Oyster reefs can outpace sea-level rise

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In the high-salinity seaward portions of estuaries, oysters seek refuge from predation, competition and disease in intertidal areas[1,2], but this sanctuary will be lost if vertical reef accretion cannot keep pace with sea-level rise (SLR). Oyster-reef abundance has already declined ~85% globally over the past 100 years, mainly from over harvesting[3,4], making any additional losses due to SLR cause for concern. Before any assessment of reef response to accelerated SLR can be made, direct measures of reef growth are necessary. Here, we present direct measurements of intertidal oyster-reef growth from cores and terrestrial lidar-derived digital elevation models. On the basis of our measurements collected within a mid-Atlantic estuary over a 15-year period, we developed a globally testable empirical model of intertidal oyster-reef accretion. We show that previous estimates of vertical reef growth, based on radiocarbon dates and bathymetric maps[5,6], may be greater than one order of magnitude too slow. The intertidal reefs we studied should be able to keep up with any future accelerated rate of SLR (ref. 7) and may even benefit from the additional subaqueous space allowing extended vertical accretion.

Oyster-reef communities (*Crassostrea virginica*) provide numerous ecosystem services, including production of oysters, water filtration[8,9], provision of habitat for fishes and crustaceans[10], shoreline stabilization[11,12], and maintenance of estuarine-water alkalinity[13]. In the face of natural and anthropogenic stressors, such as harvesting, degrading water quality, increasing rates of SLR, warming, disease, ocean acidification, and parasitism, reef habitats and associated services are becoming unsustainable. Loss of these reefs in estuaries that otherwise lack alternative hard substrates is a global problem[4].

SLR, in particular, threatens oyster reefs in the high-salinity seaward portions of estuaries because there, oysters seek refuge from biofouling (space competition), predation and disease in intertidal areas[1,2]. The importance of the intertidal area to individual oyster growth in lower estuaries is apparent from experimental work that has shown intertidal oysters grow 34% faster and exhibit an order of magnitude less fouling (percentage cover) than subtidal oysters[14]. Constructed subtidal reefs in no-harvest sanctuaries (North Carolina, USA) were also found to have few, if any, live oysters (mean density of 0–92 live oysters m^{-2}) after six years in euhaline waters, whereas intertidal reefs faired significantly better (200–225 live oysters m^{-2}; ref. 15). Restoration is a common mitigation option for historic oyster-reef loss, but project success with accelerating SLR will depend on a reef's ability to maintain an intertidal position. Model simulations presume that reef-accretion rates cannot exceed the rate of SLR, but parameterizations are not verified with direct measures of reef-scale growth[16,17]. Without direct measures of reef-scale growth, our ability to assess restoration and

conservation success, quantify the ecosystem services provided, and forecast impacts of climate change and SLR on oysters and other reef-forming shellfish species is impeded.

Although an oyster reef hosts a variety of organisms, reef structure is primarily composed of the biogenic sediment of oysters, including skeletal shell material and biodeposits[2,5,18,19] and allogenic sediment (for example, from resuspension, shoreline erosion and river discharge). Reef structure is controlled largely by reef accretion rates and erosion rates. Reef accretion is the result of sediment inputs including oyster-shell production, biodeposition and allogenic sediment, whereas reef erosion is mainly a function of bioerosion, dissolution, predation and hydrodynamic processes (Supplementary Fig. 1). Allogenic sedimentation contributes to reef accretion; however, if the sedimentation rate is too high, reef structure will be lost owing to burial and a decrease in oyster-shell production through a reduction in oyster settlement, survival and growth[20,21].

To investigate reef composition and growth, we examined cores collected in 2010–2011 from five intertidal experimental reefs constructed on sandflats in 1997 ($n = 3$) and 2000 ($n = 2$) in a coastal marine research reserve (Methods). Experimental reefs developed on 60 bushels of oyster shell (cultch) with initial dimensions of $3 \times 5 \times 0.15$ m ($W \times L \times H$) through natural settlement, growth and survivorship of oysters (Supplementary Fig. 2 and Table 1). The cores showed that the upper 15 cm of the reefs are primarily composed of live oysters, shell material, and open pore space of the taphonomically active zone (TAZ), the zone where shell modification or destruction is highest[22] (Fig. 1 and Supplementary Fig. 1). Below the TAZ, we observed the reef core, where pore space between the oyster shells is filled with sediment and shell preservation is highest. On average (by mass; ± 1 s.d.), the reef core consists of $48 \pm 9\%$ shell (>2 mm in size), $30 \pm 12\%$ sand (allogenic sediment; no agglomerates), and $19 \pm 6\%$ silt and clay (biodeposits + allogenic sediment). On the basis of the similarity of the grain-size distributions, the sand in the reef is probably sourced from the surrounding sandflat.

Reef accretion rate is commonly expressed as the change in elevation through time (cm yr^{-1}; refs 5,6). On the basis of the reef heights measured from the top of the core to the top of the cultch (assuming the top of the cultch was 15 cm above the substrate), those five reefs grew 2.7 ± 0.7 cm yr^{-1} (mean ± 1 s.d.). Examining reef growth rates exclusively using core data, however, does not scale up to whole-reef evolution given the irregular and complex patterns of oyster settlement, growth and survivorship over a range of scales (less than one to tens of metres) within reefs. In addition, maximum potential reef height and thickness depend on the elevation of the substrate and the upper limit of the tidal range where oysters cannot grow because the stress from limited inundation is too high. We name that upper limit the growth ceiling,

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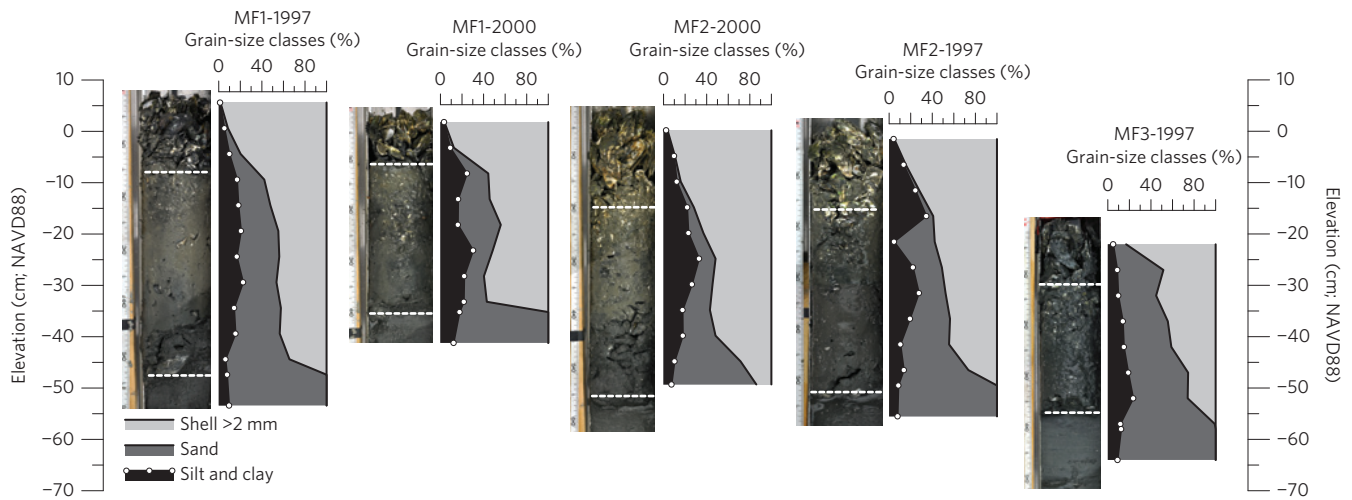
Figure 1 | Oyster-reef compositional changes with depth. Core photos and sample depths plotted relative to the North American Vertical Datum of 1988 (NAVD88). Dashed lines on photos bracket the reef core (Supplementary Fig. 1). See Supplementary Fig. 2 for locations and Supplementary Table 1 for additional information.

which probably varies across tidal ranges and climates. If the top of the reefs reached their growth ceiling sometime in the past, then those reef-height measurements from coring might underestimate vertical reef-growth rate.

Core data indicated that reefs grow at a rate that should be resolvable using direct measuring techniques across relatively short time periods. To examine changes in growth, from initial colonization to maturity, our approach shifted towards the use of remote sensing applied to those reefs constructed in 1997 and 2000, plus six experimental reefs constructed in 2011. The 2011 reefs were constructed in the same coastal research reserve and to the same specifications as the older reefs (Supplementary Fig. 2 and Table 2). Thus, we were able to closely examine changes in reef height, area and volume during the first 2 years and after ~10 years of reef development. To image the shape of the older and younger reefs, we used a Riegl terrestrial laser scanner (LMSZ210ii) and reef growth was measured from high-resolution digital elevation models (DEMs) created from the laser returns (Fig. 2 and Supplementary Fig. 3 and Methods).

Reef height is defined here as the distance between the elevation of the substrate on which the cultch was placed and the elevation of a horizontal plane intersecting the highest 1–2% of the reef's surface area quantified from the DEM. On the basis of linear regression, the 2011 reefs grew vertically 11.5 ± 1.4 cm yr^{-1} (Fig. 2). The older reefs, with the exception of MF3–1997, did not gain more than 2.0 ± 1.4 cm in elevation over the two-year observation period. The elevation across the crest of the 5 older reefs in 2012 was 0.6 ± 4.0 cm NAVD88 (mean ± 1 s.d.), which is close to local mean sea level (8.5 ± 3.7 cm NAVD88; ref. 23) and is interpreted as the growth ceiling. All of the 2011 reefs were constructed >36 cm below the ceiling, and therefore were not growth limited during our study period. Most of the older reefs were constructed on substrates of similar elevations as the 2011 reefs (Supplementary Table 2) and on the basis of the average growth rate of the 2011 reefs, the older reefs probably reached their present heights rapidly within their first 4 years of growth. Reef MF3–1997 was constructed at an elevation similar to the 2011 reefs; however, the top of the reef was still 6 cm below the growth ceiling 14 years after construction. Reef MF3–1997's vertical growth was limited by some external stress, possibly recreational harvesting, which explains why the reef gained elevation between 2011 and 2012 (Fig. 2b). When a reef reaches the growth ceiling, the top is limited by aerial-exposure stress and vertical accretion of the reef crest is reduced to the rate of SLR. Previous studies obtained samples from the tops of ancient

reefs for dating, which is probably why vertical-accretion rates of ~0.5 cm yr^{-1} were reported[5,6].

Reef growth is important to quantify in three dimensions because lateral accretion ensures continual vertical growth by providing space below the ceiling for larval settlement and subsequent accumulation of oyster biomass (Figs 2 and 3). Reef lateral accretion decreased with increasing reef age: average radial expansion was 30.1 ± 10.5 cm yr^{-1}, for the 2011 reefs, and 10.3 ± 3.5 cm yr^{-1}, for the older reefs (mean ± 1 s.d.). Lateral accretion is probably facilitated by the transport of shell from the reef's crest to perimeter and impeded by the transport and deposition of sand from the surrounding area burying the edge of the reef. Both of those processes were observed in the DEMs generated during 2010 and 2012 and were probably associated with coastal storms (for example, Hurricane Irene; 2011). Over the relatively short time frame of our study, linear regression was the best model to explain rates of surface area and volume change. Reef surface area increased 1.8 m^2 yr^{-1} and volume increased 0.54 m^3 yr^{-1}, indicating that the reefs double in area and volume from their original cultch dimensions about every 9.5 and 4.0 years, respectively (Fig. 2). Intertidal oyster reefs below the vertical growth ceiling grow rapidly in all directions (Figs 2 and 3, and Supplementary Fig. 4 and Table 2).

Reef accretion is a complex mix of oyster biology, taphonomy and depositional/erosional processes that cause growth rates to vary over time and space. The crests of the older reefs showed little vertical change through time, except for small pockets of erosion due to collisions (earlier coring and observed impacts from floating debris), predation and currents (Fig. 2a). Elevation gains on the older reefs were highest across the perimeters of the reefs, where the oysters are probably experiencing less stress from aerial exposure, but still benefit from reduced competition, predation and disease by being situated intertidally (Fig. 2a). Our results suggest that intertidal reefs have the potential to match even the highest predictions of SLR by the year 2100 (ref. 7), provided SLR does not coincide with or create additional stresses on oyster reefs that reduce productivity.

The base of the TAZ was detected at a consistent core depth (~15 cm below the reef surface), regardless of vertical position or changes in growth rates among the older reefs (reef MF3–1997 compared with the others), indicating that expansion of the reef core is keeping pace with the top of the reef. The high growth rates we document are from the oysters growing rapidly in large clusters on the reefs[18] (Supplementary Figs 4 and 5). In addition,
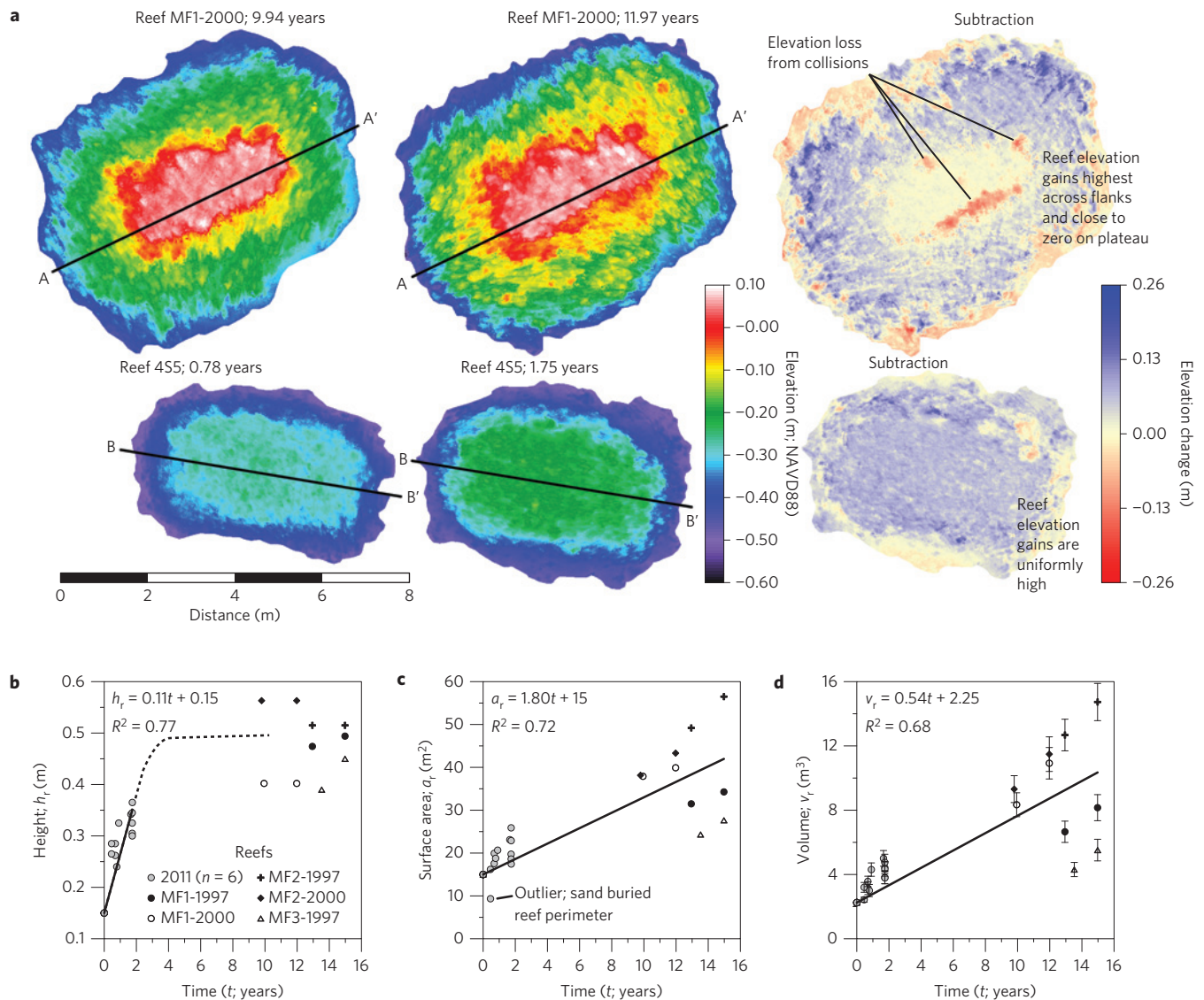
Figure 2 | Oyster-reef growth through time. a, Digital elevation models and difference maps of an older reef, MF1–2000, and a younger reef, 4S5 (see Supplementary Fig. 2 for locations). **b–d**, Regression lines of: vertical growth (± 0.014 cm; dashed line is an extrapolation; **b**), areal growth (± 0.88 m^2; **c**) and volume change ($\pm$ surface area $\times$ 0.014 cm; **d**). See Methods and Supplementary Table 2 for additional information.
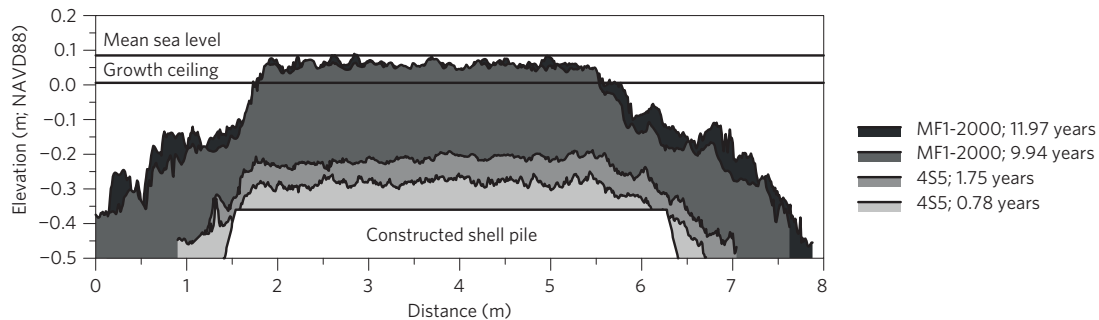

Figure 3 | Transects A–A′ and B–B′ across the reefs at different growth stages. See Fig. 2a for transect locations.

the reefs show high preservation of oyster shell in the reef core (low taphonomic loss), which is supported by our measurements (mean ± 1 s.d.) of carbonate in the TAZ (301 ± 142 kg m^{-3}) being similar to the reef core (369 ± 94 kg m^{-3}). Excluding shell material, the composition of the reef core is mostly allogenic sediment,

making reefs efficient sediment traps as they grow. Reef rugosity probably promotes sediment trapping by reducing shear stresses between the clusters of oysters and sedimentation helps bind the reef together by filling pore space. Some of the older reefs may have been at their growth ceiling for ~10 years; however, they are not buried by

allogenic sediment. Maintenance of TAZ-pore space in the absence of vertical reef growth suggests shear stresses are reduced along an increasing-depth gradient in the reef.

C. virginica reefs exist across wide geographical and environmental ranges, in diverse landscape settings, and are influenced by different types and magnitudes of stress, which certainly influence growth rates. Our results show that accretion rates of intertidal oyster reefs have the potential to surpass all other coastal ecosystem engineers, which are primarily macrophytes such as saltmarsh ($\sim$1 cm yr^{-1} in river-dominated areas)[24,25], seagrass (0.3–0.9 cm yr^{-1}; refs 26,27) and mangrove (1.35–0.1 cm yr^{-1}; ref. 28). With global warming resulting in higher rates of SLR (ref. 29), existing intertidal oyster reefs that have reached their growth ceiling could respond to SLR and the associated reduction in aerial exposure time by demonstrating enhanced vertical accretion. The high rates of reef growth suggest that the intertidal high-salinity portions of estuaries can be hotspots for oyster-reef productivity. Restoring reefs on intertidal sandflats could help preserve vegetated estuarine ecosystems sensitive to SLR and coastal structures by dampening waves and reducing estuarine shoreline erosion. Buffering shorelines from erosion is an ecosystem service reefs provided more widely in the mid-nineteenth century, before massive exploitation. The subsequent increase in coastal development, often at the shoreline, commonly uses riprap revetments and bulkheads as reef substitutes for shoreline stabilization, which is an inferior alternative because of the great natural capital reefs provide[30], including the maintenance of elevation in reference to mean sea level.

Methods

Oyster reefs were constructed in 1997 ($n=3$), 2000 ($n=2$) and 2011 ($n=6$) on 6 separate intertidal sand flats in and around Middle Marsh, North Carolina, USA, which is part of the Rachel Carson National Estuarine Research Reserve (Supplementary Fig. 2). Before constructing the 2011 reefs, we surveyed seafloor elevations at the reef sites with a Trimble 5800 global positioning system (GPS; 0.5 cm horizontal and 1.5 cm vertical error on average) to use as a base from which to measure growth. For the older reefs, we assumed that the substrate elevations were the contact between the cultch and sandflat sediment measured from the cores.

Core collection involved driving a 10-cm-diameter aluminium pipe through the centre of reefs with a jackhammer. Core location and elevation was surveyed with the Trimble GPS. To vertically characterize the reef sediment, we divided each core into 5-cm bins ($=392$ cm^3) downward from the reef top and 2-cm^3 subsamples from bins below the reef base. To separate the shell material >2 mm, we washed each core sample through a sieve, collecting all of the sediment-laden water in a bucket. Shells were dried in an 80 °C oven, weighed, photographed and identified ($>90\%$ *C. virginica*). When all of the sediment settled out of suspension in the bucket, we decanted the water, dried the sediment in an 80 °C oven, and weighed the sample. We subsampled the dry <2 mm size fraction, sonicated the subsample to break up agglomerations, and particle sizes from 2,000 to 0.04 µm were measured using a Cilas laser particle-size analyser.

Each reef was surveyed three times; the first during placement of the cultch using a level and measuring tape, and subsequent surveys between 2010 and 2013 using the terrestrial laser scanner (Supplementary Table 2). The laser scanner, mounted on a tripod adjacent to the reef, rotated 360° while collecting up to 2 million spatial (*xyz*) data points from laser returns. To sample entire reefs, we scanned from 2 to 3 different positions around each reef's perimeter during the 30 min before and after a spring low tide. Laser returns were transformed into the Universal Transverse Mercator coordinate system by positioning 8 reflectors in the scan area and surveying them with the Trimble GPS. The reefs were imaged from 600,000 to 1,000,000 laser returns (number depended on reef size) spaced <1 cm apart. Laser returns from the oyster reefs and surrounding sandflats were isolated from the entire point cloud using the manual classification tools included in the Merrick Advanced Remote Sensing software suite. We used Golden Software's Surfer 11.0 to generate grid files (1-cm spacing) of the reefs and surrounding sandflat with the Kriging algorithm, which given the high density of points resulted in nearly identical maps to those made using the Nearest Neighbor algorithm. All reef measures including height, area and volume were made from the DEMs.

The potential sources of error that could have impacted our ability to measure oyster-reef growth, included: GPS error, laser-scanner instrument error, error with manually levelling the reflectors and associating them with the surveyed points, error associated with manually editing the point cloud, and error

associated with using algorithms to create the DEMs. We quantified error experimentally from a synthetic reef, which was a pile of oyster shell in a $1.2 \times 1.2 \times 0.15$ m shape (Supplementary Fig. 3). The morphology of the synthetic reef was measured three times using two scan positions. Each set-up included repositioning and resurveying the reflectors. Those three data sets were processed in the same manner as outlined above to create DEMs and vertical error was estimated by subtracting grid cells (Supplementary Fig. 3). The mean of those 25,662 observations was zero, indicating that no bias exists, and error was therefore defined as the mean standard deviation or 0.014 m (Supplementary Fig. 3e).

Reef area and surface area were measured using Golden Software's Surfer 11.0 by digitizing the perimeter from DEMs and the perimeter was defined as the transition from smooth sandflat to irregular oyster reef. We estimated the error associated with choosing that boundary by having three individuals perform the analysis, independently, using the same DEM. Error was defined as the standard deviation of those measures or 0.88 m^2. The error associated with the volume measure was calculated as the product of the vertical error (0.014 m) and the surface area of the reef (Supplementary Table 2).

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Author contributions

A.B.R., F.J.F., J.H.G. and N.L.L. conceived of the project. A.B.R., F.J.F., J.T.R., E.J.T. and S.E.C. collected field data. A.B.R., J.T.R. and S.E.C. processed data. A.B.R. wrote the article. All authors constructed experimental reefs, contributed to discussions and interpretations of the results, and edited the manuscript.

Additional information

Supplementary information is available in the online version of the paper. Reprints and permissions information is available online at www.nature.com/reprints. Correspondence and requests for materials should be addressed to A.B.R.

Competing financial interests

The authors declare no competing financial interests.