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ARTICLE

Recruitment of a threatened foundation oyster species varies with large and small spatial scales

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Abstract

Understanding how habitat attributes (e.g., patch area and sizes, connectivity) control recruitment and how this is modified by processes operating at larger spatial scales is fundamental to understanding population sustainability and developing successful long-term restoration strategies for marine foundation species—including for globally threatened reef-forming oysters. In two experiments, we assessed the recruitment and energy reserves of oyster recruits onto remnant reefs of the oyster *Saccostrea glomerata* in estuaries spanning 550 km of coastline in southeastern Australia. In the first experiment, we determined whether recruitment of oysters to settlement plates in three estuaries was correlated with reef attributes within patches (distances to patch edges and surface elevation), whole-patch attributes (shape and size of patches), and landscape attributes (connectivity). We also determined whether environmental factors (e.g., sedimentation and water temperature) explained the differences among recruitment plates. We also tested whether differences in energy reserves of recruits could explain the differences between two of the estuaries (one high- and one low-sedimentation estuary). In the second experiment, across six estuaries (three with nominally high and three with nominally low sedimentation rates), we tested the hypothesis that, at the estuary scale, recruitment and survival were negatively correlated to sedimentation. Overall, total oyster recruitment varied mostly at the scale of estuaries rather than with reef attributes and was negatively correlated with sedimentation. Percentage recruit survival was, however, similar among estuaries, although energy reserves and condition of recruits were lower at a high- compared to a low-sediment estuary. Within each estuary, total oyster recruitment increased with patch area and decreased with increasing tidal height. Our results showed that differences among estuaries have the largest influence on oyster recruitment and recruit health and this may be explained by environmental processes operating at the same scale. While survival was high across all estuaries, growth and reproduction of oysters on remnant reefs may be affected by sublethal effects on the health of recruits in high-sediment estuaries. Thus, restoration programs should consider lethal and sublethal effects of whole-estuary environmental processes when selecting sites and include environmental mitigation actions to maximize recruitment success.

KEYWORDS
connectivity, foundation species, landscape connectivity, landscape ecology, oyster health, oyster reefs, recruitment, regional scale, *Saccostrea glomerata*, spatial scales

INTRODUCTION

Foundation species (sensu Dayton, 1972) provide critical ecosystem services and functions (Ellison, 2019). Due to anthropogenic disturbances, many foundation species and the communities they support have experienced widespread reductions in abundance at local scales and range retractions at larger, biogeographic scales (Curtis et al., 2018; Dunic et al., 2021; Murray et al., 2022). In recent years, large-scale (i.e., tens to hundreds of kilometers) restoration initiatives have been prioritized to achieve the target goals of the United Nations' "2021–2030 Decade of Ecosystem Restoration" (e.g., Diefenderfer et al., 2021). Successful, sustainable restoration and the maintenance of established populations over large scales require a detailed understanding of how key demographic processes (e.g., recruitment, growth, and survivorship) vary across the scales at which populations of foundation species occur. Indeed, the lack of success of many restoration efforts has been attributed to limited information on variation in population processes of targeted foundation species at larger spatial scales (Bayraktarov et al., 2016; Bible & Sanford, 2016). Resolving this issue may provide insight into where restoration may or may not be more successful (Lindenmayer, 2020).

Recruitment is a fundamental demographic process influencing population maintenance and resilience, and it has important implications for long-term restoration success (Connell, 1985; Roughgarden et al., 1985; Strathmann et al., 2002). The recruitment of marine foundation species, such as corals, mussels, barnacles, and oysters, can be limited by a range of bottlenecks including larval supply (Raimondi, 1990; Underwood & Fairweather, 1989), availability of substrate (Arnold et al., 2010; Tamburri et al., 2008), larval behavior (Arnold et al., 2010; Tamburri et al., 2008), and settlement and postsettlement mortality events (Connell, 1985; Taylor & Bushek, 2008), all of which can operate differently at both local and biogeographic scales. Understanding the processes that explain the most variation in recruitment is critical to optimizing management strategies and restoration efforts for marine benthic foundation species.

At regional or biogeographical scales (i.e., 10–100 s of kilometers), recruitment can be determined by larval supply. For example, greater recruitment of California mussels, *Mytilus californianus*, on the southern California coast in comparison to its northern counterpart was likely driven by regionalized oceanic upwelling that affected larval transport and temperature (Smith et al., 2009). Recruitment patterns can also be modified by the attributes of multiple patches of habitat such as patch connectivity. More connected habitat patches may exhibit higher recruitment rates because of larger landscape areas for settlement (Strathmann et al., 2002). For example, recruitment of corals in the central Great Barrier Reef was significantly greater at distances $\leq$300 m from a coral reef compared to distances $>$300 m (Sammarco & Andrews, 1989). In addition, a larger patch area increases the probability of recruitment because of greater chemical settlement cues and settling area provided by adult conspecifics (Raimondi & Morse, 2000; Tamburri et al., 2008; Whitman & Reidenbach, 2012). For example, a small decrease in spatial area of coral (0.25 m^2) led to a 46% decrease in coral recruitment (Vermeij, 2005). Other habitat attributes such as patch shape can also promote recruitment. For example, irregularly shaped mussel-bed patches can have greater recruitment because convoluted edges increase the surface area for settlement (Commito et al., 2014; Svane & Ompi, 1993). Because the factors that influence recruitment are typically studied separately, we have little information on how they may interact to control recruitment and which factors may be the most important. Resolving this may provide critical information on where processes such as habitat fragmentation or reductions in habitat area have the most significant consequences for population maintenance.

The abundance, growth, and survivorship of recruits can also vary with habitat attributes occurring within patches such as substrate morphology (e.g., Gribben et al., 2011), rugosity (e.g., Soniat et al., 2004), water flow (e.g., Bushek, 1988), elevation (e.g., Esquivel-Muelbert et al., 2022), and relative positions within patches (e.g., centers vs. edges; Campbell et al., 2014). For example, total oyster recruitment and recruit survivorship on intertidal oyster reefs were greater at lower elevations and at edges than at higher elevations and centers of patches (Baillie & Grabowski, 2019; Fodrie et al., 2014). In addition, habitat attributes can vary with abiotic processes operating at larger spatial scales (Leong et al., 2022; Lloyd et al., 2020; Stelling-Wood et al., 2021). Thus, their effects on recruitment will be dependent on the broader environmental settings in which they occur. Generally, there is limited understanding of which habitat attributes are most important for maximizing recruitment and how variation in these attributes across larger spatial scales influences recruitment (Boström et al., 2011). This could be contributing to poor outcomes from many restoration strategies (McAfee et al., 2020). This is a key knowledge gap in supporting the management and conservation of foundation species over large spatial scales (Angelini et al., 2011; Gilby et al., 2018).

Understanding spatial variation in recruitment also requires knowledge of the environmental processes that can influence recruitment, in terms of both survival and condition, which can have cascading impacts on populations by influencing subsequent growth and reproduction. Abiotic factors such as temperature can strongly influence larval development, settlement, growth and, thus, recruitment at landscape and patch scales (Dove & Sammut, 2007; Edmunds et al., 2001; Parker et al., 2017). For example, increased mortality of coral recruits was associated with elevated temperatures via premature larval metamorphosis across landscapes of coral reefs (Edmunds, 2021; Edmunds et al., 2001). The recruitment and survivorship of recruits of the Sydney rock oyster, *Saccostrea glomerata*, on spat collection units in estuaries of New South Wales (NSW), Australia, differed among estuaries but was consistently greater in shallow subtidal areas compared to intertidal areas (Esquivel-Muelbert et al., 2022; Lee et al., 2012). Recruitment can also be negatively related to turbidity (Esquivel-Muelbert et al., 2022) and can be higher on sediment-free substrata (Diggles, 2017). Indeed, higher levels of sedimentation can smother newly settled corals (e.g., Birrell et al., 2005), oysters (e.g., Kimbro et al., 2014) and mussel recruits (e.g., Österling et al., 2010). On the other hand, small amounts of sediment can nourish the growth of postsettled filter-feeding recruits such as corals and bivalves (Dodge et al., 1974). Recruitment at large spatial scales can also be influenced by the type of estuary. For example, recruitment of Olympia oyster, *Ostrea lurida*, was lower in estuaries with greater marine influences (reflected as lower summer temperature, higher winter salinity, and shorter residence time) compared to estuaries more influenced by river and catchment runoff (Wasson et al., 2016). Recruitment can also vary due to within-habitat variation in environmental conditions. Lower surface elevation on oyster reefs is also associated with lower temperatures and can promote recruit survival (Lenihan, 1999). Smaller habitat patches can also be more prone to sedimentation (Glasby et al., 2015).

In Australia, oysters previously formed extensive reef complexes up to 10 ha. It is estimated that only 10% of these reefs now remain and they are considered functionally extinct (Beck et al., 2011; Gillies et al., 2018). Thus, similar to denuded oyster reefs globally (Beck et al., 2011), there are efforts to restore oyster beds including *S. glomerata* (Howie & Bishop, 2021; Reeves et al., 2020). In this study, we used spatial variation in oyster reefs dominated by the Sydney rock oyster, *S. glomerata*, to determine the habitat attributes (i.e., patch connectivity, area, circularity, distance from edge, rugosity) that best predict recruitment and health among and within estuaries. We explored whether the recruitment of oysters to oyster reefs was related to the environmental variables of temperature and sedimentation within and across estuaries, which are indicative of river and/or catchment influences at the estuarine level. To do this, we conducted two large-scale experiments. In the first experiment, we quantified and compared the total recruitment and percentage survivorship of recruits on tiles placed on multiple reef patches within each of three estuaries. We also determined variation in the abiotic factors, that is, temperature and sedimentation. In addition, because recruit abundance and/or survivorship (in the short term) can be a poor predictor of recruit health (Gribben & Wright, 2006), we investigated whether estuaries that supported higher recruitment also supported healthier recruits (measured as energetic reserves; Gibbs et al., 2020). A second experiment explicitly investigated whether differences in sedimentation among estuaries explained variation in the recruitment of oysters to reefs. We hypothesized that total recruitment and the percentage of live recruits would (1) vary among estuaries, (2) increase with patch connectivity, shape, and size in each estuary, and (3) decrease with higher surface elevation and away from patch edges. Furthermore, we hypothesized that (4) total recruitment and the percentage of live recruits would be negatively associated with increases in temperature and sedimentation and that (5) recruit health would vary between estuaries.

MATERIALS AND METHODS

Influence of environmental and habitat attributes on oyster recruitment and health among estuaries

Oyster recruitment with habitat attributes

We quantified the total recruitment and percentage of live recruits (i.e., percentage survivorship) of oysters on tiles in oyster reefs among three estuaries covering 250 km of the coastline of NSW, Australia: Crookhaven River, Hunter River, and Port Hacking (Figure 1A,B,E,G). Recruitment tiles (110 × 110 × 5 mm) were made from prefabricated cement-fiber sheets (Anderson & Underwood, 1994). Although oyster reefs have declined throughout NSW, there remain significant populations of oysters attached to mangrove roots and on artificial substrata in all estuaries (Gillies et al., 2018). We focused on estimating recruitment and not larval supply as the population genetics of *S. glomerata* along NSW does not show high interestuary variation, indicating good mixing of populations (O'Hare et al., 2021). As larvae are not solely entrained within an estuary, larval supply (and recruitment) within an estuary is unlikely to reflect any differences in adult populations among the estuaries. Moreover, the NSW Department of Primary Industries shows high settlement on commercial collectors across all estuaries, indicating that larval supply is not limiting in any of our estuaries and is not the major factor stopping the recovery of oyster reefs (W. O'Connor, personal communication).

Within each estuary, we randomly chose a subset of reefs on which to place the recruitment tiles (Appendix S1: Figure S1). The number of recruitment tiles on each reef differed according to reef area, with a minimum of four tiles sampled on the smallest reefs (5–10 m^2) and a maximum of 48 tiles on the largest reefs (≥4000 m^2; see Appendix S1: Table S1). The location of each tile (*XY* coordinates) on the reefs was randomized prior to deployment using the spsample package in R (version 4.0.3). Tiles were attached to the reefs using wooden stakes (2 cm × 2 cm × 1 m) driven into the base of the reefs. Tiles, one per stake, were secured to the stakes with stainless steel screws at the centers and secured to the stakes perpendicular to the reef surface (Appendix S1: Figure S1). The tiles were orientated so as to reduce the potential influence of sedimentation on smothering recruits and maximizing recruitment success (Colden et al., 2017). Tiles were established ≤5 cm above the reef complexes.

Across our three estuaries, we determined the total abundance and percentage survivorship of oyster recruits over the entire *S. glomerata* recruitment period, which spans several recruitment events over approximately 7 months (Diggles, 2017; Lee et al., 2012; Underwood & Anderson, 1994). Tiles were deployed by January 2020 (see tile deployment dates in Appendix S1: Table S3) just prior to the estimated start (February 2020) of recruitment to the end of the recruitment period (August–September 2020). Tiles were checked periodically (every 2–3 months), and no missing tiles were replaced during this period. A total of 38.9%, 6.7%, and 9.9% tiles were lost at Crookhaven River, Hunter River, and Port Hacking, respectively (Appendix S1: Table S3). To determine the total abundance of oyster recruits and percentage survivorship of recruits on each tile at the end of the recruitment period (i.e., September 2020), we took photos of the front side of the tiles in the field with a camera (Olympus TG-6; 12 megapixels). For all oysters, we determined whether they were alive or dead using ImageJ software (version 153; Schneider et al., 2012). Following methods of Taylor and Bushek (2008) and Gribben et al. (2020), live recruits were defined as recruits with both valves attached and nongaping, whereas dead recruits included individuals with empty valves, single valves, and gaped valves containing oyster tissue and scars (marks left from recently detached oysters). We did not count any recruits on the screws owing to differences in settlement material and surface rugosity in comparison to the tiles. Total abundance of recruits was the sum of live and dead oysters per tile, and percentage survivorship was the percentage of live recruits per tile. To explore evidence for competition between oysters and fouling communities on tiles, we also determined the total cover of other fouling groups (i.e., turf algae, barnacle, and crustose coralline algae) on each tile. Fouling organism cover was calculated based upon 50-point annotations on each tile using Coral Point Count with Excel extensions (CPCe; Kohler & Gill, 2006).

To understand the extent to which the habitat attributes of reefs at different scales explained variation in recruitment, following Leong et al. (2022), within patches, we quantified surface elevation ("elevation") of each tile and their distances to the nearest reef edge ("dist.to.edge"). Surface elevations were mapped with a Real-Time Kinematic and differential Global Positioning System unit (RTK-dGPS, Leica GNSS 14, vertical accuracy ±8 mm; horizontal ±13 mm), and the distances to patch edges were acquired with *XY* coordinates of tiles and mapped reef contours (obtained with NearMap) using the "NEARDIST" function (version 10.3, ESRI, 2016). At the whole-patch scale, we quantified patch area ("area"), reef circularity (sensu McGarigal et al., 2012, "circle," i.e., measure of perimeter relative to a perfect circle), and two-dimensional fractal complexity (sensu Mandelbrot, 1977 "frac," i.e., the measure of edge perimeter relative to closest geometric shape) to quantify variances of whole-patch sizes and shapes. At the landscape scale, we quantified an isolation index (sensu McGarigal et al., 2012; "iso.index") as a measure of patch connectivity among the reefs. The isolation index was calculated as the weighted sum of products between nearest-neighbor distance from focal patch to other patches and the ratios of focal area to total patch area (Moilanen & Nieminen, 2002). All habitat attribute variables collected are summarized in Appendix S1: Table S2.

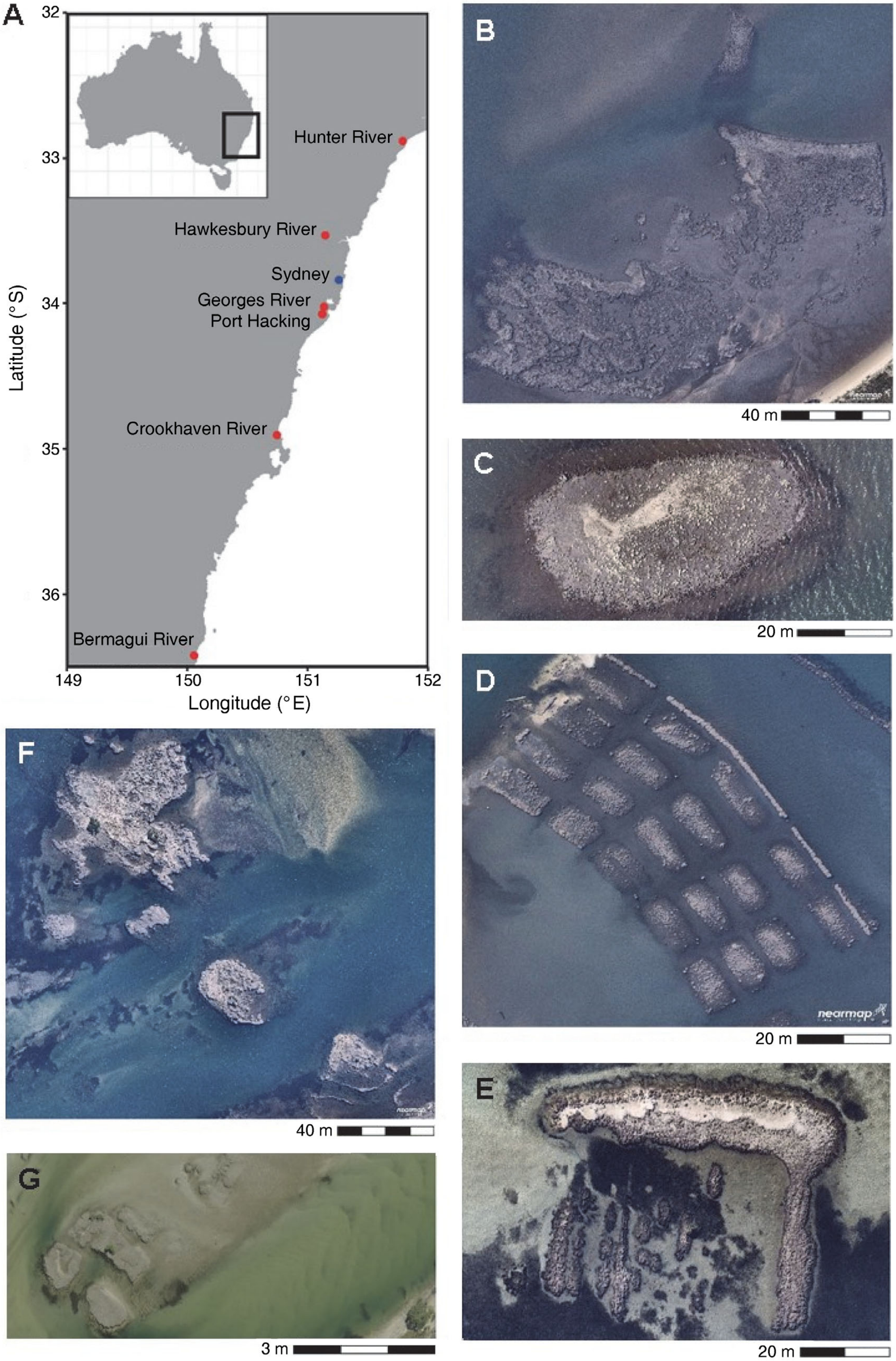

FIGURE 1 (A) Location of sampled estuaries (red dots) and satellite aerial images of *Saccostrea glomerata* reef complexes along coastline of New South Wales (inset), Australia, where oyster recruitment was determined. (B) Hunter River. (C) Hawkesbury River. (D) Georges River. (E) Port Hacking. (F) Crookhaven River. (G) Bermagui River. Aerial images (B–F) and (G) were obtained from NearMap Ltd. (https://www.nearmap.com/au/en) and NSW Government Spatial Services (https://maps.six.nsw.gov.au/), respectively.

Temperature and sedimentation across spatial scales

In each estuary, we deployed nine temperature loggers (Hobo Pendant Loggers UA-002-08, accuracy ±0.2°C) on one to three reefs that contained recruitment plates during the estimated peak recruitment period of *S. glomerata* (sensu Diggles, 2017). Loggers were calibrated to ±0.2°C prior to deployment, attached to the tile stakes that were randomly selected and rested on the reef surfaces (see location of loggers in each estuary in Appendix S1: Figure S2). Loggers recorded air and submerged temperatures continuously at 10-min intervals for 2 weeks (28 January 2020–11 February 2020; dates inclusive) in the absence of weather events (e.g., storms or floods) as confirmed by the monthly weather reports from the Australian Bureau of Meteorology (BOM) (http://www.bom.gov.au/climate/mwr/). We filtered out logged temperatures during the change of incoming tides, that is, effective shore level (ESL) heights (sensu Harley & Helmuth, 2003; Appendix S1: Section S1). We further excluded temperatures 0.15 m below and above ESLs (sensu Lathlean et al., 2011). We assumed negligible variation of day and night temperatures from the short period (2-week) of temperature logging. We then calculated the fifth ("p5temp," as a proxy of highest tides, submerged water temperatures) and 95th-percentile temperature ("p95temp," as a proxy of lowest tides, exposed aerial temperatures) for each logger. We also calculated the temperature CV to evaluate temperature variances surrounding the mean temperature of each logger. We summarize the list of temperature and sedimentation variables in Appendix S1: Table S2.

We measured sedimentation rates on *S. glomerata* reefs using sediment traps made of open-lid cylindrical specimen jars (5.0 cm diameter × 10.0 cm height for Crookhaven River and Hunter River; 3.0 cm diameter × 11.5 cm height for Port Hacking). We deployed 72 traps (26 on Crookhaven River, 28 in Hunter River, and 18 in Port Hacking) attached to the stakes of a random subset of tiles from March 2020 for 2–3 months; a total of 46 sediment traps remained to be collected (Appendix S1: Table S3). Extreme weather events (e.g., storms) were absent during the sediment-trapping period, again confirmed by monthly weather reports from BOM (see above). After collection, the contents of the traps were rinsed with freshwater on a 1-mm sieve to remove any organisms and large shell grit. Filtered sediment was then dried in an oven at 60°C until constant weight was reached. Finally, the dry sediment was weighed on an electrical balance (Australian Scientific GX-224AE; maximum capacity: 200.0 g precision: ±0.0001 g) and converted to sedimentation rate, that is, dry weight per number of deployment days (grams per day).

Recruit health between estuaries

The energy status of oysters recruited to the plates was determined by the total lipid and classes of lipids, which are an indicator of energy reserves (Gibbs et al., 2020; Parker et al., 2017). Crookhaven River was not included due to the low number of recruits collected. At the end of the experiment described earlier, all tiles were returned to the lab where oysters from each estuary were randomly selected for lipid analyses. In total, 48 oysters (24 per estuary; mean shell length: Port Hacking = 1.27 ± SE 0.07 cm and Hunter River = 1.38 ± SE 0.07 cm) were analyzed.

Lipid separation and lipid class analysis were done as described by others (Gibbs et al., 2020, 2021). Briefly, to determine the amount of lipid and lipid classes, oysters were freeze-dried (Christ Alpha 1-4 LSC) and then quantitatively extracted overnight using a modified Bligh and Dyer (1959) one-phase methanol:dichloromethane:water extraction ($MeOH:CH_2Cl_2:H_2O$) solvent mixture (20:10:7 mL). An aliquot of the extract was analyzed using an Iatroscan MK VI TH10 thin-layer chromatography-flame ionization detector (TLC-FID) analyzer (Tokyo, Japan) to quantify individual lipid classes (Ackman, 1981; Volkman & Nichols, 1991). Lipid standards were used to calibrate the flame ionization detector (FID) for each compound class. Peaks were quantified on a Windows 10-compatible computer using SIC u7 Data Station for Iatroscan software (LSI Medience Corp., System Instruments Co.). Lipid class peaks were labeled using SIC u7 Iatroscan Integrating Software version 2.1, quantified using predetermined linear regressions, and expressed as in micrograms per oyster per centimeter in size. Total lipid amounts for oysters were determined as the sum of all lipid classes for each sample. The condition index of larvae was calculated as the ratio of triacylglycerides (TAG): cholesterol, as TAG μg larva^{-1}/cholesterol ng larva^{-1} (Fraser et al., 1988).

Statistical approach

To investigate the relationships between habitat attributes and recruitment success (i.e., total number of recruits and percentage of live recruits), we fitted generalized linear mixed models (GLMMs) and conducted stepwise model selection. The total abundance of recruits and percentage live recruits were fitted with GLMMs, using negative binomial and binomial error distributions, respectively. The GLMMs were fitted using the lme4 (Bates et al., 2015) and glmmTMB packages (Magnusson et al., 2017) in R (version 4.03). "Estuary" was included as a fixed factor to assess differences at large scales.

Habitat attributes (i.e., "area," "distance to edge," "elevation," "frac," "circle," and "isolation index") were fitted as independent covariates and as interaction terms with "estuary" in the models. Habitat attributes were not strongly correlated to each other (i.e., Pearson's correlation coefficients, $r < \pm 0.7$; Zuur et al., 2009). Reef ("reef_id") was also included as a random intercept to account for potential nonindependence between sampled tiles from the same reef. After each model was fitted, stepwise model selection was conducted until the best model (lowest corrected Akaike information criterion [AIC] using the "dredge" function in the MuMIn package; Barton, 2009). Both here and for Experiment 2 (described below), the best models were validated using residual values versus the fitted plots (Zuur et al., 2009). For selected habitat attributes ("Attr" in Tables 1 and 2), we acquired their regression slopes across estuaries using "emtrends" (emmeans package; Lenth, 2016). For selected attributes with an interaction with "estuary" ("Attr:Es" in Tables 1 and 2), we acquired regression slopes for each estuary term using the same package. When only "estuary" was selected ("Es" in Tables 1 and 2), we conducted post hoc Tukey tests on the sampled estuaries using "lsmeans" (lsmeans package; Lenth, 2016).

For all estuaries combined and each estuary separately, relationships between total fouling cover and total oyster recruitment and percentage live oysters were explored using Pearson's correlation coefficients. All data were log10-transformed prior to analysis.

Model selection was also used to assess the relationships between the response variables (i.e., total recruitment and percentage of live recruits) and the abiotic variables (i.e., sedimentation rate, temperature CV, fifth-percentile temperature ["p5temp"] and 95th-percentile temperature ["p95temp"]). Sedimentation rate and temperature variables were modeled separately for each response variable. This was because there were insufficient replicates that had both a temperature logger and sediment traps based upon random deployments ($n = 6$ for joint-sediment trap and temperature tiles). Similar to the models against habitat attributes, each response variable was fitted against "estuary" and abiotic variable(s) and with interaction terms between abiotic variables and "estuary." A total of four models were therefore analyzed.

Differences in total lipids, lipid classes, and condition index between estuaries were analyzed in R using a fixed-effect linear model with the position on the reef (front, back, middle) as the first factor and "Estuary" as the second factor. One-way analysis of variance (one-way ANOVA) was used to determine significant differences between factors. Analysis showed position to have no significant effect, so this factor was removed and data reanalyzed with "Estuary" as the only factor. Cochran's

TABLE 1 Results of model selections for total live recruitment per tile (response variable) against patch attribute ("Attr"), estuaries ("Es"), and interaction between estuaries and attribute ("Attr:Es") for each attribute and its corresponding spatial scale (rows in first and second columns).

Response variable: total recruitment		A. Selected model terms					
Spatial scales	Patch attributes	"Es"	"Attr"	"Attr:Es"	B. Estuary groups for selected "Es"	C. Slope estimates for selected "Attr"	D. Slope estimates for selected "Attr: Es"
Within-patch	Surface Elevation	X	X	…	CR < HR = PH	−0.79 ± 0.25	…
	Distance to Edge	X	…	…	CR < HR = PH	…	…
Whole-patch	Circularity index	X	…	…	CR < HR = PH	…	…
	Fractal dimension	X	…	…	CR < HR = PH	…	…
	Area	X	X	…	CR < HR = PH	+0.09 ± 0.05	…
Among-patch	Isolation index	X	…	X	CR < HR = PH	…	CR: +3.51 ± 1.10 PH: +0.22 ± 0.69 HR: −0.03 ± 0.24

Note: Selected model terms for each patch attribute are denoted by "X" in "Es," "Attr," and "Attr:Es" cells in column A. Selected model terms. For models with selected "Es," post hoc test groupings for differences among estuaries, that is, Crookhaven River (CR), Hunter River (HR), and Port Hacking (PH), are denoted by <, >, and/or = in column B. Estuary groups for selected "Es." Regression slope estimates of selected "Attr" and "Attr:Es" terms are represented with trends of estimates (+ or −) with their standard errors (±) in columns C. Slope estimates for selected "Attr" and D. Slope estimates for selected "Attr: Es," respectively. For models with selected "Attr:Es" terms, we presented the regression slope estimates, estimate trends, and standard errors for each estuary.

TABLE 2 Results of model selections for percentage live recruits (response variable) against patch attribute (“Attr”), estuaries (“Es”), and interaction between estuaries and attribute (“Attr:Es”) for each attribute and its corresponding spatial scale (rows in first and second columns).

Response variable: Percentage recruitment		**A. Selected model terms**			**B. Estuary groups for selected “Es”**	**C. Slope estimates for selected “Attr”**	**D. Slope estimates for selected “Attr: Es”**
Spatial scales	**Patch attributes**	**“Es”**	**“Attr”**	**“Attr:Es”**			
Within-patch	Surface elevation	X	...	...	CR < HR = PH	...	...
	Distance to edge	X	...	X	CR < HR = PH	...	CR: −0.32 ± 0.38 HR: −0.27 ± 0.06 PH: −0.04 ± 0.07
Whole-patch	Circularity index	X	...	X	CR < HR = PH	...	CR: −11.66 ± 6.32 HR: +0.42 ± 0.35 PH: +3.40 ± 1.56
	Fractal dimension	X	X	...	CR < HR = PH	−2.44 ± 1.50	...
	Area	X	...	X	CR < HR = PH	...	CR: −3.78 ± 1.34 HR: −0.02 ± 0.04 PH: −0.34 ± 0.19
Among-patch	Isolation index	X	...	X	CR < HR = PH	...	CR: +13.13 ± 3.94 HR: +0.97 ± 0.17 PH: +0.23 ± 1.47

Note: Selected model terms for each patch attribute are denoted by “X” in “Es,” “Attr,” and “Attr:Es” cells of column A. Selected model terms. For models with selected “Es,” post hoc test groupings for differences among estuaries, that is, Crookhaven River (CR), Hunter River (HR), and Port Hacking (PH), are denoted by <, >, and/or = in column B. Estuary groups for selected “Es.” Regression slope estimates of selected “Attr,” and “Attr:Es” terms are represented with trends of estimates (+ or −) with their standard errors (denoted by ±) in columns C. Slope estimates for selected “Attr” and D. Slope estimates for selected “Attr: Es,” respectively. For models with selected “Attr:Es” terms, we present the regression slope estimates, estimate trends, and standard errors for each estuary.

test found no heterogeneity of variances, and no transformation was required for all lipid classes, total lipids, and condition index. A summary of the variables and statistical analyses in this experiment can be found in Appendix S1: Table S2.

Influence of sedimentation on recruitment among estuaries

To more explicitly investigate whether large-scale variation in abiotic environmental variables was correlated to oyster recruitment among estuaries, we simultaneously determined sedimentation rates and oyster recruitment across six estuaries containing remnant *S. glomerata* reefs. This included the three estuaries sampled above and three additional estuaries (Georges River, Bermagui River, and Hawkesbury River; Figure 1A,C,D,F). *S. glomerata* reefs in the additional estuaries (i.e., Georges River, Hawkesbury River, and Bermagui River) formed large reefs (at least one patch >100 m^2) on remnant oyster aquaculture leases, ballast heap, and natural rock, respectively (NSW Marine Estate and Authority, 2021). Our six estuaries were categorized as high or low sedimentation estuaries based on long-term monitoring of water turbidity in these estuaries by the NSW Office of Environment and Heritage (2016) (Appendix S1: Table S5). Low-sediment estuaries consisted of Bermagui River, Crookhaven River, and Port Hacking with average turbidities recorded <3 Nephelometric Turbidity Units (NTUs). Meanwhile, high-sediment estuaries recorded average turbidities of >6 NTUs and comprised Hunter River, Hawkesbury River, and George’s River.

Recruitment was assessed on tiles attached to the reefs using the same protocol as the experiment described above, but the tiles were attached horizontally to the reef to assess the influence of sedimentation on recruitment (Appendix S1: Figure S3A). To mimic recruitment on oyster reef complexes (sensu Soniat et al., 2004), two dead cupped-valve shells of *S. glomerata* shells were glued on the top surface on each tile with a marine epoxy (Megapoxy HT, Vivacity Engineering Pty. Ltd.). The shapes, sizes, and positions of shells were consistent in traps (refer to Appendix S1: Section S2), and shells were cleaned and disinfected following aquatic biosecurity protocols (INT11/7170 POMS procedure) of NSW Department of Primary Industies (2018) prior to deployment.

In each estuary, we randomly deployed 15 tiles across the entire reef area within an estuary as we were not interested in within-patch, whole-patch, or among-patch influences on oyster recruitment (Tables 1 and 2).

Randomization of the tile locations on the reef complexes was also conducted before deployment using the spsample package in R. *XY* and surface elevation of tile locations were measured with the RTK-dGPS unit. Tiles were deployed in January 2021 just prior to the period of *S. glomerata* recruitment (Anderson & Underwood, 1994; Diggles, 2017; Lee et al., 2012) and retrieved between late June and early July 2021 in all estuaries, except for Bermagui River, which was retrieved in September 2021 due to COVID-19 restrictions in Australia. Upon retrieving the tiles, we quantified the total recruitment per tile and percentages of live recruits to total recruitment, as described above.

We simultaneously estimated the levels of sedimentation among estuaries adjacent to all tiles. Standardized sediment traps were made of a 3-mm-thick, open-ended, flat-bottomed polyvinyl chloride (PVC) cylinder lid. Each trap had a low diameter-to-height aspect ratio, that is, 100 mm in internal diameter and 25 mm in height, to capture sediment resuspension and maximum net deposition in intertidal areas (Flower, 1991). As described above, we attached dead cupped-valve shells to mimic the surface rugosity of *S. glomerata* to the base of each trap. Traps were secured on the reef surface with cable ties attached to 10-mm-diameter PVC pipes staked into the complexes; (Appendix S1: Figure S3A). Traps were deployed within the same tidal cycle and remained for ~30 days (see Appendix S1: Table S4 for deployment and retrieval dates). During the sediment-trapping period, no extreme weather events (i.e., storms, rainfall, or floods) were recorded, as confirmed by monthly weather reports from BOM. Intact, nonoverturned traps (100% recovered from all estuaries, except Crookhaven River with 25% recovered; Appendix S1: Table S4) from the estuaries were returned to the laboratory for processing. Sediments were sieved and weighed as described above and results converted to dry weight (in grams).

Statistical approach

We fitted GLMMs to test whether total oyster recruitment and percentage of live recruits varied among estuaries, that is, "estuaries" categorized as a fixed factor having high or low sedimentation. "Estuary" was included as a nested random factor within "estuary type" (two levels: high and low). We also included surface elevation ("elevation") of tiles and traps as a covariate in each model to account for its influence on recruitment (Baillie & Grabowski, 2019; Colden et al., 2017). GLMMs were run using the same packages and procedures as described above. Instead of model selection, however, statistical significance used to test for the effect of "estuary type" using likelihood ratio tests (LRTs) from GLMMs. To confirm that our observed rates of sedimentation to oyster reefs varied as expected among the nominally high- and low-sedimentation estuaries, we used a similar model but with sediment weight as the response variable.

RESULTS

Influence of environmental and habitat attributes on oyster recruitment and health among estuaries

Oyster recruitment and spatial characteristics

The total recruitment and percentage of live oyster recruits on tiles differed among estuaries, and both were lower in Crookhaven River compared to Hunter River and Port Hacking, which did not differ from each other (Figure 2A,B; Tables 1 and 2). The average percentage cover of area occupied by other species on the tiles was low (17.4 ± SE 1.6%). Pooled across estuaries and within

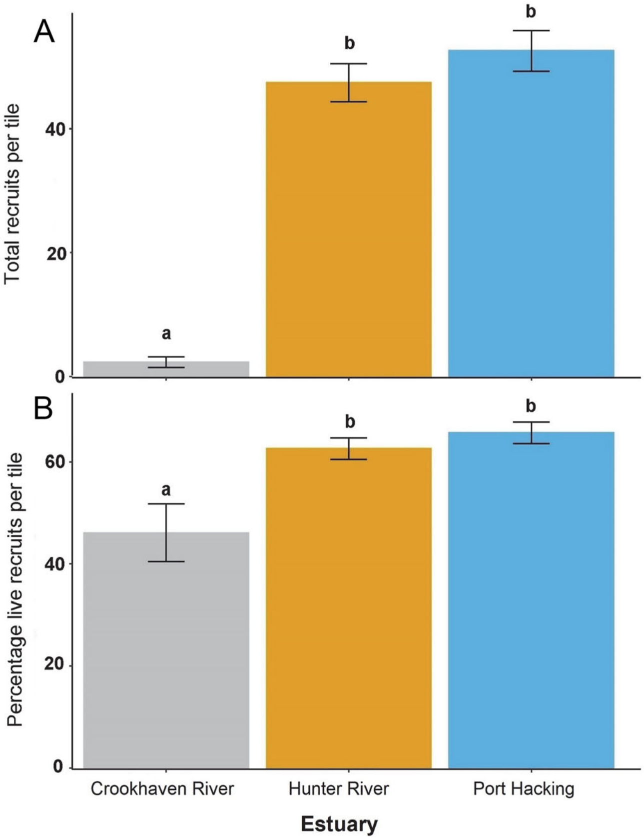

FIGURE 2 Mean and SE of (A) total no. recruits per tile and (B) percentage of live recruits per tile on oyster reefs in Crookhaven River, Hunter River, and Port Hacking. Letters represent results of pairwise post hoc Tukey tests between estuaries.

estuaries, the relationships between total oyster recruitment and percentage of live oysters on tiles and area occupied by fouling organisms were all weak (all $r^2 < 0.21$; Appendix S1: Table S6).

Within patches, the total number of recruits reduced with increasing surface elevation in all estuaries (Figure 3A, Table 1), but there was no relationship between total recruits and distance from the edge (Figure 3B, Table 1). For patch attributes, there was a positive relationship between the total number of recruits and reef area (Figure 3C, Table 1) but no significant differences in total recruits and circularity or fractal dimension of the patch (Figure 3D,E, Table 1). In contrast, as the isolation of reefs increased, there were more recruits in Hunter River and Crookhaven River, but the opposite trend was observed for reefs in Port Hacking (Figure 3F, Table 1).

Within patches, the percentage of live recruits (i.e., survivorship) did not vary with surface elevation (Figure 4A, Table 2). The relationship between patch connectivity and the percentage of live recruits varied among estuaries. Within patches, the percentage of live recruits decreased farther away from reef edges in all estuaries; this relationship was stronger in Crookhaven River and Hunter River compared to Port Hacking (Figure 4B, Table 2). Increases in reef area were associated with lower percentages of live recruits in all estuaries, with a stronger negative relationship at Crookhaven River (i.e., larger slope estimate) compared to Hunter River and Port Hacking (Figure 4C, Table 2). The percentage of live recruits increased with reef circularity in Crookhaven River and Hunter River, but the opposite relationship was found in Port Hacking (Figure 4D, Table 2). The percentages of live recruits varied with patch attributes such as reef area and two-dimensional reef fractional dimensionality, although the relationships varied among the estuaries. The percentages of live recruits decreased with increasing reef fractal dimensionality in all estuaries (Figure 4E, Table 2). The percentage of live recruits increased with increasing isolation in the Hunter River and Crookhaven River, but the opposite trend was observed for reefs in Port Hacking (Figure 4F, Table 2).

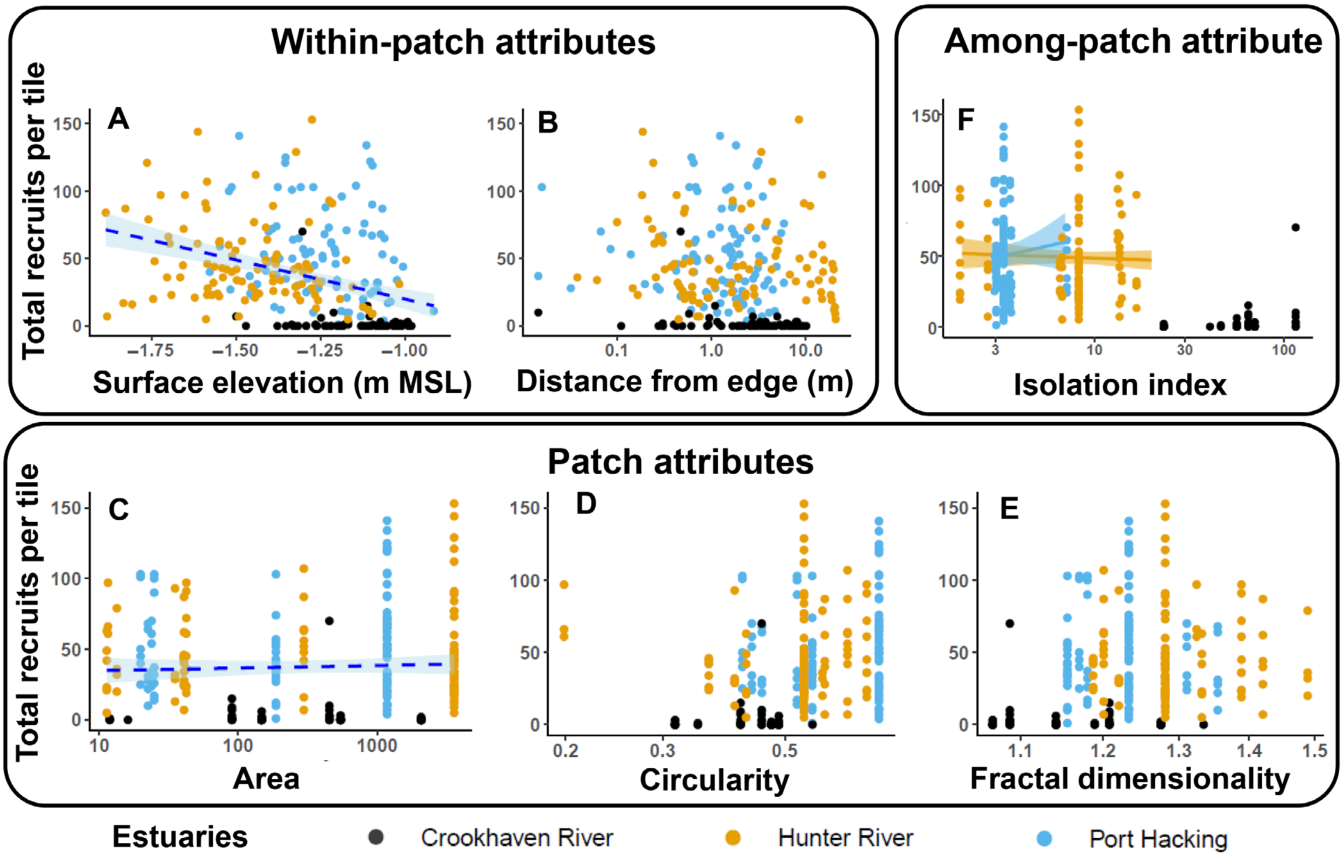

FIGURE 3 Relationships between total abundance of recruits per tile and within-patch ([A] elevation; [B] distance to reef edge), whole-patch ([C] area [D] circularity; [E] fractal dimension), and among-patches ([F] isolation index) attributes at Crookhaven River, Hunter River, and Port Hacking. Dashed regression lines and standard errors (shaded areas) in blue represent those of selected attribute terms ("Attr" in Table 1). Full regression lines and standard errors (shaded areas) represent those of selected interaction terms between estuaries and attributes ("Attr:Es" in Table 1). All *x*-axes except for surface elevation are base-10 logarithmic-scaled.

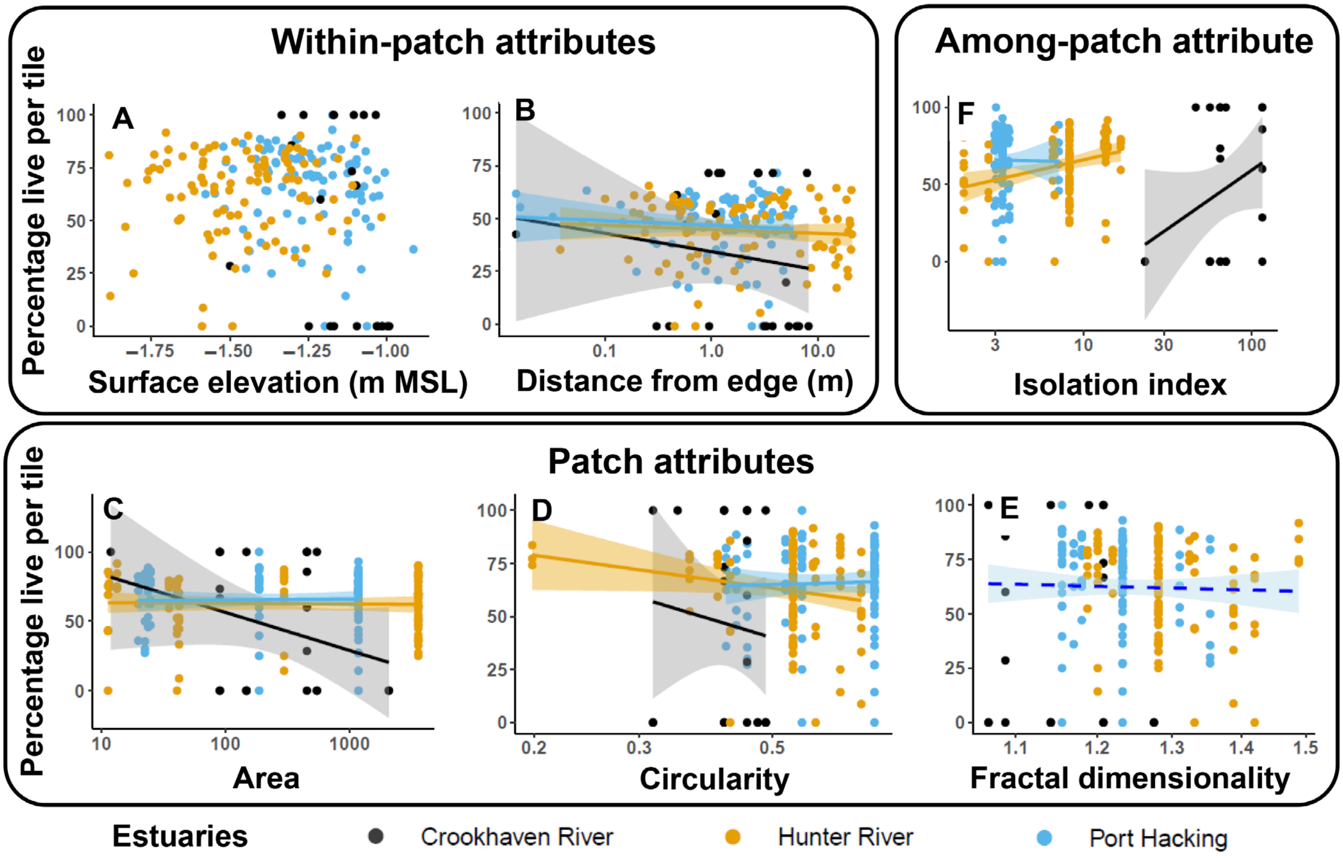

FIGURE 4 Relationships between percentage of live recruits on tiles and within-patch ([A] elevation; [B] distance to reef edge), whole-patch ([C] area; [D] circularity; [E] fractal dimension), and among-patches ([F] isolation index) attributes at Crookhaven River, Hunter River, and Port Hacking. Dashed regression lines and standard errors (shaded areas) in blue represent those of selected attribute terms ("Attr" in Table 2) from the models. Full regression lines and standard errors (shaded areas) represent those of selected interaction terms between estuaries and attributes ("Attr:Es" in Table 2). All *x*-axes except for surface elevation are base-10 logarithmic-scaled.

Temperature and sedimentation across spatial scales

Sedimentation was positively correlated with total recruits in all estuaries (Figure 5; Table 3). However, the relationship was stronger in Hunter River and Port Hacking compared to Crookhaven River (Table 3). Change in temperature as indicated by the coefficient of temperature was also correlated with increased percentages of live recruits (Figure 5E; Table 3) and fifth-percentile temperatures (Figure 5K: Table 3) irrespective of estuaries. Meanwhile, higher 95th-percentile temperatures were associated with lower proportions of live recruits in all estuaries (Figure 5H; Table 3).

Recruit health between estuaries

Overall, total lipids and the lipid classes of triacyglycerides (TAGs), polar lipids (PLs), and steryl esters (SEs) and the condition index of oysters were significantly greater at Port Hacking compared to Hunter River (Figure 6A,D,E,H,I; Appendix S1: Table S7).

Influence of sedimentation on recruitment among estuaries

Sedimentation on oyster reefs was higher on nominally high- compared to low-sedimentation estuaries (LRT $X^2 = 42.4$, $df = 1$, $p < 0.005$; Figure 7A). Low-sediment estuaries (Bermagui River, mean weight 1.7 ± SE 0.5 g; Port Hacking, 1.4 ± SE 0.4 g; Crookhaven River, 2.0 ± SE 1.6 g) recorded sediment weights in traps below 2.00 g, whereas those in the high-sediment estuaries were an order of magnitude higher (Hunter River, 20.8 ± SE 3.7 g; Hawkesbury River, 25.9 ± SE 7.0 g; George's River, 25.5 ± SE 5.0 g). Oyster reef surface elevation did not vary been high- or low-sediment estuaries (Figure 7B).

Low-sediment estuaries had almost 18 times higher total oyster recruitment (72 ± SE 9 recruits per tile) on tiles compared to high-sediment estuaries (4 ± SE

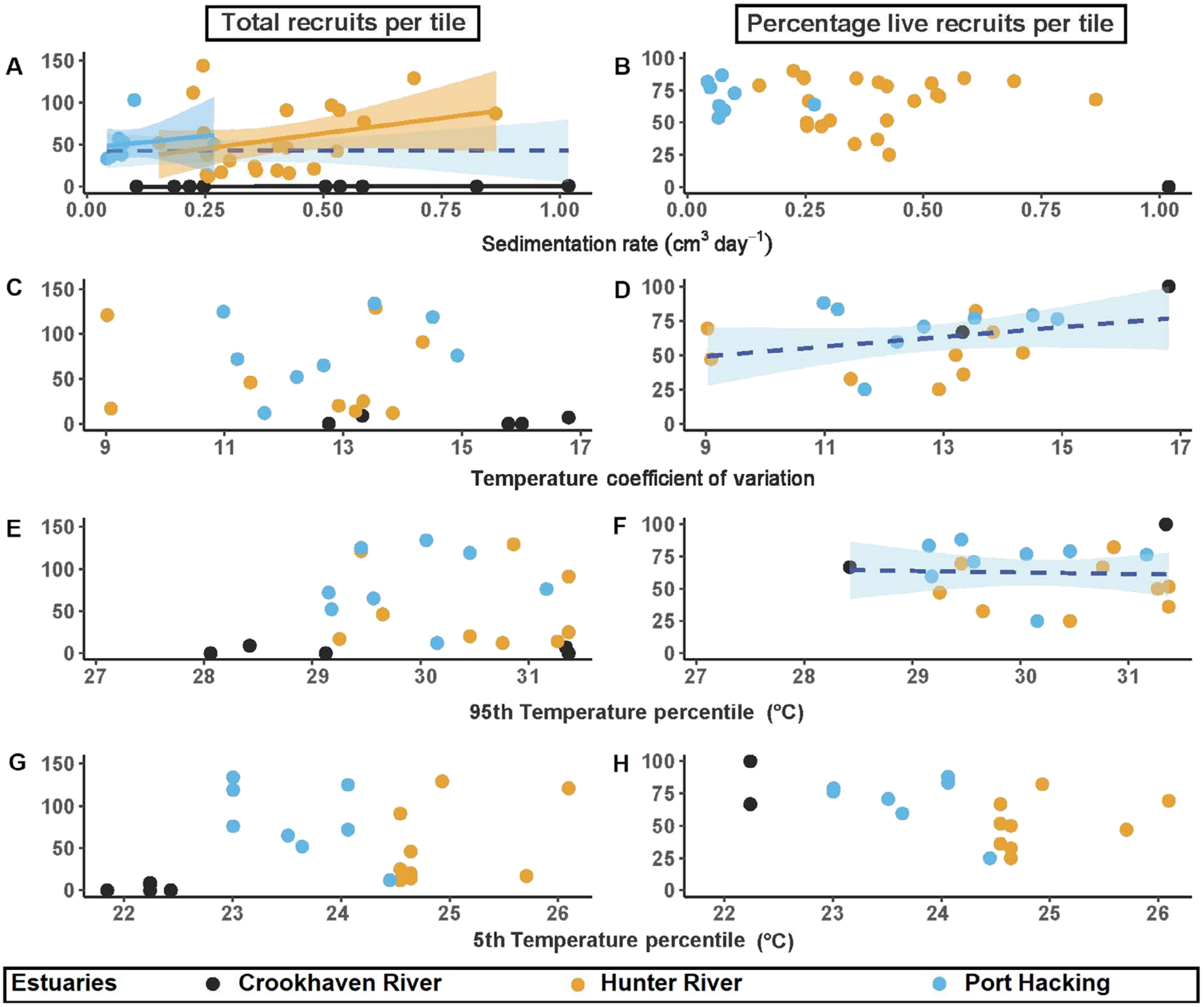

FIGURE 5 Relationships between recruitment success variables (left panel: total recruitment on each tile; right panel: percentage of live recruits on each tile) with other abiotic factors (i.e., [A, B] sedimentation rate; [C, D] temperature coefficient of variation; [E, F] 95th-percentile temperature; [G, H] 5th-percentile temperature). Full regression lines and standard errors (shaded areas) for each estuary represent significant estuary-only term ("Es" in Table 3). Dashed regression line and standard errors (shaded areas) in blue represent selected abiotic variable terms ("Abio" in Table 3) from the models.

1 recruits, LRT $X^2 = 9.39$, df = 1, $p = 0.003$; Figure 7C). An exception was Crookhaven, which had low recruitment and was classified as a low-sedimentation estuary. Percentages of live recruits ranged from 64.9% per tile at Hunter River to 100% per tile in the Hawkesbury River and did not differ between high- and low-sediment estuaries (LRT $X^2 = 0.04$, df = 1, $p = 0.857$; Figure 7D).

DISCUSSION

Understanding which habitat attributes determine recruitment success, and how they might interact with environmental setting, is critical for managing and restoring foundation species (Fahrig, 2003, 2017), particularly those that have broad distributions (Angelini et al., 2011; Byers et al., 2015). We found support for our hypotheses that oyster recruitment and recruit health would vary among estuaries. At the level of the estuary, total recruitment was broadly negatively correlated with sedimentation on oyster reefs. Postrecruitment survival was, however, similar among estuaries. Within estuaries, we also found support for the hypotheses that recruitment is negatively related to surface elevation and positively correlated to distance to the edge of patches. Our data suggest that, although within-estuary attributes of oyster reefs may influence recruitment, recruitment patterns are largely determined by larger-scale variation in

TABLE 3 Results of model selections for total live recruitment per tile and percentage live recruitment per tile (response variables) against abiotic variable (“Abio”), estuaries (“Es”), and interaction between estuaries and abiotic variable (“Abio:Es”) for each variable measured in this study (rows in first left column).

	A. Selected model terms			B. Estuary groups for selected “Es”	C. Slope estimates for selected “Abio”	D. Pearson’s correlation coefficients (*r*)
Abiotic variables	**“Es”**	**“Abio”**	**“Abio:Es”**			
Response variable: Total recruitment						
Coefficient of Variation temperature	...	...	...	...	...	$r = -0.06$
5th-percentile temperature	...	...	...	...	...	$r = +0.21$
95th-percentile temperature	...	...	...	...	...	$r = +0.44$
Sedimentation rate	X	X	...	PH = HR > CR	+1.68 ± 0.61	$r_{\mathrm{CR}} = +0.66^{\mathrm{X}}$ $r_{\mathrm{PH}} = +0.19^{\mathrm{X}}$ $r_{\mathrm{HR}} = +0.31^{\mathrm{X}}$
Response variable: Percentage live recruitment						
Coefficient of variation Temperature	...	X	...	...	+0.88 ± 0.19	$r = -0.29^{\mathrm{X}}$
5th-percentile temperature	...	X	...	...	+2.21 ± 0.37	$r = +0.48^{\mathrm{X}}$
95th-percentile temperature	...	X	...	...	−0.85 ± 0.30	$r = -0.03^{\mathrm{X}}$
Sedimentation rate	...		...	...	...	$r = -0.31$

Note: Selected model terms for each patch attribute are denoted by “X” in “Es,” “Abio,” and “Abio:Es” cells of column A. Selected model terms. For models with selected “Es,” post hoc test groupings for differences among estuaries, that is, Crookhaven River (CR), Hunter River (HR), and Port Hacking (PH) are denoted by <, >, and/or = in column B. Estuary groups for selected “Es.” Since “Abio:Es” was not selected in all models, only regression slope estimates of selected “Abio,” with their corresponding trends (+ or −) and their standard errors (±) are reported in column C. Slope estimates for selected “Abio.” Pearson’s correlation coefficients (*r*) between each abiotic variable and the response variable coefficient trends (+ or −) and statistical significance (superscripted X via selected “Abio” and/or “Es” terms) are reported in column D. Pearson’s correlation coefficients (*r*). Correlation coefficient and coefficient trend of each estuary, that is, r_{CR}, r_{PH}, and r_{HR}, are listed when “Es” term was selected.

estuarine-wide processes affected by environmental conditions. This supports other studies that also found that oyster recruitment was related to processes operating at regional scales (Byers et al., 2015; Kimbro et al., 2014).

Our data also suggest that recruitment is correlated with sedimentation, which may explain the significant differences found among estuaries at most sites. At Crookhaven River, however, recruitment was low despite having low sedimentation, possibly because the unusually strong currents and the higher elevation of the reef surface at this site (Leong et al., 2022) may hinder recruitment, as demonstrated in other studies (e.g., Thomsen & McGlathery, 2006). However, in our study, estuaries with high sedimentation also had longer periods of low salinity and high turbidity (Appendix S1: Table S5). Thus, sedimentation may be a proxy for a range of other abiotic variables related to the level of catchment influence on estuarine water quality that may affect oyster recruitment and health. In contrast, pH and temperature do not differ greatly among estuaries (NSW Office of Environment and Heritage, 2016; Appendix S1: Table S5) and do not explain the patterns of recruitment among estuaries we observed. This suggests that estuaries with low sedimentation may be more suitable targets for restoration as higher recruitment and healthier recruits may lead to faster reef development and sustainable long-term restoration. Regardless, measuring sedimentation may be a good general proxy for predicting potential recruitment in different estuaries. Such information would be invaluable to managers and restoration practitioners wishing to maximize restoration success.

In estuaries, recruitment of marine invertebrates can also be a function of larval supply (Ross, 2001; Satumanatpan & Keough, 2001) and can directly affect the number of settlers and recruits at all spatial scales (Underwood & Fairweather, 1989). Bivalve larvae and hydrodynamics can interact and determine larval dispersal and retention in natural habitats, and understanding larval sources and sinks for oyster reef restoration activities may be important to ensure viable oyster populations (McIntyre et al., 2021). The high levels of oyster settlement and strong genetic mixing of *S. glomerata* populations among the estuaries included in our study suggest that larval supply is not determined by within-estuary oyster populations and is not the main factor limiting restoration of oyster reefs. However, this may not always be the case, and understanding oyster larval supply–recruitment relationships is an important avenue for future research. Although oyster larvae can be sampled via passive and active sampling (McIntyre et al., 2021) for *S. glomerata*, we have limited information on the timing of spawning of adults and when larvae are present in the water column. Moreover, sampling larvae

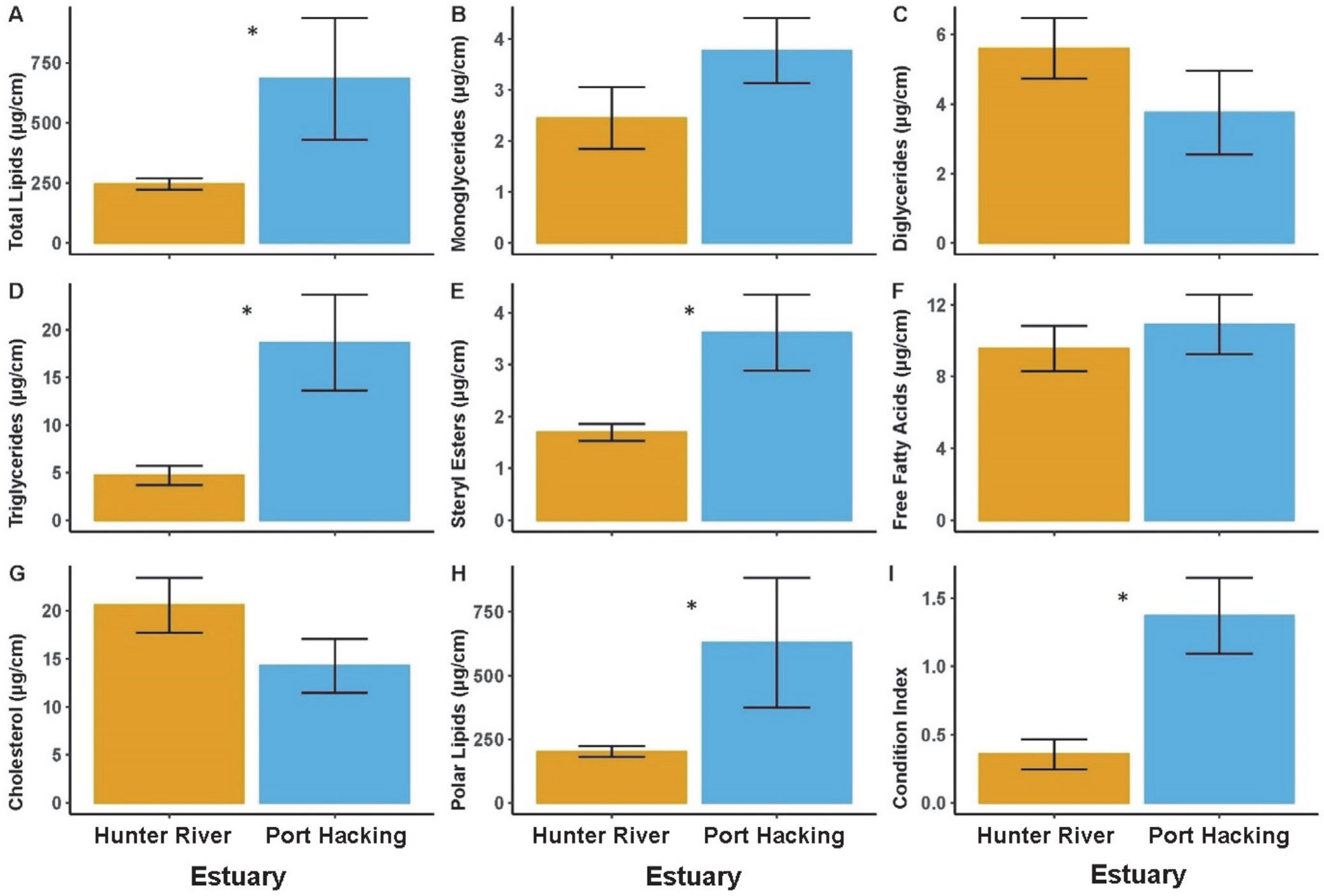

FIGURE 6 Mean and SE of (A) total lipids, (B) monoacylglycerides, (C) diacylglyceride, (D) triacylglycerides, (E) steryl esters, (F) free fatty acids, (G) cholesterol, (H) polar lipids, and (I) condition index of subsets of live oyster recruits in Hunter River and Port Hacking. An asterisk indicates statistical significance at $\alpha = 0.05$ of lipid response variables between estuaries (see Appendix S1: Table S7).

over the same spatial scales we used and the temporal scales needed to capture variation in larval supply among estuaries would be challenging.

Interestingly, recruit survivorship was independent of whether estuaries had high or low sedimentation or temperature, indicating that, once recruited to a surface, recruits may be able to tolerate various sedimentation levels. This supports other studies that found that, although high sedimentation levels can prevent oyster larvae settlement (Taylor & Bushek, 2008; Thomsen & McGlathery, 2006), postsettled recruits can survive various levels of sedimentation (Baillie & Grabowski, 2019; Soniat et al., 2004). However, from the first experiment, oyster recruits from Port Hacking (a low-sedimentation estuary) had a higher condition index and higher fast-burning energy reserves (as indicated by greater levels of triacyglyceride; Gibbs et al., 2020, 2021) than recruits collected in the Hunter River (a high-sedimentation estuary). They also had higher levels of PLs and SEs, which are major sources of reserve fuel and can also be used to regulate cellular activities (Fraser et al., 1988; Korber et al., 2017; Lee et al., 1971). This may indicate differences in food supply or metabolism of oysters between these two estuaries, with sublethal effects on recruits having important consequences for recruit fitness. Understanding the mechanisms underpinning these findings and the longer-term consequences of these findings for recruit growth and reproduction is an important avenue for future research.

Temperature differences at the patch but not the estuary scale were correlated with recruitment survival between settlement plates in all estuaries. Specifically, the proportions of live recruits increased with higher high-tide temperatures (i.e., fifth-percentile temperatures) but decreased with higher low-tide temperatures (i.e., 95th-percentile temperatures). Our results support other studies showing *S. glomerata* survivorship can increase with elevated water temperatures (Pereira et al., 2020) but are also negatively impacted by higher temperatures during aerial exposure (Bishop & Peterson, 2006; Dove & Sammut, 2007; Scanes et al., 2020). In our study, a larger temperature CV (i.e., a larger range between

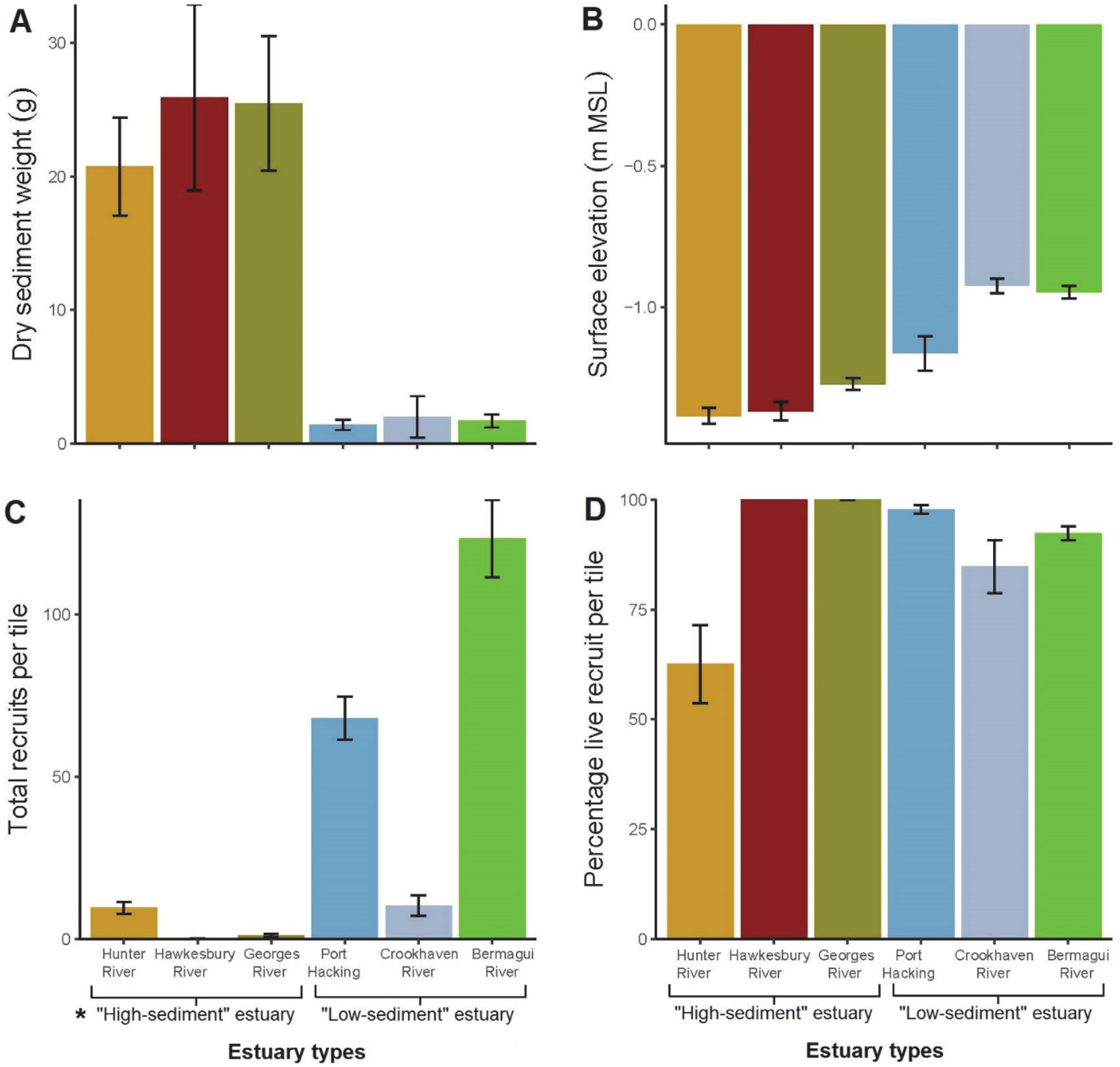

FIGURE 7 (A) Mean (±SE) dry sediment weight. (B) Surface elevation in sampled estuaries at "high-sediment" estuary (i.e., Hunter River, Georges River, and Hawkesbury River) and "low-sediment" estuary (i.e., Port Hacking, Crookhaven River, and Bermagui River). (C) Total recruitment on top surface of tiles and (D) percentage of live recruits on top surface of tiles. An asterisk denotes statistical significance of estuary type at α = 0.05 for total recruitment (panel C).

high-tide water temperature and low-tide air temperature) was also correlated to higher survival of recruits. Although this relationship was unexpected, the larger temperature variations could be linked to larger tidal ranges and water fluxes, which increase seston and oxygen and promotes sediment movement, all of which are linked to increased oyster growth survivorship (Colden et al., 2017; Fodrie et al., 2014; Grabowski et al., 2005). In addition, recruitment was not influenced by competition for space relationships between the cover of fouling organisms, total recruitment, and percentage live oysters on tiles were all weak, indicating limited competition between oysters and other fouling organisms.

Although differences among estuaries had the strongest influence on recruitment, some factors operating at smaller scales also had consistent relationships within estuaries. Our results support other studies showing that higher abundances of recruits are often associated with lower surface elevation (Baillie & Grabowski, 2019; Bishop & Peterson, 2006; Lenihan, 1999) as they are submerged for a longer period, thereby prolonging feeding and reducing desiccation stress (Bahr & Lanier, 1981; Bartol et al., 1999; Roegner & Mann, 1995). Larger reefs were associated with more recruits in all estuaries and may provide more surface area for settlement and increase the possible settlement cues from existing adults (Raimondi, 1988; Tamburri et al., 2008; Whitman & Reidenbach, 2012). It is uncertain why increasing fractal dimension (i.e., increasingly irregular shapes patches) was correlated to decreased recruit survivorship but it may influence hydrodynamics around patches leading to lower survivorship possibly via reducing food supply or promoting refuges for mesopredators.

Our study also supports inconsistent relationships between patch connectivity and total recruitment for other species of oysters found in other studies (e.g., Carson, 2010; Haase et al., 2012; Lagarde et al., 2019) However, increases in reef isolation were associated with higher proportions of live oysters in all estuaries, suggesting that where restoring oyster reefs involves multiple patches, spacing them farther apart may increase oyster survivorship, possibly by reducing predation pressure (Lanham et al., 2020). In addition, within patches, we found higher proportions of live recruits closer to reef edges in two estuaries, as found for high densities of recruits observed at edges of *C. virginica* reefs (Hanke et al., 2017). Recruits at intertidal reef edges experience more volume fluxes of water, seston, and oxygen with incoming tides, thereby promoting their growth and survivorship (Fodrie et al., 2014; Grabowski et al., 2005; Lenihan, 1999).

Our results showed that estuary-scale factors have the largest influence on oyster recruitment and potentially recruit health, and that this was possibly related to environmental processes operating at the catchment level. Although high survival was observed across all estuaries, high-sediment estuaries had low recruitment and may also have poor recruit health, which can further affect population maintenance of remnant reefs and restoration success. If the goal of oyster restoration is to achieve greater survival and faster reef growth, then restoration programs for *S. glomerata* should prioritize selection of estuaries with low sedimentation rates or where sediment stress can be mitigated. If restoration is to be successful in estuaries where sedimentation is high, recruitment may need to be assisted by reducing reef elevations, increasing the size of reefs and decreasing the fractional dimensionality of patches. We also found that connectivity of reefs was related to oyster recruitment and their survival, but patterns were variable among estuaries, suggesting that pilot studies would help in exploring the local effects of connectivity and how they can be harnessed to maximize recruitment success.

AUTHOR CONTRIBUTIONS

RCL, PEG, ABB, WAO, and PMR conceived the ideas and designed methodology. RCL, MCG, and KRE collected the data. RCL, MCG, ES, ABB, EMM, and LMP analyzed the data. RCL, PEG, ABB, and PMR led the writing of the manuscript. All authors contributed critically to the drafts and gave their final approval for publication.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

Data and code (Leong et al., 2023) are available in UNSWorks, the University of New South Wales' Library repository, at https://doi.org/10.26190/unsworks/25335.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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