

ARTICLE

Coastal squeeze on temperate reefs: Long-term shifts in salinity, water quality, and oyster-associated communities

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Funding information

North Carolina Division of Marine Fisheries Coastal Recreational Fishing License Program; National Science Foundation, Grant/Award Number: 1926395

Handling Editor: Ilsa B. Kuffner

Abstract

Foundation species, such as mangroves, saltmarshes, kelps, seagrasses, and oysters, thrive within suitable environmental envelopes as narrow ribbons along the land–sea margin. Therefore, these habitat-forming species and resident fauna are sensitive to modified environmental gradients. For oysters, many estuaries impacted by sea-level rise, channelization, and municipal infrastructure are experiencing saltwater intrusion and water-quality degradation that may alter reef distributions, functions, and services. To explore decadal-scale oyster–reef community patterns across a temperate estuary in response to environmental change, we resampled reefs in the Newport River Estuary (NRE) during 2013–2015 that had previously been studied during 1955–1956. We also coalesced historical NRE reef distribution (1880s–2015), salinity (1913–2015), and water-quality-driven shellfish closure boundary (1970s–2015) data to document environmental trends that could influence reef ecology and service delivery. Over the last 60–120 years, the entire NRE has shifted toward higher salinities. Consequently, oyster–reef communities have become less distinct across the estuary, manifest by 20%–27% lower species turnover and decreased faunal richness among NRE reefs in the 2010s relative to the 1950s. During the 2010s, NRE oyster–reef communities tended to cluster around a euhaline, intertidal-reef type more so than during the 1950s. This followed faunal expansions farther up estuary and biological degradation of subtidal reefs as NRE conditions became more marine and favorable for aggressive, reef-destroying taxa. In addition to these biological shifts, the area of suitable bottom on which subtidal reefs persist (contracting due to up-estuary intrusion of marine waters) and support human harvest (driven by water quality, eroding from up-estuary) has decreased by >75% since the natural history of NRE reefs was first explored. This “coastal squeeze” on harvestable subtidal oysters (reduced from a 4.5-km to a 0.75-km envelope along the NRE’s main axis) will likely have consequences regarding the economic incentives for future oyster conservation, as well as the suite of services delivered by remaining shellfish reefs (e.g., biodiversity maintenance, seafood supply). More broadly, these findings exemplify how “squeeze” may be a pervasive

concern for biogenic habitats along terrestrial or marine ecotones during an era of intense global change.

KEYWORDS

coastal narrowing, community assembly, ecotones, environmental stress gradients, saltwater intrusion, sea-level rise, shellfish closures, water quality

INTRODUCTION

Predicting the responses of ecosystems to global change is bolstered by understanding how the distributions of habitat-forming foundation species will shift across depths, elevations, or latitudes in response to changes in the position of suitable abiotic (fundamental niche) and biotic (realized niche) environmental conditions (Parmesan & Yohe, 2003; Snedaker, 1995). In particular, the global redistribution of more mobile terrestrial and marine taxa, manifest as whole-community shifts, may be linked to the distribution and prevalence of specific biogenic structures that serve as foraging, mating, refugia, and resting habitats (Asch & Erisman, 2018; Morley et al., 2018).

Over the next several decades, the impacts of global and local environmental shifts on biogenic habitats and associated communities may be magnified in dynamic coastal and estuarine environments where steep physicochemical and biological gradients exist between terrestrial and marine biomes (i.e., concentrated over meter-to-kilometer scales) (Gunter, 1956). For example, in response to relative sea-level rise (RSLR), temperate saltmarshes must either accrete vertically or transgress landward to persist (Morris et al., 2002). For saltmarshes otherwise capable of landward retreat in response to RSLR, human development/infrastructure can obstruct natural migration corridors. As such, these saltmarshes become “squeezed” between rising water on the seaward edge and coastal development on the landward margin, which truncates the zone of suitable environmental niche space (for saltmarshes, primarily vertical position relative to tidal inundation) (Doody, 2004; Pontee, 2013). Broadly speaking, the potential for squeeze may be a fundamentally relevant concern for all coastal biogenic habitats existing along strong gradients of temperature (rocky intertidal mussels [Barry et al., 1995]; kelp [Dayton, 1985]), light (seagrass [Ochieng et al., 2010]), dissolved oxygen (oysters [Lenihan & Peterson, 1998]), and storm-generated physical disturbance (coral [Fabricius et al., 2008]).

Estuaries are classically defined as the mixing zones between rivers and the sea; thus, salinity gradients are first-order drivers of local floral and faunal distributions (Odum, 1988). The eastern oyster (*Crassostrea virginica*) typically occupies subtidal zones within brackish

estuarine waters and intertidal zones in the lower estuary, where salinities are characteristically marine (Bahr & Lanier, 1981). Brackish water and aerial exposure ultimately provide these bivalves with refugia from enemies, such as predators, space competitors, and bioeroders, across these prominent environmental stress gradients (Fodrie et al., 2014; Walles et al., 2016).

Many temperate estuaries have been significantly modified by local development and global change, including by pervasive bathymetric modifications to accommodate commercial ports, development of intra-coastal waterway networks for boating/shipping transit, and marina construction, as well as RSLR and human population growth throughout most watersheds (Kennish, 2002). These activities are profoundly altering salinity and related water-quality regimes that may have cascading impacts on biogenic habitats such as oyster reefs. For instance, dredging/channelization generally increases tidal prism and, combined with RSLR, can lead to up-estuary saltwater intrusion (Ralston & Geyer, 2019). The Newport River Estuary (NRE) in North Carolina is a model system for exploring the consequences of these dynamics since many of these anthropogenic alterations define the NRE. Additionally, long-term place-based research—often linked to the presence of field stations (Able, 2016; Sagarin et al., 1999)—is a critical requisite for detailed investigations of multidecadal ecosystem change in response to human influences (e.g., fishing, urbanization, climate change). Owing to the extended presence of university and government marine labs nearby, studies documenting the distribution and natural history of eastern oyster reefs in the NRE date back to the 1880s (e.g., Grave, 1901, 1905; McDougall, 1943; Winslow, 1889). In conjunction with these biological reports, there is a substantial library of environmental data collected from the NRE over the last 100+ years. Regulated by the salinity regime of the NRE at the start of the 20th century, the transition from primarily intertidal reefs (lower estuary) to chiefly subtidal reefs (upper estuary) occurred 12 km upstream of Beaufort Inlet (the nearest ocean connection) a century ago (Grave, 1901, 1905) and was characterized for both economic and ecologic purposes. Grave (1905) postulated that subtidal oyster cultivation was feasible only upstream of this “line” due to periodic freshets that limited the distribution of common oyster enemies, such as

predatory marine gastropods and bioeroders. Additionally, Grave (1901) qualitatively noted the enhancement of biodiversity in the NRE due to the distinct invertebrate assemblages supported by subtidal versus intertidal reefs. Building from these observations, Wells (1961) sampled both subtidal and intertidal oyster reefs of the mesohaline and euhaline (5–35 practical salinity units) regions of the NRE and quantified the distribution of 300+ reef-associated fauna across this salinity gradient.

To assess how oyster–reef communities in the NRE have changed in nature or distribution over decadal scales, potentially in response to human-driven salinity shifts, we resampled reefs during 2013–2015 that were previously sampled in 1955–1956 by Wells (1961). We made direct comparisons of reef-associated faunal communities between 1955–1956 and 2013–2015 to evaluate taxon- and assemblage-level distributions across the NRE during this six-decade interval. We combined these faunal data with multidecadal NRE salinity records to address the following questions: (1) Has the structure and distribution of NRE oyster–reef communities changed over time? (2) Which faunal groups account for differences among reefs or through time? and (3) For any changes we observed across estuary or time, did faunal shifts correspond to spatiotemporal patterns of NRE salinity gradients? We also incorporated ancillary data, such as presence/absence of intertidal and subtidal reefs during the 1880–2015 period and water-quality closures throughout the historical record to consider the following additional questions: (4) Has the transition line between subtidal and intertidal reefs shifted up or down estuary in response to changes in salinity regimes? and (5) How have water-quality closures interacted with the subtidal–intertidal reef transition line to determine the extent of NRE bottom suitable for restoration, maintenance, and cultivation of subtidal reefs.

METHODS

Study system and field collections

Despite modifications, the NRE remains a shallow (1-m mean depth at mean low water) drowned-river system covering 134 km² and defined by extensive intertidal mudflat and saltmarsh areas (Kirby-Smith & Costlow, 1989). The NRE extends 16.5 km from Beaufort Inlet to the bayhead delta, receives freshwater from a relatively small watershed (250 km²) via a 15-km long main-stem river (~20 m wide), and has a 0.75-m tidal range (Ensign et al., 2013). In historical surveys, subtidal reefs dominated the upper 4.5 km of the NRE across broad shallow flats, although the crests of these reefs

could/can infrequently (as a proportion of total reef extent) extend intertidally along raised bars given the tidal range in this section of the NRE (Grave, 1901, 1905; Winslow, 1889). Conversely, intertidal reefs with shallow subtidal flanks dominated the lower 12 km. Wells (1961) sampled oyster–reef associated communities at five sites throughout the NRE during 1955–1956, with the specific focus of relating the composition and distribution of fauna to salinity. In the lower, euhaline portion of the estuary (based on measurements made at the time of study), Wells (1961) sampled Shark Shoal (SS) and Pivers Island (PI) (Figure 1). In the polyhaline NRE, Wells (1961) sampled Gallants Point (GP) and White Rock (WR) (Figure 1). Near the mesohaline–polyhaline transition in the upper NRE, Wells (1961) sampled Cross Rock (CR) (Figure 1). We conducted visits to all reefs specifically described in Winslow (1889), Grave (1905), and Wells (1961) to qualitatively determine whether reefs remained extant as of 2013 (Table 1). Since Wells (1961), the SS and GP sites have been dramatically altered with near-total loss of oyster reefs: SS has been transformed into Radio Island via dredge-spoil deposits from the adjacent channel serving the Port of Morehead City, and GP is now occupied by multiple boat marinas and a bridge span over the former oyster–reef sites (Table 1). Therefore, we focused our 2010s sampling revisits on Wells' (1961) PI, WR, and CR sites, which nearly span the entire NRE (Figure 1). Based on our interpretation of Wells' (1961) site descriptions, the specific patch of reef he sampled for WR was absent at the time of our 2013–2015 revisits; therefore, we moved 1 km south-southwest to sample a comparable reef in the middle region of the estuary termed White Rock replacement (WRR) (Figure 1).

To sample oyster–reef associated communities, Wells (1961) employed a simple sampling methodology: *“During each station visit, a gallon [3.78-liter] jar was filled with oysters, their associates, and shell. An effort was made to collect from each of the minor variations in the habitat, such as tidal zones, and to have the sample reflect the faunal diversity of the bed.”* During 1955–1956, Wells (1961) collected 13, 6, and 15 samples at PI, WR, and CR, respectively. Collections from PI and CR spanned all seasons, while WR collections were made only during summer (Table 1). Samples were returned to the laboratory, where Wells (1961) identified all fauna at the lowest taxonomic level possible, which was ultimately published as a taxon-specific presence/absence matrix across reefs and over time. To generate data comparable with those of Wells (1961), we followed the same collection approach and collected material from the reef crest down to the reef base (including subtidal fringe as possible) to capture faunal composition and diversity on

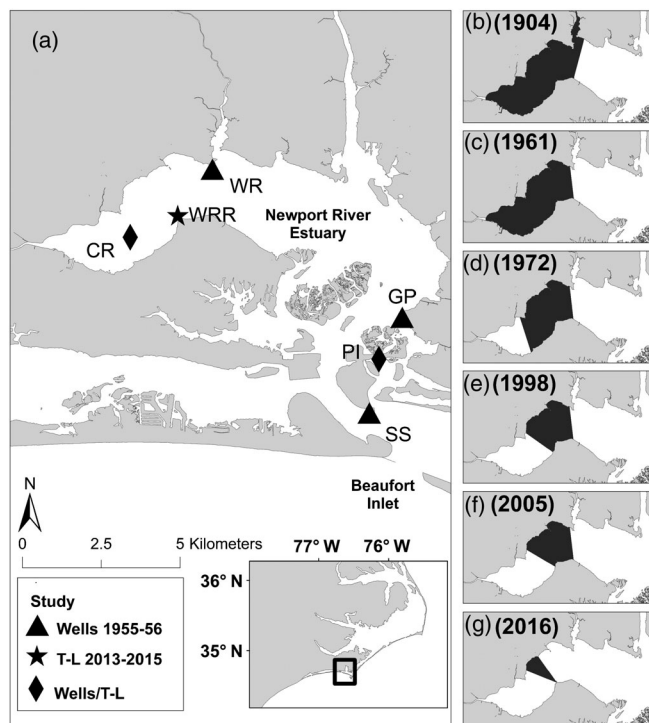


FIGURE 1 (a) Eastern oyster (*Crassostrea virginica*) reefs in Newport River Estuary (NRE) sampled for reef-associated fauna during 1955–1956 (Wells, 1961) or 2013–2015 to assess multidecadal stability or change in this temperate coastal system. Reef sites included Shark Shoal (SS), Pivers Island (PI), Gallants Point (GP), White Rock (WR) or White Rock replacement (WRR), and Cross Rock (CR). Distinct symbols represent reefs sampled during the 1950s only, 2010s only, or 1950s and 2010s. (b–g) Area within NRE, 1904–present, where subtidal oysters can persist and be harvested for human consumption (black shaded regions). This area, which has experienced “coastal squeeze” over time, is defined by the subtidal–intertidal oyster transition zone (downstream margin) and shellfish harvest closure boundaries (upstream margin) and is shown at the time of (b) Grave’s (1905) and (c) Wells’ (1961) reef surveys; following (d) water-quality-related permanent shellfish harvest closures in 1972; with downstream extensions of permanent harvest closures in (e) 1998 and (f) 2005. In (g) 2016, this area appeared to have truncated further in accordance with reef surveys during 2013–2015, as well as undergone an additional downstream extension of permanent harvest closures

each reef. The number of samples we collected was comparable to Wells (1961): 16 trips to both PI and CR that spanned all seasons, and 14 trips to WRR spanning all seasons (Table 1). Generally, 2013–2015 sampling followed a bimonthly schedule (a single 3.78-L sample per reef per interval), with some deviations due to factors such as storm events (e.g., Hurricane Arthur in 2014). Similarly, sampling during 1955–1956 occurred coincident with storm landfalls (Hurricanes Connie, Diane, and Ione 1955) (Wells, 1961). All 2013–2015 samples

were transported to the laboratory, where we identified fauna to the lowest taxonomic level possible.

Historical records of salinity, water-quality closures, and reef longevity

Given the central role of salinity in regulating across-estuary distributions of reef types (subtidal versus intertidal) and associated fauna (reviewed in Baggett et al. [2015] and Walles et al. [2016]), we explored if and how salinity gradients have shifted in the NRE over time by coalescing a 1913–2015 time series from multiple published and regulatory agency sources. To leverage these historical salinity data and provide greater context for our faunal investigations, we evaluated all known records taken from within 0.5 km of PI, WR/WRR, or CR reefs (separately for each site). For PI, sources included (1) Hoyt (1920), who reported monthly salinity recordings during 1913–1914 ($N = 42$); (2) Wells (1961), who reported monthly salinity observations during 1955–1956 ($N = 124$ across all sites); and (3) North Carolina Division of Marine Fisheries Shellfish Sanitation (NCDMFSS) program, which provided point-measure salinities at fixed NRE sampling sites during 1965–2015 ($N = 1900$ across all sites) (NCDEQ, 2021). Generally, NCDMFSS sampling near each reef site followed a biweekly schedule, although sampling frequency ranged from 0 to 60 observations in any given year based on management needs and weather patterns throughout the survey. A final source is (4) the present study, which provided point-measure salinities taken during faunal sampling efforts at each reef site ($N = 44$ across all sites). For WR/WRR and CR, salinity data were limited to the aforementioned Sources 2–4. We could not completely standardize these salinity data in terms of sampling seasonality, storm events, diel periodicity, and water-level context. As a check against potential biases associated with this low degree of standardization, we also explored salinity patterns in the NRE using only the NCDMFSS database. Conclusions drawn from that more-standardized subset of salinity data regarding spatiotemporal patterns are entirely consistent with conclusions drawn from the complete, coalesced NRE salinity record.

NCDMFSS also provided records regarding the boundaries of permanent shellfish harvest closure areas in the upper NRE in response to changes in water quality over time. These closures are mandated by the Food and Drug Administration when counts of indicator fecal coliform bacteria exceed a geometric mean of 14 most probable number (MPN) per 100 ml or a 90th-percentile reading >43 MPN per 100 ml (National Shellfish Sanitation Program, 2017).

TABLE 1 Summary of Newport River Estuary oyster reef site characteristics. Insights from Grave (1901) are provided to give historical context to oyster reef sites relevant to the multidecadal analysis

Reef	Grave (1901)	Wells (1961)	This study 2013–2015	Distance to inlet (km)	Reef type	Aerial exposure regime	Months (January–December noted as 1–12) sampled	
							Wells (1961)	Current study
Shark Shoal	Not noted	Extant	Nonextant	1.8	Groin	Intertidal, subtidal fringe	1955: 7, 8, 9, 10, 11 1956: 1, 2, 3, 4, 5, 6, 7, 9	Not sampled
Pivers Island	Not noted	Extant	Extant	3.5	Fringing	Intertidal, subtidal fringe	1955: 7, 8, 9, 10, 11 1956: 1, 2, 3, 4, 5, 6, 7, 9, 10	2013: 7, 8, 10, 12 2014: 2, 4, 6, 8, 10 2015: 1, 3, 5, 7, 10, 10, 12
Gallants Point	Not noted	Extant	Nonextant	6.6	Bar	Intertidal, subtidal fringe	1955: 7, 8, 9 1956: 7, 8, 9	Not sampled
Green	Extant	Not noted	Nonextant	9.9	Patch	Not noted	Not sampled	Not sampled
White Rock	Extant	Extant	Nonextant	12.5	Patch	Intertidal, subtidal	1955: 7, 8, 8, 9 1956: 8, 9	Not sampled
White Rock replacement	Extant	Not noted	Extant	13.1	Patch	Intertidal	Not sampled	2013: 7, 8, 10, 12 2014: 2, 4, 6, 8, 10 2015: 1, 3, 5, 7, 12
Turtle Rock	Extant	Extant	Nonextant	13.4	Not noted	Not noted	Not sampled	Not sampled
Lime Kiln	Extant	Not noted	Extant	14.5	Flats connected to bar	Subtidal, few intertidal crests	Not sampled	Not sampled
Cross Rock	Extant	Extant	Extant	14.7	Flats connected to bar	Subtidal, few intertidal crests	1955: 5, 7, 8, 8, 9, 10, 11 1956: 1, 2, 4, 5, 6, 7, 9, 10	2013: 7, 8, 10, 12 2014: 2, 4, 6, 8, 10 2015: 1, 3, 5, 7, 10, 10, 12

Statistical analyses

We used several multivariate statistical approaches to examine patterns in oyster-reef associated faunal communities across the NRE in the 1950s and 2010s. All multivariate analyses were based on the presence/absence of taxa in individual samples. For Wells (1961) to include a species in his publication, that taxon had to be present in at least 20% of all samples. To achieve as accurate a comparison as possible, we also excluded “rare” or transient taxa observed in <20% of samples collected during 2013–2015. To not overestimate differences between the 1950s and 2010s, however, all species reported by Wells (1961) were included in the 2013–2015 database regardless of their occurrence frequency in our sampling. Oysters were themselves excluded from the community analysis because they were present in every sample and, thus, would have no impact on multivariate differences among communities. To avoid reporting spurious differences between communities over time driven by differences in

taxonomic expertise among researchers or shifts in accepted phylogenetic relationships at the species or genus level, we conducted all analyses at the family level, except Actiniara (anemones) and Nemertea (ribbon worms), which were grouped at the Order and Phylum levels, respectively. At this resolution, we are confident that faunal identities were conserved over time.

To evaluate evidence of statistical differences among samples, we used a crossed permutational multivariate analysis of variance (PERMANOVA) with NRE site (PI, WR/WRR, CR), period (1950s, 2010s), and site $\times$ period as fixed factors. PERMANOVA post-hoc procedures were used to evaluate pairwise differences as necessary based on statistical results in PERMANOVA. To determine which families were driving differences among NRE sites and between study periods, we calculated similarity percentages (SIMPER) among samples. We also used non-metric multidimensional scaling (nMDS) of reef-associated faunal presence/absence to explore similarity in samples collected across the NRE during 1955–1956

and 2013–2015. Environmental and temporal variables of salinity, Julian Day (a proxy for seasonal effects), and year were fitted to the data using ENVFIT to determine how these variables correlated with observed community groupings in nMDS space. The salinity value assigned to a particular sample was taken from the corresponding spot measures taken by Wells (1961) or our research team at the time of sampling at each reef.

To assess community turnover (beta diversity) at multiple scales, we calculated multivariate dispersions for within-reef samples, across the NRE, and between study periods (Anderson et al., 2006). To further quantify taxonomic turnover among NRE sites (i.e., beta diversity across PI, WR/WRR, and CR) as an indicator of the strength of environmental/community gradients across these reefs and through time, we calculated Jaccard distances (1-Jaccard index) for all PI-WR/WRR, PI-CR, and WR/WRR-CR pairwise combinations of samples collected in the 1950s and 2010s, with time periods handled separately. Using each sample-by-sample dissimilarity score as a replicate for site-pair comparisons, we assessed statistical differences in between-site turnover during the 1950s versus the 2010s using the Mann-Whitney U test (separate tests for PI vs. WR/WRR, PI vs. CR, WR/WRR vs. CR). This nonparametric approach was used because variances of site-versus-site Jaccard scores were heteroscedastic between study periods for all three site-pair comparisons.

To further evaluate the statistical correlation between NRE salinity gradients and the level of taxonomic turnover across reefs, and through time, we conducted a single Mantel test. This correlation paired two variables drawn from separate but identically structured matrices (i.e., site-pair $\times$ period): Jaccard dissimilarity in faunal communities and Euclidean differences in mean salinities across sites and time (i.e., 1950s vs. 2010s). Mean salinities for each site $\times$ period were calculated from the replicate point-based measurements taken during each sampling visit at each site in Wells (1961) or the present study, separately.

To evaluate multidecadal salinity patterns across the NRE, we calculated annual minimum, maximum, and mean (as possible) salinities from monthly values provided by each data source for PI, WR/WRR, and CR. For PI, least-squares regressions were conducted for annual minimum, maximum, and mean salinities during 1913–2015. For WR/WRR and CR, least-squares regressions were conducted for annual minimum, maximum, and mean salinities during 1955–2015.

We used the following statistical packages to explore spatiotemporal dynamics of NRE oyster reef communities: nMDS, PERMANOVA, SIMPER, ENVFIT, PERMDISP, Jaccard distances, and the Mantel test were conducted

using the R package, *vegan* version 2.5–7 (Oksanen et al., 2019). Least-squares regressions and Mann-Whitney U tests were conducted using R version 4.04 (R Core Team, 2020). Patterns of water-quality closures and reef persistence through time in the NRE did not require quantitative statistical tests.

RESULTS

Spatiotemporal patterns of reef-associated fauna

There were notable differences in NRE reef-associated faunal communities over time. Fewer taxa (families or lowest possible taxonomic resolution) of reef-associated fauna were collected in 2013–2015 ($N = 36$) than in 1955–1956 ($N = 54$). Wells (1961) collected 52, 44, and 33 taxa at PI, WR, and CR, respectively. By comparison, during 2013–2015 we collected 27, 26, and 26 taxa at PI, WRR, and CR, respectively.

Given these community-level differences, 1955–1956 and 2013–2015 faunal samples were distinct in multivariate space (SIMPER = 56% different; PERMANOVA $df = 1$, $F = 18.67$, $p < 0.001$) (Figure 2). Indeed, sample year (nMDS Axis 1) and salinity (nMDS Axis 2), but not Julian Day, were significantly correlated with community variability (year: $R^2 = 0.700$, $p < 0.001$; salinity: $R^2 = 0.366$, $p < 0.001$; Julian: $R^2 = 0.002$, $p = 0.91$). Taxa contributing the most to the community difference between 1955–1956 and 2013–2015 (50% cumulative contribution) were hydrozoa (Campanulariidae), bryozoans (Electridae, Victorellidae, and Bugulidae), sedentary polychaetes (Sabellariidae and Spionidae), burrowing amphipods (Corophiidae), sessile protists (Folliculinidae), anemones (*Actiniaria* spp.), errant polychaetes (Phyllodocidae and Eunicidae), bivalves (Veneridae), ribbon worms (Nemertea), gastropods (Pyramidellidae), isopods (Sphaeromatidae), and parasitic barnacles (Sacculinidae).

We documented up-estuary movement of several taxa from 1955–1956 to 2013–2015. Four families (Tellinid clams, Tubificid worms, Sacculinid barnacles, and Muricid snails) were observed at WRR in 2013–2015 that were not at WR in 1955–1956. Notably, Atlantic oyster drills (*Urosalpinx cinerea*, Muricidae), an important predator of oyster spat (Chestnut & Fahy, 1953), were collected in 21% of samples at WRR in 2013–2015 but absent in Wells' (1961) surveys. Wells (1961), however, did record oyster drills in 66% of samples at GP, 7 km downstream from WRR, and 86% of samples at PI, 10 km downstream from WRR. Together, these data indicate an upriver shift in drill distribution. We also documented

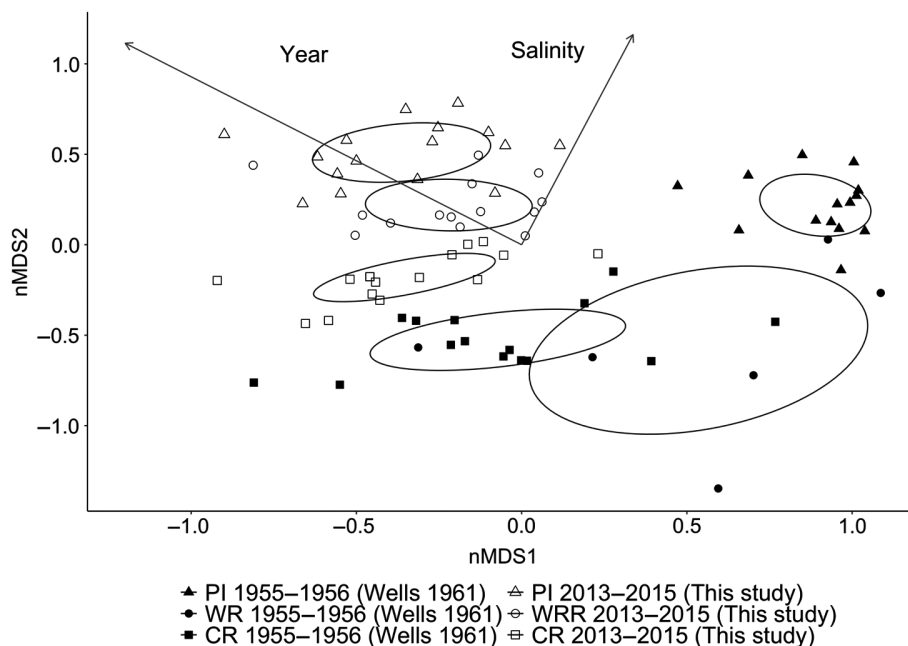


FIGURE 2 Community composition patterns of reef-associated fauna across NRE during 1955–1956 and 2013–2015 based on nonmetric multidimensional scaling (nMDS, stress = 0.15). Each datum represents a single reef sample, with symbol shapes and fill (open/closed) delineating reef identity and sampling period. Environmental factors that correlate with faunal community patterns are included as vectors (moving in the direction of increasing year and salinity across nMDS space). Ellipses represent 95% confidence intervals for each of the six site $\times$ period groups. Oyster reefs included Pivers Island (PI), White Rock (WR) or White Rock replacement (WRR), and Cross Rock (CR)

the up-estuary migration of five taxa from WR in 1955–1956 to CR in 2013–2015, including Caprellid amphipods, Leptocheliids, Venerid clams, and Eunicid and Terebellid polychaetes.

Despite these overarching differences between study periods, some things appeared consistent between the 1950s and 2010s. Common reef-associated fauna in the NRE across all sites and both study periods included barnacles, Balanidae (*Amphibalanus eburneus*); amphipods, Melitidae (*Melita nitida* and *Dulichieilla appendiculata*); xanthid crabs, Panopeidae (*Panopeus herbstii* and *Eurypanopeus depressus*); gastropods, Calyptraeidae (*Crepidula* spp.) and Pyramidellidae (*Boonea impressa*); polychaetes, Nereididae (*Alitta succinea* and *Nereis falsa*); and Mytilid bivalves (*Geukensia demissa* and *Brachidontes exustus*) (Table 2). Spionid polychaetes (*Polydora websteri*) were abundant at all sites across both studies, except PI in 1955–1956 (25% of samples). Anemones (*Actiniaria* spp.) and Venerids (*Mercenaria* spp.) were similarly abundant at all sites in both studies, except CR in 1955–1956 (13.3% and 0%, respectively). Notably, PI, WR/WRR, and CR could be distinguished from each other in multivariate community space during both 1955–1956 and 2013–2015 (Figure 2). Moreover, during both the 1950s and 2010s (as with sampling overall), community composition was significantly correlated with salinity, primarily across nMDS Axis 2. Unsurprisingly, PI samples were typically associated with

higher salinities, CR samples were generally associated with lower salinities, and WR/WRR samples fell in between PI and CR extremes.

Fundamentally related to our core questions, among-site faunal differences for PI, WR/WRR, and CR truncated over time. Indeed, between-reef dispersions (mean distance of samples to group centroid) during 2013–2015 were 14% smaller than during 1955–1956 ($F = 0.952$, $p < 0.001$). Relatedly, 2013–2015 samples/sites appeared to cluster more tightly in nMDS space that was correlated with higher salinities, relative to 1955–1956 analogs (Figure 2).

These patterns were also clear in species-turnover metrics among reef sites (Figure 3). Jaccard distance between PI and WR in 1955–1956 (52%) was nearly $1.4\times$ greater than PI-versus-WRR distance in 2013–2015 (38%) ($U = -6.62$, $p < 0.001$). Between PI and CR, Jaccard distance was $1.25\times$ greater in 1955–1956 (60%) than in 2013–2015 (48%) ($U = -7.23$, $p < 0.001$). Similarly, WR versus CR Jaccard distance in 1955–1956 (49%) was $\sim 1.3\times$ higher than for WRR versus CR in 2013–2015 (37%) ($U = -5.89$, $p < 0.001$). Notably, the degree of faunal turnover (Jaccard distances) among reefs and over time was significantly correlated with the magnitude of salinity difference recorded between reef-sampling events (Mantel $R = 0.16$, $p < 0.001$).

TABLE 2 Oyster–reef associated fauna and their frequencies of occurrence (0%–100% scale) in Newport River Estuary (NRE) during 1955–1956 (Wells, 1961) and 2013–2015 surveys. Oyster reefs included Pivers Island (PI), White Rock (WR) or White Rock replacement (WRR), and Cross Rock (CR). Taxa reported by Wells (1961) include those in >20% of all NRE samples (five sites), although 1955–1956 frequency of occurrence may be <20% across the three sites included here

Taxonomic group	1955–1956			2013–2015		
	PI	WR	CR	PI	WRR	CR
Arthropoda						
Amphipoda						
Caprellidae	86	33	0	0	0	13
Corophiidae	57	67	87	0	14	94
Gammaridae	64	33	20	6	7	6
Melitidae	100	100	93	38	79	88
Tanaidacea						
Leptocheliidae	36	33	0	0	0	13
Isopoda						
Sphaeromatidae	21	33	93	13	100	94
Decapoda						
Diogenidae	36	17	0	6	0	0
Panopeidae	100	67	80	100	100	100
Diptera						
Tabanidae	0	17	20	6	0	0
Maxillopoda						
Balanidae	93	100	87	81	79	88
Chtamalidae	36	0	0	0	0	0
Sacculinidae	0	0	0	44	79	56
Pycnogonida						
Nymphonidae	29	0	0	0	0	0
Bryozoa						
Cheilostomatida						
Bugulidae	64	67	20	6	7	0
Electridae	29	100	93	0	0	0
Membraniporidae	86	17	0	0	0	0
Schizoporellidae	86	17	0	0	0	0
Ctenostomatida	0	0	0	0	0	0
Alcyonidiidae	21	67	7	0	0	0
Nolellidae	0	33	0	0	0	0
Victorellidae	29	33	47	0	0	0
Ciliophora						
Heterotrichea						
Folliculinidae	93	67	53	0	0	0
Clitellata						

(Continues)

TABLE 2 (Continued)

Taxonomic group	1955–1956			2013–2015		
	PI	WR	CR	PI	WRR	CR
Oligochaeta						
Tubificidae	0	0	0	6	21	44
Cnidaria						
Anthozoa						
Actiniaria spp.	100	33	13	38	50	38
Gorgoniidae	57	17	0	0	0	0
Hydrozoa						
Campanulariidae	50	67	47	0	0	0
Mollusca						
Bivalvia						
Anomiidae	36	33	7	6	0	0
Arcidae	21	0	0	0	0	0
Mytilidae	100	50	100	100	100	100
Pholadidae	43	0	0	0	0	0
Tellinidae	0	0	0	0	7	19
Veneridae	57	33	0	38	57	75
Gastropoda						
Buccinidae	7	0	0	0	0	0
Calyptraeidae	36	50	13	0	43	25
Cerithiidae	57	0	0	0	0	0
Columbellidae	93	50	7	0	7	0
Fascioliariidae	50	0	0	0	0	0
Fissurellidae	71	0	0	6	0	0
Muricidae	86	0	0	6	21	0
Pyramidellidae	100	33	33	75	79	38
Nemertea						
Nemertea spp.	86	50	13	0	21	25
Platyhelminthes						
Polycladida						
Stylochidae	43	17	20	0	0	0
Polychaeta						
Errantia						
Eunicidae	93	17	0	94	79	6
Nereididae	100	100	100	100	100	100
Phyllodocidae	100	33	13	44	79	19
Syllidae	64	33	7	6	0	0
Sedentaria						
Capitellidae	71	33	20	6	0	19
Sabellariidae	93	50	13	0	0	0
Sabellidae	86	50	13	13	0	6
Serpulidae	100	50	27	25	36	13

(Continues)

TABLE 2 (Continued)

Taxonomic group	1955–1956			2013–2015		
	PI	WR	CR	PI	WRR	CR
Spionidae	79	50	80	25	64	69
Terebellidae	79	17	0	13	21	6
Porifera						
Demospongia						
Chalinidae	29	33	0	0	0	0
Clionaidae	100	33	7	6	0	0
Halichondriidae	93	0	0	0	0	0
Tunicata						
Ascidacea						
Molgulidae	57	50	20	0	7	0
Styelidae	29	50	7	0	0	0
Vertebrata						
Actinopterygii						
Gobiidae	7	17	20	0	14	44

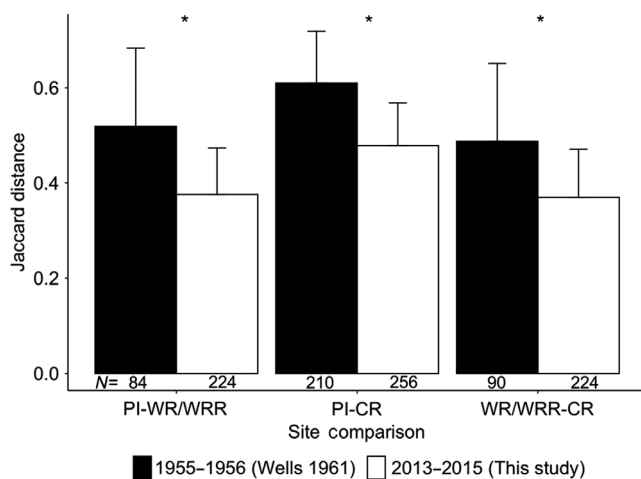


FIGURE 3 Jaccard distance as a measure of between-reef species turnover (beta diversity) in 1955–1956 (Wells, 1961) and 2013–2015. Data are presented as means $\pm$ 1 SD. Oyster reefs included Pivers Island (PI), White Rock (WR) or White Rock replacement (WRR), and Cross Rock (CR). Statistically significant ($\alpha = 0.05$) differences in species turnover across PI–WR/WRR, PI–CR, and WR/WRR–CR in the 1950s versus 2010s, based on Mann–Whitney U analyses, are indicated by asterisks. Sample sizes used for between-reef comparisons are also provided

Salinity, water quality, and reef persistence

NRE salinity regimes have shifted over multidecadal scales in terms of extremes and averages. Across all sites,

only PI, the site nearest to Beaufort Inlet, did not experience a shift in annual mean and maximum salinities over time (mean: $R^2 = 0.02$, $p = 0.37$; maximum: $R^2 = 0.02$, $p = 0.18$); both metrics consistently approached full marine salinity throughout the entire record (Figure 4a). Conversely, annual minimum salinities recorded at PI increased notably across the 1913–2015 time span ($R^2 = 0.21$, $p = 0.01$), from annual minimum readings <20 parts per thousand (ppt) in the early to mid-20th century toward >25 ppt by 2015 (Figure 4a). At the mid-estuary WR/WRR reefs, annual mean, maximum, and minimum salinities all increased across 1955–2015 (mean: $R^2 = 0.26$, $p < 0.001$; maximum: $R^2 = 0.20$, $p < 0.01$; minimum: $R^2 = 0.097$, $p < 0.05$). Early in the record, annual salinities at WR/WRR typically ranged between 10 and 25 ppt, while by the end of the record salinities consistently ranged between 15 and 30 ppt (Figure 4b). At CR, our farthest upstream NRE study site, annual mean, maximum, and minimum salinities also rose through time, but only mean and maximum trends were statistically unambiguous (mean: $R^2 = 0.27$, $p < 0.001$; maximum: $R^2 = 0.21$, $p < 0.01$; minimum: $R^2 = 0.07$, $p = 0.07$). Salinities ranged between 5 and 20 ppt early in the record at CR and shifted toward 15–30 ppt by 2015 (Figure 4c).

Prior to the 1970s, the entire 16.5-km (along main stem) NRE was open to oyster harvest. Following a failure of the Newport Municipal Sewage Treatment plant in 1969 and subsequent standardized water-quality sampling by NCDMFSS, shellfish harvest was permanently prohibited just upstream of CR in 1972. This closure line, running perpendicular to the NRE main-stem axis, was located 15.5 km from Beaufort Inlet. In 1998, as water-quality testing continued, this closure line moved 0.9 km down estuary. In 2005, the closure line moved an additional 0.25 km down estuary. Finally, as we were concluding our reef sampling in 2015, the closure line moved once more, 0.1 km farther down estuary. By 2016, only the lower 14.25 km of the NRE was open to oyster harvest and cultivation. Finally, reefs such as Green Reef and Turtle Rock mapped by Grave (1901), as well as SS, GP, and WR sampled by Wells (1961), were extirpated by 2013 (Table 1). In addition, across 2013–2015, the subtidal fringes of PI no longer matched the spatial extent as described in Wells (1961).

DISCUSSION

Temperate oyster reefs and associated fauna in the NRE have exhibited remarkable changes in composition and distribution during the last 60–120 years. These changes have been driven primarily by shifts in underlying abiotic

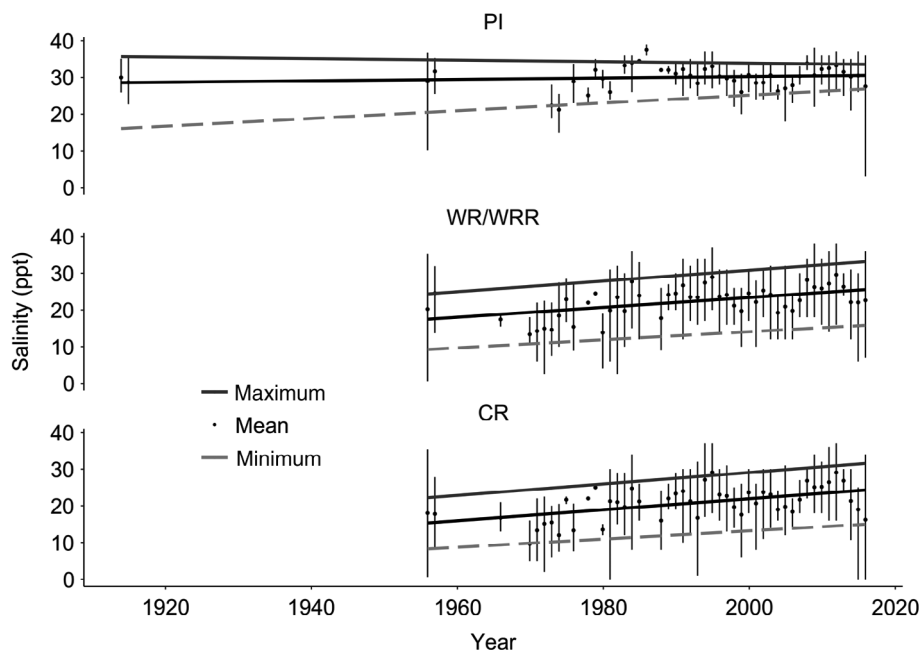


FIGURE 4 Multidecadal trends in annual mean, maximum, and minimum salinity across the Newport River Estuary, in the vicinity of Pivers Island (PI), White Rock and White Rock replacement (WR/WRR), and Cross Rock (CR) oyster reefs. For PI, sources included Hoyt (1920), Wells (1961), North Carolina Division of Marine Fisheries Shellfish Sanitation (NCDMFSS) program, and the present study. For WR/WRR and CR, salinity data were sourced from Wells (1961), NCDMFSS, and the present study. In each panel, data are depicted as a scatterplot for annual means (solid black line), with bars extending above and below mean values to represent annual maximum and minimum salinity records, respectively. For each reef, solid and dashed gray lines show the least-squares regressions for annual maximum and minimum values, respectively

environmental gradients (i.e., salinity). These dynamics have occurred coincidentally with NRE water-quality degradation, resulting in a squeeze on subtidal, harvestable oyster reefs along the river-to-ocean axis. This oyster-reef squeeze phenomenon is analogous to the compression of suitable habitat for saltmarsh plants along developed estuarine shorelines in an age of accelerated sea-level rise (Pontee, 2013). Building from these examples, we stress that coastal squeeze is likely to broadly impact shallow-water and intertidal biogenic habitats that exist along steep environmental gradients and are subject to multiple anthropogenic perturbations. More broadly, we speculate that the distribution and extent of many foundation species existing primarily along ecotones in terrestrial or aquatic systems may be relatively sensitive to anthropogenic environmental perturbations.

The squeeze on NRE oyster reefs has manifested in two ways. First, reef communities along the NRE main axis have become less distinct from each other since the 1950s, with between-reef faunal turnover (beta-diversity) and whole-estuary richness (alpha diversity for the entire NRE) decreasing over time. Second, the area within the NRE in which subtidal-reef communities can persist (ultimately driven by higher-salinity waters intruding at the down-estuary margin) and support human harvest

(driven by expanding water quality degradation, impinging along the up-estuary margin) has decreased by >75% since the distribution and natural history of reefs in this system were described a century ago (Grave, 1901; Winslow, 1889). These community shifts corresponded to a long-term decrease in NRE environmental heterogeneity (i.e., estuarine salinity gradient), which has been reported to be a fundamental driver of spatial community turnover in diverse marine and terrestrial contexts (Chase & Myers, 2011). Throughout the NRE, reefs have become more marine and intertidal in physical nature and faunal composition. Notably, this homogenization of reef communities decreased NRE-scale species richness, contrary to the paradigm of increased species diversity associated with higher salinities, versus brackish waters, in estuarine systems (Odum, 1988).

Without planned manipulative experiments at whole-estuary scales to evaluate (i.e., serially discount) a suite of oyster stressors, the links we have drawn between oyster-reef community patterns and salinity through time are somewhat correlative by nature. In the context of a broader literature that greatly informs our observations, however, we consider it reasonable to acknowledge salinity as a first-order driver of oyster reef dynamics in the NRE. Indeed, for >100 years the distribution of oyster

reefs in the context of salinity regimes has been realized (e.g., Baggett et al., 2015; Winslow, 1889), with mechanisms documented at physiological (La Peyre et al., 2013) through community (reviewed in Bahr & Lanier [1981]) levels. Over geologic horizons, seaward–landward migration of reefs is also thought to be driven by RSLR and salinity regimes (Goff et al., 2015). Moreover, many of the reef-associated community members shifting their distribution in the NRE are defined by well-described salinity tolerance envelopes that match observed environmental shifts. In this regard, the mechanistic link we draw between shifts in salinity and reef communities based on long-term observations and well-documented organism–environment relationships is analogous to the direct connections made between poleward range shifts and global warming (sensu Morley et al. [2018]). Furthermore, existing data do not support other known oyster stressors such as disease, hypoxia/anoxia, or oversedimentation as limiting in this system (note that harvest impacts are also considered separately in what follows). Despite active wild-harvest and shellfish farming operations in the NRE throughout the last century, there are no reports of pervasive disease outbreaks in this system. The NRE is relatively shallow and well mixed, and bottom-water oxygen concentrations remain above 6 ml L^{-1} ($>75\%$ saturation) year round in the mesohaline and euhaline portions of the system (Kirby-Smith & Costlow, 1989). Finally, high sediment-accumulation rates over the last 50 years are confined to the head of the NRE (9.7 mm year^{-1}) and decrease downstream approaching RSLR in the vicinity of CR ($<5.0 \text{ mm year}^{-1}$) (Mattheus et al., 2009) and therefore would not explain the disproportionate loss of reefs farther down estuary.

While we also readily acknowledge the limits and dangers of extrapolating findings from a single study system too broadly (Hurlbert, 1984), we also emphasize that the basic relationship between salinity and the intertidal-versus-subtidal distribution of eastern oyster reefs is robust (Baggett et al., 2015; Walles et al., 2016). Therefore, any system experiencing natural or human-driven shifts in salinity might be informed by lessons drawn from multidecadal patterns in the NRE. In particular, we anticipate that other small drowned-river estuaries and tidal creeks with relatively small watersheds and little freshwater input, or estuaries in low-lying coastal plains particularly vulnerable to RSLR, are mostly likely to see upstream migration of eastern oyster reefs because those systems are most vulnerable to saltwater intrusion (excluding reverse estuaries). Additionally, even some large estuarine embayments, such as San Francisco Bay, are subject to saltwater intrusion given the system-specific levels of ocean connectivity and freshwater inflows (Cloern & Jassby, 2012). Conversely, some

estuaries with large watersheds and high freshwater inputs, such as Mobile Bay, may see increased frequency, duration, or magnitude of freshets (sensu Park et al. [2007]) that could potentially drive the area suitable for subtidal reefs seaward. Notably, the extent of bottom habitat suitable for subtidal reef persistence in these deeper, river-dominated systems may be more significantly regulated by the development and expansion of low-oxygen conditions (Lenihan & Peterson, 1998).

Multiple taxa contributed to the differences we observed across time and space, indicative of major community-level changes. For instance, we documented fewer desiccation-intolerant fauna during 2013–2015 across the NRE than did Wells (1961) and observed several species with distributions shifted up estuary between sampling in the 1950s and 2010s. For instance, the majority (17 of 25) of families that drove community-level differences at PI between 1955–1956 (Wells, 1961) and 2013–2015 are characteristically subtidal (Ruppert & Fox, 1989) and were less frequently observed in recent sampling relative to six decades ago. Most notably, these included taxa such as boring sponges (Clionaidae), gastropods (three families, including oyster drills), mossy and encrusting bryozoans (Bugulidae, Membraniporidae, Schizoporellidae), tunicates (Molgulidae), and sedentary polychaetes (Sabellariidae and Terebellidae). Similarly, 10 out of 23 families that drove community-level shifts between WR (1950s) and WRR (2010s) were characteristically subtidal and decreased in abundance over time, including mossy and encrusting bryozoans (Bugulidae, Electridae, and Alcyonidiidae), tunicates (Molgulidae and Styelidae), hydrozoans (Campanulariidae), and sedentary polychaetes (Sabellidae, Sabellariidae, and Serpulidae).

In practical terms, the loss of subtidal habitat at PI and WR/WRR is a proximate reason for both the NRE-wide shifts in community structure between 1955–1956 and 2013–2015, as well as the compositional squeezing of reef-associated communities across the NRE over time (i.e., decrease in across-NRE beta and entire-NRE alpha diversity). During the 1950s, most intertidal oyster reefs in the euhaline NRE also supported subtidal reef skirts that extended to depths $\sim 0.5 \text{ m}$ below mean low water (Wells, 1961). While these fringe subtidal reef habitats in the lower NRE may have been sourced primarily from dislodged oyster clumps shed from the intertidal sections of the reefs (combined with some in situ oyster recruitment/growth), these living biogenic structures persisted consistently enough to support subtidal reef-associated fauna, such as bryozoans and anemones. As salinity regimes in the to middle NRE have trended higher over time, we speculate that marine-adapted predators and pests, such as stone crabs (*Menippe mercenaria*), oyster drills, and *Clionid* boring sponges, exerted strong predation (Chestnut & Fahy, 1953) and bioerosion

(Lunz, 1943) pressures that extirpated subtidal reef structure and, subsequently, associated subtidal fauna. Even though the WRR station sampled during 2013–2015 was ~0.5 km farther up estuary relative to the WR reef sampled in the 1950s, we observed no significant subtidal fringe reef during our repeated, year-round visits to that site. By comparison, Wells (1961) specified that he was able to locate and sample from both intertidal and subtidal reef zones at WR.

Salinity-related shifts in faunal distributions also contributed to the decline in species turnover across the NRE over time. In 1955–1956, 10 families had up-estuary limits at WR, but by 2013–2015, five of those families had expanded their ranges up estuary to CR. Two of those families, Caprellids and Leptochellids, are closely associated with mossy bryozoans, such as *Bugula neritina*, which themselves are excluded by low salinity (Kitamura & Hirayama, 1985). Similarly, Eunicid polychaetes (Garcês & Pereira, 2011) and Venerid clams (Davis & Calabrese, 1964) both moved up estuary between the 1950s and 2010s and generally exhibit low fitness at salinities <15 ppt. Thus, the shift in mean salinities at CR from ~16 ppt in 1955–1956 to ~21 ppt in 2013–2015 would almost certainly reflect a decrease in abiotic stress for those taxa. Atlantic oyster drill distribution also shifted up estuary over the last 60+ years. In 1955–1956, drills were not documented farther up estuary than GP, but during 2013–2015 this species was routinely collected at WRR (~7 km up estuary from GP). Owing to the nature of our stratified-haphazard sampling across reef zones, and since drills typically avoid aerial exposure (Johnson & Smee, 2014), we suspect drills were collected from the low perimeter of the WRR reef. Still, their up-estuary expansion is doubly notable: drills are important low-intertidal and subtidal predators, and they are limited by salinities <18 ppt (Federighi, 1931; Manzi, 1970). While our statistical analyses operated at the family level, it was also significant that Wells (1961) collected the Balanid barnacle *Amphibalanus improvisus* at CR, while this species was absent during 2013–2015 throughout the NRE. *A. improvisus* populations are generally limited to areas with salinities <15 ppt (Gordon, 1969), which makes this species another potentially important “canary in the coal mine” reflecting saltwater intrusion into the upper NRE.

As in many human-dominated coastal systems, the drivers of NRE environmental change (e.g., salinity) are multifaceted and include channelization, sea-level rise, rainfall, and stormwater drainage infrastructure. Mechanical dredging of navigational channels alters coastline bathymetry and, in the case of the NRE, contributed to an increase in tidal range and tidal prism and decreased estuarine water residence time, potentially leading to saltwater intrusion (Johnston 1981). To serve

the state port in Morehead City, NC (in the lower NRE), Beaufort Inlet has been dredged to new depths at least five times since 1911 (years and depths: 1911, 6.0 m; 1936, 9.1 m; 1961, 10.7 m; 1978, 12.2 m; and 1994, 13.7 m), a cumulative inlet depth increase of more than 100% over time (Zervas, 2003). Zervas (2004) explored long-term trends in water levels across North Carolina and noted that three locations defined by inlet/channel dredging (Oregon Inlet, Beaufort Inlet, Wilmington) saw large and statistically significant increases in tidal ranges, while other locations saw no such increases. For the Beaufort Inlet–NRE system, this increase in tidal range has approached 10 cm since the early 1970s (Zervas, 2003), increasing ocean–estuary exchange during each tidal cycle. Additionally, to create the port and adjacent ship-turning basin, extensive deltaic salt marshes that formerly dampened connectivity between the NRE and ocean have been converted to relatively deep open water. Despite important differences in embayment size/orientation and tidal regime between systems, dredge/fill activities in Tampa Bay were projected to account for a 4-ppt increase in estuarine salinity (Zhu et al., 2015), akin to the long-term shifts in the NRE (>5 ppt). Exacerbating these changes, RSLR may change whole-estuary volume, with increased oceanic influence (i.e., potential saltwater intrusion if bottom bathymetry does not keep pace with SLR). Immediately adjacent to PI reefs, the National Oceanic and Atmospheric Administration (NOAA) Tide Station 8656483 revealed an 18-cm increase in mean sea level across 1973–2015 (~3.5 mm year⁻¹ RSLR) (NOAA, 2021). Finally, Beaufort Inlet dynamics may have also contributed to the salinity-driven faunal patterns we observed in 2013–2015 (but not long-term salinity patterns per se), as Beaufort Inlet widened from 1.15 km in 2010 to 1.75 km in 2015 (Seymour et al., 2019), furthering the coastal ocean influence in the NRE.

Alterations to the physical and environmental structure of estuaries also have implications for the magnitude and duration of freshwater pulses, called freshets, that are critical in limiting predators and pests that attack subtidal oysters (while oysters exhibit greater environmental tolerance for these low-salinity events) (Bahr & Lanier, 1981; sensu Bender et al., 1984). In this respect, the long-term increases in mean and minimum salinities in the NRE run counter to projected higher annual rainfall (Polsky et al., 2000) and the occurrence of wetter tropical cyclones (Paerl et al., 2019) in this region. This disconnect may be explained by the more rapid flushing of major pulse freshets in the NRE over time due to stormwater infrastructure, channelization, and RSLR. Following the passage of Hurricanes Connie and Diane in August, 1955 (combined, >400 mm rainfall), salinities throughout the entire NRE were ≤10 ppt for at least

14 consecutive days (Wells, 1961). This period of reduced salinity was highlighted by Wells (1961) to cause some oyster mortality throughout the NRE but, more notably, significant reductions in the abundance of oyster drills—including within subtidal fringing reefs near Beaufort Inlet (i.e., SS, PI, GP). By comparison, hurricane events during the 2013–2015 sampling effort—Dorian (2013, 200 mm), Arthur (2014, 100 mm), Ana (2015, 100 mm)—lowered NRE salinities by <3 ppt, while those modest effects were completely absent within two to three tidal cycles of storm passage (Tice-Lewis, 2018). We conclude that physical modifications of the NRE (e.g., channelization/ditching, higher sea levels), combined with the relatively small size of this watershed, outweigh the long-term changes in precipitation patterns in regulating local salinity regimes.

Following these shifts in estuarine environmental envelopes, the net movement of the subtidal–intertidal transition line appears to be up estuary in the NRE. We estimate that the transition line between subtidal (up-estuary) and intertidal (down-estuary) reefs has shifted from 12 to 13.5 km from Beaufort Inlet. This estimate is based on several lines of evidence, including the magnitude of community shifts at WR/WRR and CR; NRE-wide salinity patterns available from the NCDMFSS database (i.e., former and present-day locations of ~15 ppt within the estuary); current extent of subtidal and intertidal reefs in the NRE; and recent targeted experiments on the settlement, growth, and survival of subtidal oysters across the NRE (Sorg, 2017). In 2012, Sorg (2017) deployed oyster settlement substrates (e.g., oyster shell, marl) at five sites across the salinity gradient of the NRE running from near the PI site to up estuary of the CR site. By 2016, Sorg (2017) found that constructed reefs ~1 km up estuary of the WR/WRR sites exhibited substantial oyster mortality and reef degradation after 5 years due to extensive *Cliona celata* impacts, while two sites near CR demonstrated only modest bioerosion impacts. Additionally, constructed reef down estuary from WR/WRR failed to develop due largely to intense drill predation, bioerosion, and other mortalities of juvenile oysters (Sorg, 2017).

Present-day subtidal and intertidal reef distributions in the NRE are likely also impacted by the legacy of destructive shellfish harvest (zu Ermgassen et al., 2013). In this context, however, the patterns reported in Sorg (2017) are critical in highlighting the first-order importance of environmental drivers of oyster reef distributions because those constructed reefs were not subject to harvest pressure. Similarly, Powers et al. (2009) conducted surveys in the waters immediately around the NRE and found that oyster sanctuaries only met conservation success thresholds in euhaline regions when reefs were sited intertidally. Even in the absence of destructive

harvest, subtidal eastern oyster reefs did not, and do not, flourish in NRE regions defined by relatively high salinities. Thus, it seems unlikely that destructive harvest is the primary causal agent for the multidecadal patterns of reef distributions we have documented.

Long-term physicochemical alterations to the NRE have led to a form of coastal “narrowing” for subtidal reefs (Pontee, 2013) because the envelope of suitable environmental conditions for these reefs has migrated into the more constricted “neck” of the NRE. Given the strong preference for oysters with a subtidal morphology for human harvest (thicker, more rounded shells, with less cementing among oysters), this shift has important economic consequences. Moreover, water-quality degradation and resultant shellfish harvest closures—encroaching on oysters from the up-estuary end—have exacerbated the impacts of saltwater intrusion in the NRE regarding the benefits these reefs confer on humans. As such, subtidal, harvestable oyster reefs are not just experiencing narrowing driven by shifts in their downstream margin but, rather, a coastal squeeze along both upstream (water quality) and downstream (salinity) margins. While water-quality-related closures do provide shellfish with some de facto reserve protection in the upper regions of systems like the NRE, these closures also reduce seafood supply and economic opportunities for fishers. Moreover, there is often reduced incentive for shellfish habitat enhancement in closed waters, given the absence of potential direct economic returns related to future harvest (Fodrie et al., 2018). Furthermore, water-quality closures in the upper NRE are correlated with high sedimentation rates (Mattheus et al., 2009), which can further degrade oyster fitness under any conservation or restoration initiatives (Beck et al., 2011; Rothschild et al., 1994; Thomsen & McGlathery, 2006).

A century ago, the upper 4.5 km of the NRE was suitable for subtidal reef growth/persistence and harvest (Grave, 1905). Today, the combination of saltwater intrusion and water-quality closures has truncated this zone to an ~0.75-km remnant (along the main axis of estuary, Figure 1). Extrapolating these shifts forward suggests that the transition line for subtidal–intertidal reefs may someday occur up estuary of the shellfish-closure line, completely eliminating the area of the NRE suitable for subtidal reef persistence and harvest. While salinity records and reef presence/absence data suggest the up-estuary movement of this transition line over decadal scales, we consider it likely that the location of the break between subtidal and intertidal reefs may “wobble” in the NRE based on conditions during any few select years. For instance, the North Atlantic Oscillation (NAO) is correlated with winter rainfall patterns that should increase (positive NAO) or decrease (negative NAO) freshets in

the NRE over the course of 3- to 5-year horizons (Ottersen et al., 2001). However, we do not think that NAO phase had a major effect on the community-level shifts we observed because both the late 1950s and mid-2010s were defined by moderately negative NAO conditions (National Centers for Environmental Information on the NOAA website). Even more sporadically, strong wet storms, such as Hurricane Florence in 2018, could temporarily relocate the NRE transition line farther down estuary if oyster pests are extirpated following these major pulse events (*sensu* Wells [1961]).

Because the causes of NRE shifts are multifaceted in nature, so must be the actions to abate or reverse “squeeze” on oysters. Limiting saltwater intrusion will likely require increased efforts to halt global climate change and associated RSLR (Douglas, 1991). We also encourage managers to balance the economic drivers of channel/inlet dredging with the suite of environmental costs or benefits that these estuarine modifications stimulate—in particular, changes in the amount and quality of natural capital or infrastructure. We perceive that during the next decade, improving up-estuary water quality may be the most effective means of combatting squeeze on subtidal, harvestable oysters. This may be achieved through continued or expanded efforts to reduce non-point-source pollutants, improve wastewater/stormwater management, and implement low-impact development (Fodrie et al., 2018; Kennish, 2002). Finally, an important caveat is that subtidal reef enhancement projects in the middle and lower NRE may still support oyster harvests for a few years before predators, bioeroders, and pests degrade reef productivity, given lags between when oysters colonize available substrate and when their enemies subsequently recruit to young reefs (Fodrie et al., 2014). In this context, the use of novel, mobile substrates to support oyster settlement, survival, and growth could be explored. These mobile substrates could be periodically transferred upstream of the subtidal–intertidal transition (or just into the intertidal) to enhance subtidal reef structure, function, and persistence in the middle and lower NRE.

As subtidal reefs retreat up estuary, intertidal reefs are becoming a relatively more dominant component of this temperate estuary. Importantly, intertidal reefs are distinct from subtidal reefs in terms of the suite and magnitudes of ecosystem services they provide. In addition to being less marketable than their subtidal analogs, and owing primarily to their time out of water, intertidal reefs can be expected to provide relatively lower water filtration/purification capacity (Bahr & Lanier, 1981), reduced provision of habitat for mobile nekton (Byers et al., 2015), and decreased organic carbon burial (Fodrie et al., 2017). Yet intertidal reefs may be efficient nitrogen sinks (Piehler &

Smyth, 2011) and be significantly more important in shoreline stabilization (Grabowski et al., 2012) relative to subtidal counterparts. While intertidal reefs provide their own form of resilience to climate change via their ability to outpace RSLR (Rodriguez et al., 2014), it is also notable that reduced diversity of reef types and reef-associated fauna at the estuary scale may have complex, poorly understood impacts on ecological resilience in estuaries like the NRE (Elmqvist et al., 2003; Stachowicz et al., 2007). Using oyster reefs as a model, but applicable to all biogenic habitats that exist along strong environmental gradients, these dynamics exemplify how human-driven shifts in key abiotic properties, such as salinity, temperature, and water level, can have profound effects on coastal ecosystem structure and functions.

AUTHOR CONTRIBUTIONS

Maxwell Tice-Lewis, Niels L. Lindquist, Antonio B. Rodriguez, Clare M. Fieseler, and F. Joel Fodrie conceived the study. Maxwell Tice-Lewis, Y. Stacy Zhang, S. Gray Redding, and Quentin A. Walker conducted field and laboratory work. Maxwell Tice-Lewis and F. Joel Fodrie analyzed the data. Maxwell Tice-Lewis and F. Joel Fodrie drafted the manuscript and all coauthors provided editorial input. Comments from two anonymous reviewers helped strengthen and clarify the manuscript.

ACKNOWLEDGMENTS

We are grateful to field and laboratory hands, as well as J. Plumlee, who created Figure 1. Funding was provided by the North Carolina Marine Resources Fund (supported by the Division of Marine Fisheries Coastal Recreational Fishing License program) and the National Science Foundation (no. 1926395). This work was conducted under Protocol 16-123.0 of the University of North Carolina at Chapel Hill’s Office of Animal Care and Use.

CONFLICT OF INTEREST

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

Data (Tice-Lewis et al., 2022) are available from Dryad: <https://doi.org/10.5061/dryad.sj3tx9665>.

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How to cite this article: Tice-Lewis, Maxwell, Y. Stacy Zhang, S. Gray Redding, Niels L. Lindquist, Antonio B. Rodriguez, Clare M. Fieseler, Quentin A. Walker, and F. Joel Fodrie. 2022. “Coastal Squeeze on Temperate Reefs: Long-Term Shifts in Salinity, Water Quality, and Oyster-Associated Communities.” *Ecological Applications* e2609. <https://doi.org/10.1002/eap.2609>