflows with benthic terrain modeler. *Geosciences* 8:94. <https://doi.org/10.3390/geosciences8030094>
- Walles B, Fodrie FJ, Nieuwhof S, Jewell OJD, Herman PMJ, Ysebaert T (2016) Guidelines for evaluating performance of oyster habitat restoration should include tidal emersion: reply to Baggett et al. *Restoration Ecology* 24: 4–7. <https://doi.org/10.1111/rec.12328>
- Waycott M, Duarte CM, Carruthers TJB, Orth RJ, Dennison WC, Olyarnik S, et al. (2009) Accelerating loss of seagrasses across the globe threatens coastal ecosystems. *Proceedings of the National Academy of Sciences* 106:12377–12381. <https://doi.org/10.1073/pnas.0905620106>
- Westby S, Geselbracht L, Pogoda B (2019) Restoration guidelines for shellfish reefs. Pages 36–48. In: Fitzsimons J, Branigan S, Brumbaugh RD, McDonald T, Zu Ermgassen PS (eds) *Restoration guidelines for shellfish reefs*. The Nature Conservancy, Arlington, Virginia
- Whitman E, Reidenbach M (2012) Benthic flow environments affect recruitment of *Crassostrea virginica* larvae to an intertidal oyster reef. *Marine Ecology Progress Series* 463:177–191. <https://doi.org/10.3354/meps09882>
- Wilkie EM, Bishop MJ, O'Connor WA (2012) Are native *Saccostrea glomerata* and invasive *Crassostrea gigas* oysters' habitat equivalents for epibenthic communities in south-eastern Australia? *Journal of Experimental Marine Biology and Ecology* 420–421:16–25. <https://doi.org/10.1016/j.jembe.2012.03.018>
- Zambrano J, Garzon-Lopez CX, Yeager L, Fortunel C, Cordeiro NJ, Beckman NG (2019) The effects of habitat loss and fragmentation on plant functional traits and functional diversity: what do we know so far? *Oecologia* 191:505–518. <https://doi.org/10.1007/s00442-019-04505-x>
- Zuur A, Ieno EN, Walker N, Saveliev AA, Smith GM (2009) *Mixed effects models and extensions in ecology with R*. Springer, New York

Supporting Information

The following information may be found in the online version of this article:

Figure S1. Photo depicting how burst-shot photos for photogrammetry were taken by a field assistant (Katie Erickson) for a sampled reef.

Figure S2. Top view of a three-dimensional mesh model of Crookhaven River Reef 4 captured from Agisoft Metashape PhotoScan photogrammetry software.

Figure S3. Multi-correlation plots of all patch-attributes tested in each estuary.

Table S1. List of estuary site, reefs, reef area, reef-shape, corresponding number of cores sampled, and range of edge-proximity within each reef.

Table S2. Reef area ranges and corresponding number of samples per reefs, number of reefs per area range within each estuary site, and the total number of samples per site.

Table S3. Formulae of patch-connectivity metrics.

Table S4. Output of GLMM and LMMs of oyster population characteristics as function of biovolume and estuaries as main effects.

Table S5. Pair-wise post hoc least square means tests with Tukey correction across estuaries with Bonferroni corrected *p*-values.

Table S6. Pair-wise correlation comparison between response variables to assess co-linearity among oyster population characteristics.

Table S7. List of noncollinear spatial attributes.

Table S8. Selected patch attributes from each “best” model selection for oyster density.

Table S9. Model outputs within $\Delta AICc < 2$ from stepwise regression of oyster density.

Table S10. Model outputs within $\Delta AICc < 2$ from stepwise regression of 95th percentile oyster lengths.

Table S11. Model outputs within $\Delta AICc < 2$ from stepwise regression of median oyster lengths.

Supplement S1. High-resolution mapping and photogrammetry procedure.

Supplement S2. Assessing co-linearity between spatial attributes in each estuary.

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