

Research



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Author for correspondence:

Stephen G. Hesterberg
e-mail: shesterberg2013@gmail.com

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Conservation biology

Prehistoric baseline reveals substantial decline of oyster reef condition in a Gulf of Mexico conservation priority area

Stephen G. Hesterberg¹, Gregory S. Herbert², Thomas J. Pluckhahn³, Ryan M. Harke³, Nasser M. Al-Qattan², C. Trevor Duke^{3,4}, Evan W. Moore^{2,5}, Megan E. Smith^{2,5}, Alexander C. Delgado³ and Christina P. Sampson⁶

¹Department of Integrative Biology, ²School of Geosciences and ³Department of Anthropology, University of South Florida, 4202 East Fowler Avenue, Tampa, FL 33620, USA

⁴Department of Anthropology, University of Florida, PO Box 117305, Gainesville, FL 32611, USA

⁵Department of Marine Geosciences, University of Miami Rosenstiel School of Marine and Atmospheric Science, 4600 Rickenbacker Causeway, Miami, FL 33149, USA

⁶The Department of Anthropology, University of Michigan, 101 West Hall, 1085 South University Avenue, Ann Arbor, MI 48109, USA

SGH, 0000-0002-3607-1789

The Gulf of Mexico (GoM) is home to the world's largest remaining wild oyster fisheries, but baseline surveys needed to assess habitat condition are recent and may represent an already-shifted reference state. Here, we use prehistoric oysters from archaeological middens to show that oyster size, an indicator of habitat function and population resilience, declined prior to the earliest assessments of reef condition in an area of the GoM previously considered pristine. Stable isotope sclerochronology reveals extirpation of colossal oysters occurred through truncated life history and slowed growth. More broadly, our study suggests that management strategies affected by shifting baselines may overestimate resilience and perpetuate practices that risk irreversible decline.

1. Introduction

Oyster reefs provide critical ecosystem services in estuaries around the world, including water filtration, shoreline stabilization and fisheries habitat [1,2]. However, most of the world's oyster reefs have been lost in the last 200 years, and nearly one-third of those that remain are functionally extinct [1]. Thus, conservation efforts must be directed towards identifying the increasingly few locations where oyster reefs remain at or near past levels of ecosystem structure and function [3].

In North America, the Gulf of Mexico (GoM) is home to the world's largest remaining wild oyster fisheries [1]. Zu Ermgassen *et al.* [4,5] estimate that while Atlantic coast oyster reefs experienced declines in extent and function greater than 60% since 1900, GoM oyster habitat has fared better, with some areas relatively stable in terms of these metrics or even improved. This, combined with relatively undeveloped stretches of coastline, has contributed to the perception that oyster reefs of the GoM, such as in Florida's Big Bend, remain somewhat 'pristine' and well managed [6,7].

Existing baseline data (e.g. [7–9]), however, post-date intensive oyster harvest and widespread landscape change by at least a half-century [10–12], leaving open the possibility that reefs experienced earlier, undocumented degradation [4]. Archival data from archaeological and palaeontological sources offer pathways to reconstruct past ecology where recent historical records are deficient or anecdotal [13]. Fitness-related phenotypic traits, such

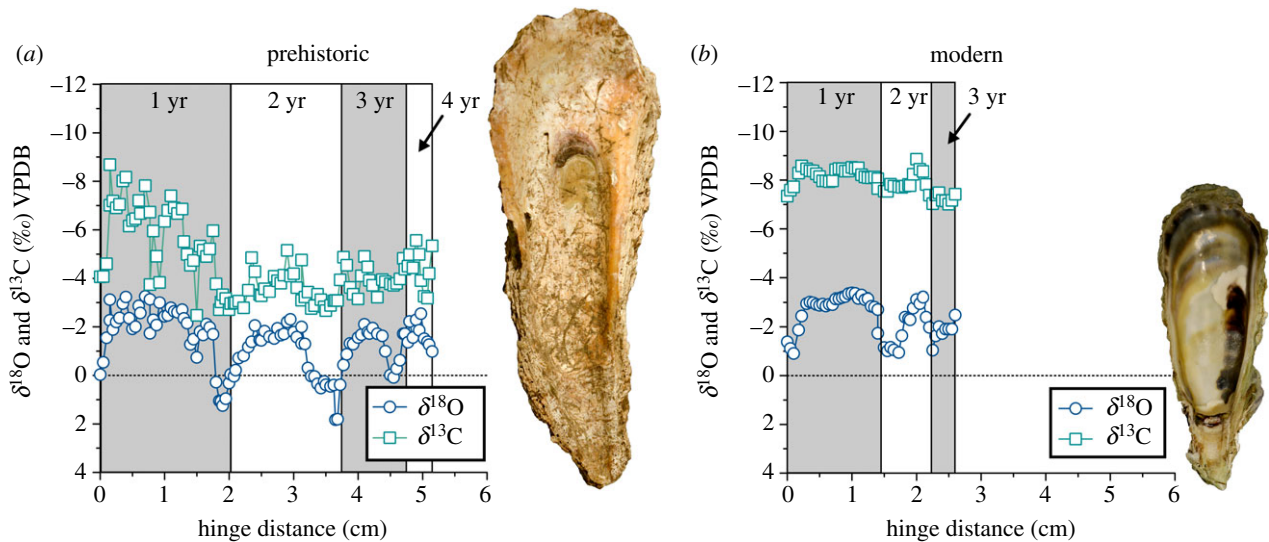


Figure 1. Largest prehistoric and modern oysters collected near Crystal River, Florida and included in isotope analyses (188.1 mm and 113.5 shell height, respectively). Life-history traits were reconstructed using temperature-dependent oxygen isotope profiles derived from the growth axis on each individual's ligamental area (i.e. hinge distance), a known sclerochronologic record. (a) Prehistoric specimen's oxygen isotope profile showing a longevity of nearly four complete years with annual hinge growth represented by alternating grey and white shading. (b) Modern specimen's oxygen isotope profile showing a contracted lifespan of only 3 years and smaller annual hinge growth relative to the prehistoric oyster. See electronic supplementary material, appendix S3 for the complete set of oxygen isotope profiles from all replicate shells. (Online version in colour.)

as body size, are frequently preserved in these records and condense key performance and life-history aspects into a single dimension [14]. For oysters, large individuals disproportionately contribute to reef ecosystem services and fecundity [5,15,16]. Thus, tracking oyster shell size through time provides a straightforward way to assess reef quality and resilience over extended timescales and complements existing baseline data focused more on metrics of habitat quantity [4].

Here, we compare archaeological and modern oyster sizes from Florida's Big Bend, a conservation priority area within the GoM, to extend Zu Ermgassen *et al.*'s [4] century-scale baseline for oyster habitat condition to over a millennium. We also perform stable isotope sclerochronology on a subsample of large oyster shells to determine the life-history basis of declining oyster size and reconstruct the palaeoenvironments of large, prehistoric oysters.

2. Material and methods

(a) Study area

Crystal River, Florida, USA, was selected as our study location based on the proximity of the Nature Conservancy-defined priority area of Florida's Big Bend [6] and two, well-studied archaeological sites consisting of midden and mound features formed from oyster shells (*Crassostrea virginica*). Indigenous peoples occupied these two sites sequentially from AD 50 to 1050 [17]. Detailed descriptions of the study area are in the electronic supplementary material.

(b) Body size reconstruction

Prehistoric oyster shells were obtained from 15 radiocarbon-dated levels exposed within four trenches at the Crystal River archaeological site ($n = 752$) [17]. At the neighbouring Roberts Island site, oysters were collected from a stratigraphic trench in the mound and from smaller stratigraphic excavations ($n = 915$) [18]. Modern oysters were obtained in 2015–2016 from intertidal

oyster reefs spanning the full range of available oyster habitat within Crystal River, including nine lower salinity reefs within the river ($n = 1750$), six inshore reefs ($n = 1419$) and six higher salinity offshore ($n = 1019$) reefs (electronic supplementary material, S1). No subtidal reefs are known to occur within the study area. On each reef, two 0.25 m² quadrats were haphazardly placed at the reef crest and near mean low water, and the matrix was excavated to an approximately 10-cm depth.

(c) Life-history reconstruction

As oxygen and carbon isotope ratios of *C. virginica* shells record seasonal temperature and salinity fluctuations, respectively [19,20], we analysed five midden and five modern oysters from the largest size classes to reconstruct annual growth patterns, estimate maximum age and infer general position within the estuary (figure 1). Of the five modern oysters, two were from the river, two were from inshore reefs and one was from an offshore reef (electronic supplementary material, figure S1). Three prehistoric oysters were obtained from Crystal River and two from Robert's Island archaeological sites (electronic supplementary material, figure S3). All 10 oysters selected for isotope analyses have a standard, common growth form (shell height: width range between 2:1 and 3:1). Oysters were mounted in epoxy resin and cross-sectioned along the growth axis of the hinge. A MicroLux drill press with a 1.0 mm carbide bit was used to mill consecutive 80–120 μg samples at increments of 2–3 samples mm⁻¹ along the entire length of the hinge. Each sample was dissolved in 104% H₃PO₄ at 90° C for 24 h, and the resulting gas analysed for $\delta^{18}\text{O}$ and $\delta^{13}\text{C}$ using a GasBench device coupled to a Thermo Finnigan Delta V Advantage IRMS in the School of Geosciences at the University of South Florida. Data are reported in standard per mil (‰) notation relative to the Vienna Pee Dee Belemnite (V-PDB) standard. Analytical precision was $\pm 0.09\text{‰}$ for oxygen and $\pm 0.08\text{‰}$ for carbon based on repeated analyses of an in-house standard.

A strong linear relationship between the length of the ligamental area (hinge distance) and shell height (electronic supplementary material, S2) was used to convert the amount of hinge accreted each year over one temperature-driven $\delta^{18}\text{O}$ cycle into annual increases in shell height. Age was determined by

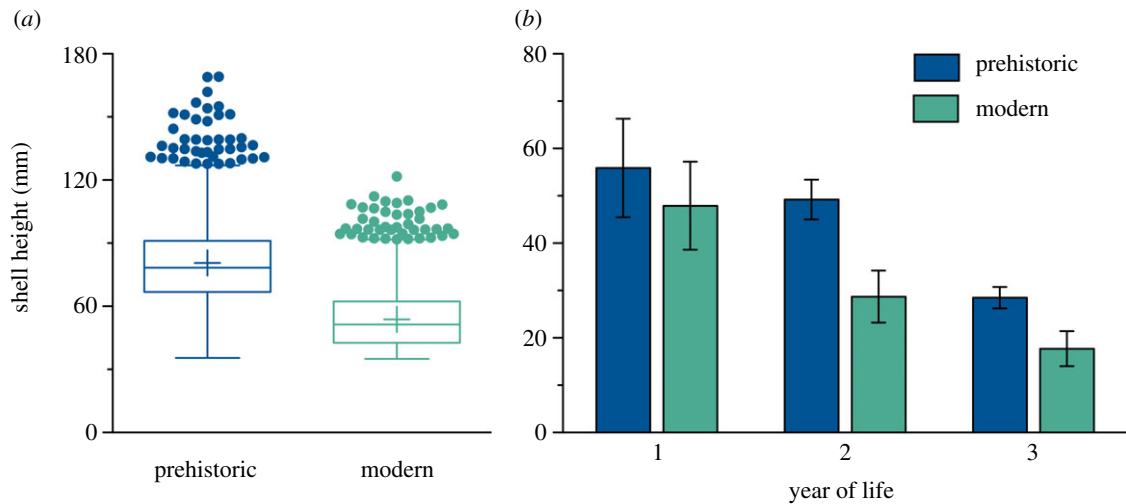


Figure 2. (a) Box and whisker plots of prehistoric ($n = 1667$) and modern ($n = 4188$) oyster shell height measurements from the Crystal River, Florida, estuary. Box and whisker plots show the median (central line), mean (cross), first and third quartiles (box), as well as $1.5\times$ the interquartile range (whiskers). Circles are measurements within $3\times$ the interquartile range of the median. (b) Mean (\pm s.e.) shell height growth per year of life for a subset of large archaeological and modern shells ($n = 5$). (Online version in colour.)

totalling the number of annual cycles in each $\delta^{18}\text{O}$ profile and estimating age to the nearest half-year. We rely upon $\delta^{18}\text{O}$ profiles instead of morphological proxies of age, which are unreliable in Florida oysters (electronic supplementary material, S4) [19].

(d) Statistical analysis

A Wilcoxon rank-sum test was used to examine differences between shell height distributions for prehistoric and modern oyster samples. For all distributions, we follow the methods of Rick *et al.* [21] and only include individuals greater than 35 mm in shell height due to preservation bias against small oysters in the archaeological sample. Welch-corrected t -tests were also used to examine whether annual additions in shell height for midden and modern oysters differed within their first, second and third years of life. All statistical analyses were performed in R [22].

3. Results

A Wilcoxon rank-sum test shows a difference in location of 25.9 mm (25.0–26.8 (95% CI)) between prehistoric and modern shell height distributions ($U = 826120$, $p < 0.001$). Shell height for the sample of prehistoric oysters ($n = 1667$, 80.5 ± 19.3 mm (mean \pm s.d.)) was larger than that observed in the modern population near Crystal River ($n = 4188$, 53.7 ± 13.5 mm (mean \pm s.d.)) (figure 2a). The maximum prehistoric shell height recovered was 188.1 mm compared to the modern maximum of 121.7 mm.

Oxygen isotope profiles of large prehistoric and modern individuals (figure 1; electronic supplementary material, figure S3) exhibit similar first-year growth patterns ($t = 0.59$, d.f. = 7.75, $p = 0.571$), but modern oysters grew 35% and 38% less in years 2 ($t = 3.15$, d.f. = 7.81, $p = 0.014$) and 3 ($t = 2.70$, d.f. = 7.11, $p = 0.030$), respectively, compared to prehistoric shells (figure 2b). The largest prehistoric shells ranged from 3.5 to 7.5 years old, with a median age of 4.5 years, while the largest modern oysters exhibited a narrower age range (2.5–4.5 years) and a shorter median age by a full year (3.5 years). Carbon isotopes in prehistoric shells are heavier ($n = 5$, $-3.96 \pm 0.49\text{‰}$ (mean \pm s.d.)) than in modern oysters ($n = 5$, $-7.27 \pm 0.30\text{‰}$ (mean \pm s.d.)). The four modern oysters

sampled from near river mouths averaged $-7.87 \pm 0.15\text{‰}$ (mean \pm s.d.), whereas the oyster collected from a modern offshore reef averaged $-4.88 \pm 0.44\text{‰}$ (mean \pm s.d.).

4. Discussion

Oyster reef ecosystem services and resilience are a function of the quantity of oysters but also the presence of larger, older individuals. Services such as water filtration and fisheries production greatly improve when oysters reach market size [4,5]. Moreover, the high proportion of females in large size classes and the nonlinear relationship between oyster size and both shell mass and reproductive output means that reefs with large oysters are more likely to outpace destructive processes, such as sea-level rise and burial, and avoid recruitment failure [15,16,23–26]. Here, we find compelling evidence that oyster habitat quality near Crystal River, Florida declined before the first ecological assessments had even begun and at a magnitude far greater than natural fluctuations in oyster size related to background climate variation [26]. The mean body size on modern reefs in Crystal River is just two-thirds of the pre-European contact baseline due to complete loss of ‘colossal’ oysters 120–190 mm in shell height (figure 2a). Truncated size has also been observed on oyster reefs elsewhere in the region [27], substantiating what may be a general phenomenon throughout the wider northern and eastern GoM (e.g. [28,29]).

Oxygen isotope-derived estimates of life history indicate that both shortened lifespan (figure 1; electronic supplementary material, figure S3) and slower growth after the first year (figure 2b) contribute to smaller oyster body sizes relative to prehistoric shells. Declining body size and related life-history shifts are characteristic of populations experiencing high adult mortality and among the best early warning signs of a population approaching collapse [30,31]. Carbon isotope values of prehistoric oysters at Crystal River are substantially heavier than those of modern oysters from the lower salinity river mouth at Crystal River but overlap with those of a shell sampled from the higher salinity offshore reefs (electronic supplementary material, figure S3). Assuming a Suess effect

offset of 0.8‰ for modern oysters [32] and assuming a similar salinity– $\delta^{13}\text{C}_{\text{DIC}}$ relationship, all of our sampled prehistoric oysters would have been collected from offshore reefs. The presence of colossal, fast-growing oysters on offshore reefs in the past is opposite of today, where the largest, fastest growing oysters are concentrated near river mouths (electronic supplementary material, figures S3 and S5).

Although we do not yet know the specific cause(s) and timing of shifts in body size, anecdotal evidence of colossal oysters in the Big Bend appear as late as the late nineteenth or early twentieth centuries [33]. A commercial fishery existed in Crystal River before 1950 [8,34], and overharvest of large oysters could have extirpated colossal individuals long before ecological assessments were ever conducted. However, landscape changes in the Crystal River watershed affecting nutrient concentrations, sediment loads and river discharge occurred over the same timescale [12,35] and possibly contributed to mass mortalities of Crystal River oysters in the 1950s [8]. Reductions in freshets provide ideal conditions for outbreaks of the oyster parasite *Perkinsus marinus* and other oyster predators, which ultimately slow oyster growth and truncate size-structure through adult mortality [36–38]. Higher salinity offshore reefs, where Crystal River's prehistoric colossal oysters likely lived, would be most sensitive to such effects.

Florida's Big Bend is thought to represent one of the last areas where limited development and proper management has allowed today's habitats to reflect a wilder past [1,6]. However, our study documents significant degradation of oyster reef function and resilience in this area by rediscovering a long-lost, prehistoric baseline of oyster body size.

The loss of the largest oysters in the Big Bend mirrors size declines in oysters elsewhere in North America [21,39], suggesting that reef quality and resilience eroded prior to more widely known historical declines in oyster aerial extent [1,4,10,11]. Although no-take reserves have been successful at protecting large oyster size classes [25], colossal individuals may never be restored in the Big Bend and wider GoM region due to irreversible changes in adjacent watersheds and climate [30]. If so, habitat management strategies that replicate the functions and adaptive capacities of past oyster reefs by means other than size restoration will be needed.

Ethics. All live oysters in this study were collected with permission from Florida Fish and Wildlife Conservation Commission (SAL-14-1633-SR, SAL-15-0901B-SR). One prehistoric shell was loaned from the Florida Bureau of Archaeological Research (no. 2016-19).

Data accessibility. Data are available from the Dryad Digital Repository: <https://doi.org/10.5061/dryad.66t1g1jz4> [40].

Authors' contributions. All authors contributed to study design, data acquisition, analysis and interpretation. All authors contributed to the manuscript writing and revisions. All authors gave the manuscript final approval before publication and agree to be held accountable for the content therein.

Competing interests. We declare we have no competing interests.

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