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Nineteenth-century collapse of a benthic marine ecosystem on the open continental shelf

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The soft-sediment seafloor of the open continental shelf is among the least-known biomes on Earth, despite its high diversity and importance to fisheries and biogeochemical cycling. Abundant dead shells of epifaunal suspension-feeding terebratulid brachiopods (*Laqueus*) and scallops on the now-muddy mainland continental shelf of southern California reveal the recent, previously unsuspected extirpation of an extensive offshore shell-gravel ecosystem, evidently driven by anthropogenic siltation. Living populations of attached epifauna, which formerly existed in a middle- and outer-shelf mosaic with patches of trophically diverse muds, are restricted today to rocky seafloor along the shelf edge and to the sandier shelves of offshore islands. Geological age-dating of 190 dead brachiopod shells shows that (i) no shells have been produced on the mainland shelf within the last 100 years, (ii) their shell production declined steeply during the nineteenth century, and (iii) they had formerly been present continuously for at least 4 kyr. This loss, sufficiently rapid (less than or equal to 100 years) and thorough to represent an ecosystem collapse, coincides with intensification of alluvial-plain land use in the nineteenth century, particularly livestock grazing. Extirpation was complete by the start of twentieth-century urbanization, warming, bottom fishing and scientific surveys. The loss of this filter-feeding fauna and the new spatial homogeneity and dominance of deposit- and detritus-feeders would have altered ecosystem functioning by reducing habitat heterogeneity and seawater filtering. This discovery, attesting to the power of this geological approach to recent ecological transitions, also strongly increases the spatial scope attributable to the negative effects of siltation, and suggests that it has been under-recognized on continental shelves elsewhere as a legacy of coastal land use.

1. Introduction

The soft-sediment seafloors of the open continental shelf (less than 200 m) support diverse benthic communities critical to commercial fisheries and to the function of marine ecosystems through such processes as secondary production, water filtering, and bioadvection of fluids and materials [1,2], but this biome remains one of the least known on Earth. Benthic surveys are widely scattered, controlled experiments are extremely challenging and observational time-series are short (less than or equal to a few decades) and usually start only after the onset of most human stresses, such as harvesting of wild populations, nutrient runoff from watersheds, pollution, climate change, and habitat modification from dumping and bottom trawling [3–5].

However, paleoecological analysis is also challenging. Whereas sedimentary cores are a powerful means of assessing anthropogenic and natural changes in estuarine and coastal ecosystems [6–8], sediment accumulation rates on the open shelf are usually too slow to allow sufficient temporal resolution. Sediment reworking by bioturbators and storms tends to admix durable shelly remains from successive community states into time-averaged assemblages of past community composition and diversity on a decadal to millennial scale [9–12].

Here, we use a new approach of unmixing time-averaged death assemblages by radiocarbon-based and other age-dating of individual dead shells to resolve temporal changes in shell production and community composition [13–17], allowing us to test for ecological legacies of human stresses on the southern California shelf, one of the best-studied shelf systems in the world. Comparing time-averaged death assemblages with 60 years of biomonitoring data on living benthos, we discover the loss of a formerly widespread and now effectively extinct shell-gravel community on the mainland shelf many decades before monitoring began. After thriving for millennia, the shelf ecosystem shifted in the nineteenth century from a spatial mosaic of shell-gravel with abundant epifaunal and sedentary suspension feeders to widespread muddy sediments dominated by detritus-based benthic communities. This loss coincides with the rise of livestock grazing and agriculture in coastal watersheds, and was thus probably driven by siltation rather than by the nutrient influxes and climate change responsible for late twentieth-century changes on these and other shelves (e.g. [18–21]). The negative effects of siltation are thus not limited to lakes and small coastal water bodies [22] and are probably under-recognized on continental shelves elsewhere as legacies of watershed land use.

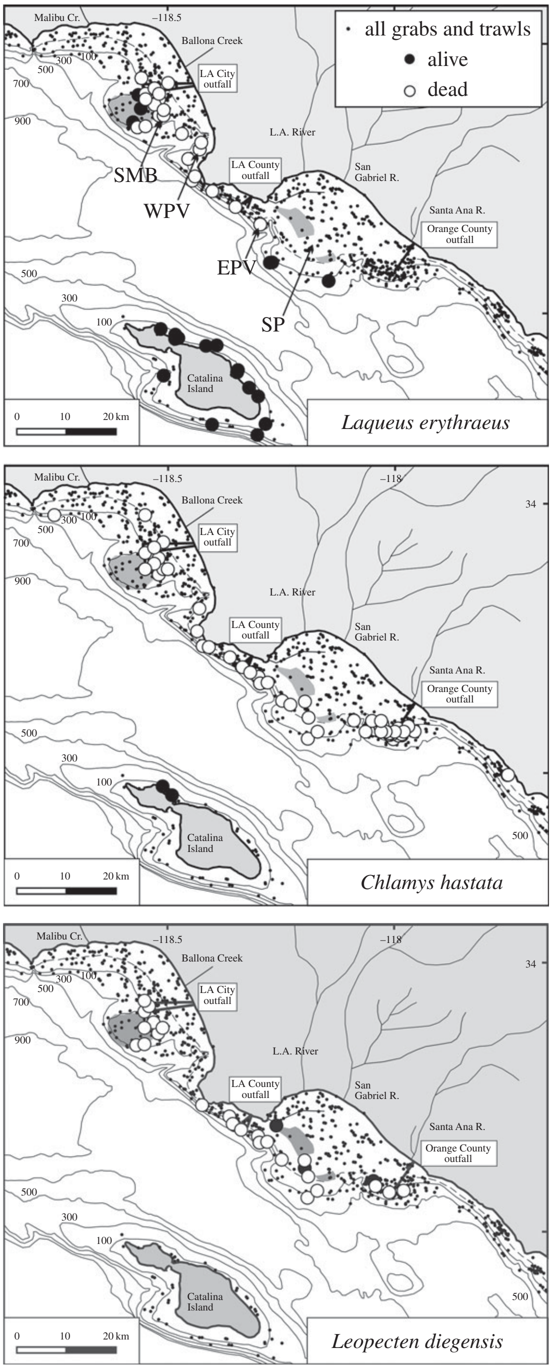

Figure 1. Empty shells of the epifaunal suspension-feeding brachiopod *L. erythraeus* and scallops *C. hastata* and *Le. diegensis* occur in more samples on the mainland shelf, over a broader area, and extend into shallower waters (less than 90 m) than do living specimens, despite intense sampling. Live occurrences are limited to rare individuals along the mainland shelf-slope break and other rocky seabeds (shaded Short Bank within Santa Monica Bay, approx. 90 m) and to the shelves of offshore islands. Three primary sites are located distant from wastewater-effluent outfalls in Santa Monica Bay (SMB) and the western and eastern ends of the Palos Verdes shelf (WPV, EPV). SP, San Pedro Shelf (with shaded rocky Horseshoe Reef at 30–40 m).

2. Material and methods

Abundances and functional groups in *living* assemblages reflect our summing of data generated by annual monitoring of benthic communities (collected with Van Veen grabs) at three sites that have the same spatial coordinates as the samples used (i) to quantify composition of shelly *death* assemblages and (ii) to estimate the post-mortem ages of brachiopod shells. These three sites are Short Bank in Santa Monica Bay (SMB; live data from 1987 to 1991 and 2000 to 2014), and the western (WPV) and eastern parts of the Palos Verdes shelf (EPV; both with live data from 1972 to 2009) (figure 1). Death assemblages based on shells sieved from Van Veen grab samples (top approx. 10 cm of seabed, 1 mm mesh) were collected in 1975, 2012 and 2014 in SMB ($n = 849$ individuals) and in 2003, 2010 and 2012 in WPV ($n = 743$) and EPV ($n = 4220$; see electronic supplementary material). To quantify the taxonomic and functional composition of a dead-shell assemblage, shell fragments of bivalves and brachiopods must include at least half of the hingeline to be counted as dead individuals and must be identifiable to the genus level (comprising greater than 95% of all individuals).

The spatial distribution of living individuals of the epifaunal, suspension-feeding brachiopod *Laqueus erythraeus* and scallops *Chlamys hastata* and *Leopecten diegensis* since the late twentieth century is based on data from 2419 grabs, dredges and trawls collected on the approximately 400 km-long mainland shelf of the Southern California Bight (San Diego to Santa Barbara) between 1956 and 2014. The distribution of dead individuals of the same species is based on data from a subset (463) of the grabs collected between 1975 and 2014. Bathymetric data for living and dead *Laqueus* are supplemented with information from bottom photographs of the mainland shelf between Malibu (northern edge of SMB) and the southernmost limit of the San Pedro Shelf (south of EPV) [23,24] and on the island shelf of Santa Catalina [25].

The extent of amino acid racemization (AAR) was analysed in 190 specimens of *Laqueus* at Northern Arizona University using reverse-phase high-pressure liquid chromatography [26]. To calibrate AAR data, one live-collected specimen of *Laqueus* collected in 1994 was used to establish baseline ratios, and 11 of the 190 dead shells were subjected to AMS radiocarbon dating (electronic supplementary material, table S1). These 12 specimens were used to calibrate the rate of aspartic acid with a simple power-law kinetic model and a lognormal uncertainty, and correction for calibration error was applied to estimates of time averaging [27] (electronic supplementary material).

We reconstruct the timing of decline in production of *Laqueus* by (i) fitting the frequency distribution of the 190 shell ages to an exponential model that permits two phases of shell loss (by disintegration and/or by burial) from the surface layer [28] and one or more abrupt changes in shell production [17], and then

(ii) dividing the AFD by a survival function (equation (14) in [17]) to quantify the effect of age-dependent shell loss, which will cause the timing of maximum production observed in AFD (its mode) to be shifted towards the recent from the true timing of maximum production (electronic supplementary material). To reconstruct original population densities, we estimate, for each 25-year window of past time, the number of dead shells that would have existed *before* shell loss (assuming a two-phase loss model), and then transform this number to a yearly standing density assuming that *Laqueus* had a lifespan of 12 years (electronic supplementary material).

3. Results

(a) Live–dead discordance

Regional surveys of benthic macrofauna since 1956 reveal that living assemblages on the modern mainland shelf of the Southern California Bight are dominated by infauna (predominantly annelids, crustaceans and molluscs [29,30]) and by mobile epifauna (crabs, sea cucumbers, urchins, seastars and brittle stars [31]), which are mostly deposit- and detritus-feeders and predators. Sedimentary samples from these seabeds include the skeletal remains of these taxa, especially of bivalves, which accurately capture spatial variability in the composition of living communities [12].

However, especially at sites with slow sedimentation located either far from the White Point outfall on the PV shelf and/or at depths below 50 m in SMB, death assemblages in benthic grab samples also contain and can be dominated by the shells of epifaunal suspension-feeders that are extremely rare or absent in living assemblages (figure 1). Shells of the large brachiopod *L. erythraeus* (greater than 3 cm) and the scallops *C. hastata* and *Le. diegensis* (greater than 5 cm) occur, respectively, at 9%, 21% and 12% of the 463 shelf sites where we have data on death assemblage composition; considering only the 328 stations in middle- and outer-shelf depths (greater than 35 m), where the shells occur preferentially, these occupancies increase to 13%, 24% and 16%. The dead shells are either densely or loosely dispersed within a muddy matrix, and are present from southern San Diego to Santa Barbara, a coastal extent of approximately 400 km. These frequencies almost certainly underestimate the true occurrence of dead shells, and of former shell-gravel communities. A large part of the shelf between Santa Monica Bay and San Pedro Shelf, the focus of our shell-dating effort, is characterized by sedimentation rates above approximately 0.1 cm yr^{-1} [32], so that shells older than 100 years are likely to be below the penetration depth of Van Veen grabs (approx. 10–15 cm). These three species were encountered alive in less than 0.1% of these same Van Veen samples, and, combining all sampling gear (2419 grabs, trawl and dredges collected since 1956), occur alive in just 0.6%, 0.2% and 0.3% of mainland shelf samples in this same area.

Bathymetrically, live individuals of *Laqueus* occur only in small patches of rocky, cobble- and boulder-rich seabeds on the narrow outer shelf (greater than 90 m) of Santa Monica Bay and on the outer edges of the San Pedro and Mugu shelves [23–25], and are sparse even there (mean 6 individuals in trawls, 95% confidence intervals = 2–12 individuals). No live occurrences are shallower than 87 m, whereas dead *Laqueus* shells are frequent on the broad, muddy middle shelf between 50 and 90 m (electronic supplementary material, figures S1 and S2).

Live–dead discordance in proportional abundance is also strong. At our three primary study sites in SMB, WPV and EPV (figures 1 and 2), as at other mainland sites of comparable depth, the most abundant guilds in living assemblages are infaunal bivalves that (i) employ a combination of deposit feeding and chemosymbiosis (*Parvilucina tenuisculpta*, *Lucinoma annulatuma*, *Thyasira flexuosa*), (ii) shift facultatively between surface deposit and suspension feeding (*Tellina carpenteri*, *Macoma yoldiformis*), or (iii) live commensally with infauna (*Rochefortia tumida*) (electronic supplementary material, figure S3). These infaunal guilds constitute 93%, 90% and 97% of living individuals at our three sites, respectively, and are also important in those death assemblages (48%, 11% and 64% of dead shells). By contrast, epifaunal suspension-feeders as a group (brachiopods and scallops), which were never detected in the living assemblages at these sites despite 6 decades of sampling, are numerically abundant in death assemblages (figure 2*a*), constituting 30%, 74% and 15% of all dead shells, and occur among the top 10 most abundant species (figure 2; electronic supplementary material, figure S4).

Death assemblages containing *Laqueus* and/or large scallops typically contain additional epifaunal suspension-feeding bivalves (*Delectopecten*, *Limaria*, *Crenella*, *Pseudochama*, *Hiatella*) and permanently attached forms such as cheilostome and cyclostome bryozoans (*Cellaria*, *Nevianipora*), bundles of serpulid worm tubes (*Salmacina tribranchiata*) and balanid barnacles. These taxa are also all rare or absent in the living assemblages at these sites today. Infaunal suspension-feeding bivalves, such as venerid and cardiid bivalves, are also more abundant dead than alive (figure 2). Species-level differences in living and death assemblages at these sites thus correspond to a major reduction in the abundance and diversity of suspension-feeders, not simply to a decline in the abundance of epifaunal guilds. These and other death assemblages on the muddy middle shelf also include a disproportionate number of obligate siphonate deposit feeders (*Nuculana*) (figure 2).

Restriction of living *Laqueus* to small numbers of individuals along the edge of the mainland shelf (greater than or equal to 90 m) contrasts with the wide bathymetric range of abundant populations on the middle to outer shelf of Santa Catalina Island, which is separated from the mainland by 30 km of abyssal seafloor (figure 1). The mean abundance of living brachiopods is two orders of magnitude higher in island trawls (mean = 602 individuals, 95% confidence interval = 122–1322 individuals) than on the mainland shelf. Camera surveys show dense aggregations of living *Laqueus* on sandy seabeds between 50 and 90 m (electronic supplementary material, figure S4).

(b) Post-mortem ages of brachiopod shells

All *Laqueus* shells from muddy seabeds (SMB, WPV and EPV; figure 1) are from 61 to 81 m water depth, and are disarticulated, incomplete and discoloured, and mostly consist only of the thick and robust hinge area. Their geological age–frequency distribution (AFD) (figure 3) shows that (i) no *Laqueus* shells are younger than approximately 1910 AD, (ii) the mode of the AFD is at approximately 160 years ago (approx. 1850 AD, 95% confidence intervals 1770–1900 AD) (electronic supplementary material, figures S5 and S6), and (iii) shell production occurred over a prolonged rather than brief interval (95% range = 5500 years, inter-quartile range = 860 years) (figure 3). The oldest shells in the death assemblages

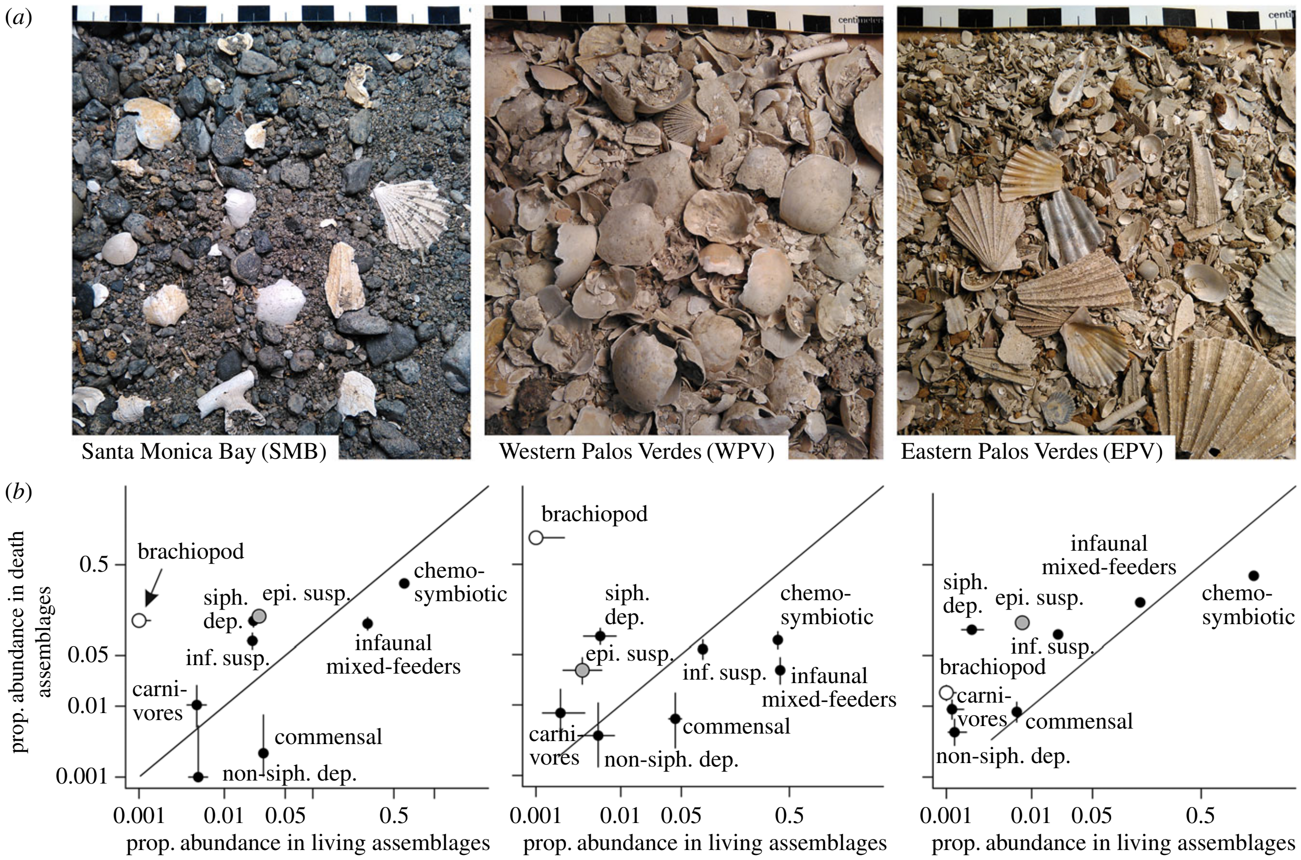

Figure 2. (*a*) Sediment residues greater than 1 mm showing abundant shells of brachiopods and scallops from three sites on the mainland shelf, sieved from Van Veen grabs of the top approximately 10 cm of the seabed. (*b*) The functional composition of living and death assemblages differs strongly: epifaunal suspension-feeders (brachiopods with white circles, bivalves with grey circles) are significantly more abundant as dead shells than living individuals. Composition of living assemblages is based on pooling annual surveys of middle-shelf communities between 1987 and 1991 and between 2000 and 2014 in Santa Monica Bay, and between 1972 and 2009 on the Palos Verdes shelf. epi. susp.—bivalve epifaunal suspension-feeders; inf. susp.—infaunal suspension-feeders; siph. dep.—infaunal siphonate deposit-feeders; non-siph. dep.—infaunal non-siphonate deposit-feeders. (Online version in colour.)

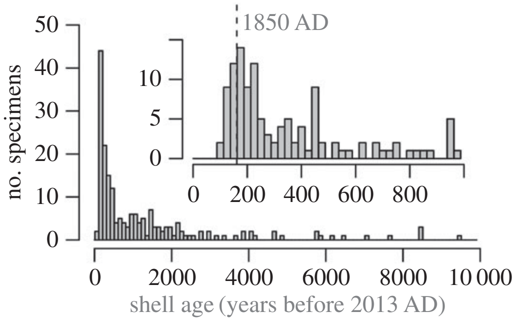

Figure 3. Frequency distribution of post-mortem ages of *L. erythraeus* (years before 2013 AD) collected from the middle shelf of Santa Monica Bay and off the Palos Verdes peninsula, determined by radiocarbon-calibrated AAR dating. Inset graph shows that death assemblages do not contain shells younger than approximately 100 years (1910 AD); the mode at approximately 160 years ago (approx. 1850 AD) indicates the last time when shells were produced in abundance (approx. 1820s after correction for taphonomic bias).

date to the time of submergence of these sites to greater than 50 m depths approximately 7000 years ago [33]. The rarity of shells younger than approximately 1850 AD and the lack of dated shells younger than 1910 AD in the AFD can only be explained by lower production of shells since approximately 1850 AD, whereas the declining abundance of shells older than approximately 1850 AD can be explained by (i) smaller populations or (ii) post-mortem loss of shells under conditions of constant production that was comparable to that of approximately 1850 AD. The latter explanation is most likely, given experimental and other observations of rapid processes of shell destruction in this [28] and other modern seabeds.

Fitting the AFD with the two-phase exponential model of shell loss that permits abrupt changes in shell production reveals that *Laqueus* shells initially disintegrate with a half-life of approximately 110 years, and that the oldest specimens reflect preferential preservation of a very small subset of the original cohorts, with a much longer half-life (approx. 1000 years). Shell loss from older cohorts has pulled the observed timing of maximum production (the mode of the AFD, approximately 1850 AD) towards the Recent by approximately 25–30 years, so that the true timing of the last interval of maximum production—the true onset of population decline—was approximately 1820–1825 AD. Assuming that *Laqueus* has a lifespan of 12 years, the population density at times of maximum production was approximately 20 individuals m^{-2} of seafloor (black curve in figure 4*a*). Uncertainty in the AAR calibration indicates that these population sizes, comparable with those of previous millennia, might have persisted until the late nineteenth century (approx. 1870s is the upper 95% confidence interval on the true, 1820–1825 mode; electronic supplementary material figure S6). However, by the earliest twentieth century, shell production had dropped too low for dead shells to be sampled, making the decline in *Laqueus* on the mainland shelf a fully pre-urban phenomenon.

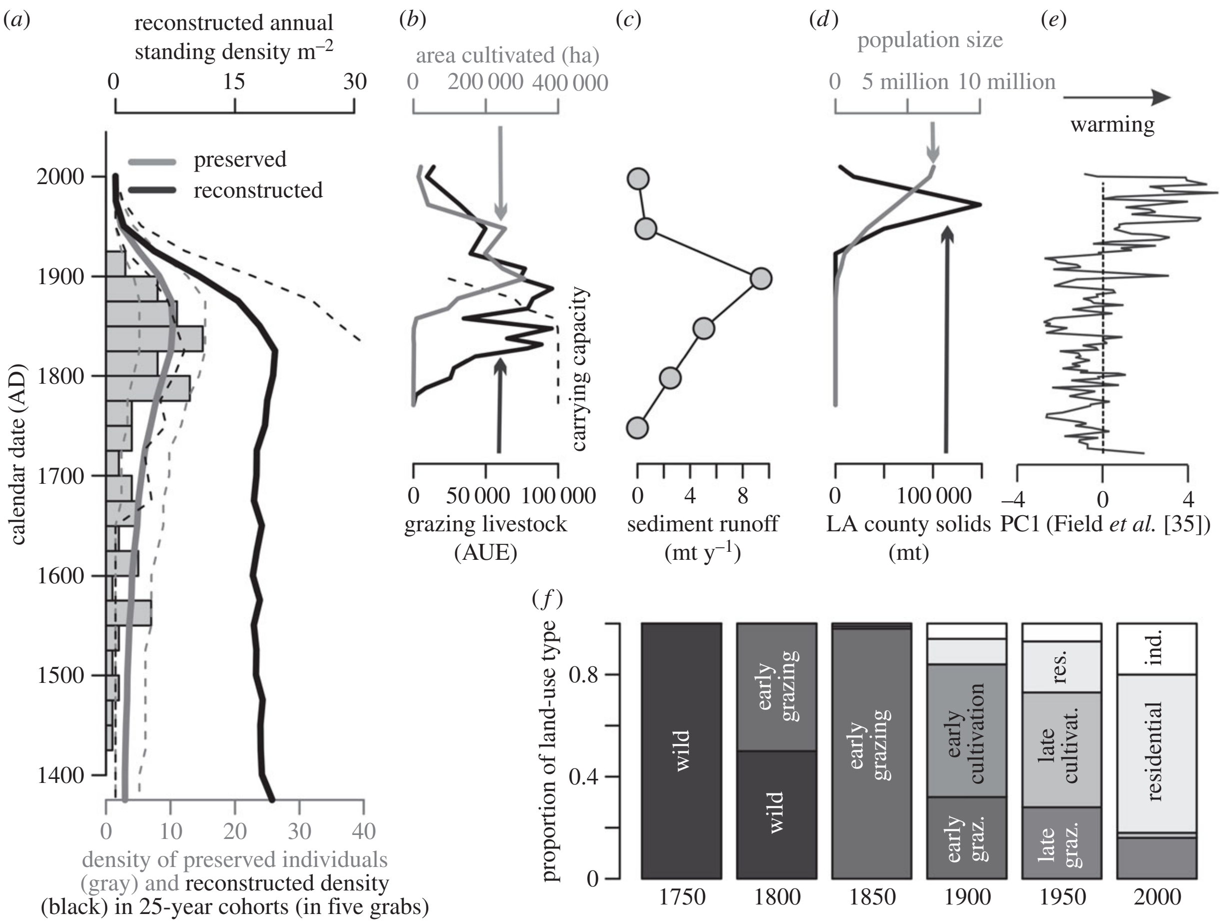

Figure 4. Chronology of (*a*) the nineteenth-century decline in brachiopod production on the mainland shelf, (*b*) changes in land use from hunting–gathering to commercial livestock and crop production, (*c*) changes in suspended sediment delivery to the ocean from land use, (*d*) size of human population and magnitude of wastewater solid-sediment emissions, (*e*) warming of Bight waters starting in the early twentieth century and (*f*) change in land use (see electronic supplementary material for details). (*a*) AFD in years AD, using 25-year cohorts; grey curve and dashed lines show this distribution when incorporating two-sigma uncertainties on the calibration of AAR; black curve and dashed lines reconstruct the density of individuals in 25 year cohorts in five grabs (rescaled to annual density m^{-2} on the top axis). (*b*) Livestock (cattle, horse, sheep) measured in Animal Unit Equivalents (AUE) for 1771–1832 AD on Los Angeles–Orange county coastal plain based on decennial data from Spanish Missions; AUE and area of cultivated land (hectares) for 1850–2000 AD based on decennial data from US Census reports; carrying capacity, assuming 10 acres per AUE, declines as land is converted to cultivation. (*c*) Sediment eroded in megatons per year, calculated using published data on sediment yields per land type applied to (*f*) our estimates of proportional land use on the alluvial plain (total 1 million acres). Early and late categories for grazing and cultivation denote before and after the early twentieth-century development of forage and soil conservation methods. (*d*) Human population size and wastewater emission of suspended solids to ocean are for Los Angeles County [34]. (*e*) Warming of California Current based on principal component analysis of planktonic foraminifera preserved in varved sediments from the nearby Santa Barbara Basin [35].

4. Discussion

(a) Non-analogue benthic ecosystem rather than an artefact of sampling and preservation

The high abundance of dead-only epifaunal suspension-feeders on the muddy mainland shelf of the Southern California Bight, especially in areas of relatively low sediment accumulation, cannot be explained by inadequate sampling of living individuals by Van Veen grabs. This shelf has been subject to repeated surveys and intensive biomonitoring over the last 60 years, and extensive trawls and bottom photography reliably detect epifaunal predators and detritus-feeders, corroborating the true rarity of epifaunal suspension-feeders [29–31]. By contrast, these same methods regularly detect large populations of *Laqueus* living on the middle to outer shelves of offshore islands (figure 1) [25].

The abundant dead shells of epifaunal suspension-feeders also cannot be explained by a post-mortem bias favouring preservation of the relatively large calcitic brachiopods (greater than 3 cm) and scallops (greater than 5 cm). The post-mortem half-lives of *Laqueus* shells (approx. 100 years) are an order of magnitude longer than those of the relatively small (less than 2 cm) and thin-shelled aragonitic infaunal bivalves *Nuculana* and *Parvilucina* in the same region (approx. 10 years [28]). However, if calcitic taxa were always rare in the California shelf community (e.g. always less than 1% of individuals), even their 10-fold preservational advantage could not shift them to apparent dominance in the death assemblage, where infaunal bivalves (comprising the other 99% of living individuals) would still be expected to constitute greater than 90% of the death assemblage (electronic supplementary material, figure S7).

Our use of death assemblages sieved from the uppermost approximately 10–15 cm of the seabed (Van Veen grabs) almost certainly underestimates the original, pre-nineteenth-century spatial distribution and abundances of epifaunal suspension-feeders on the mainland shelf. Sedimentation rates for the twentieth century vary among sites on the Santa Monica, Palos Verdes and San Pedro shelves, with an average of approximately 0.1–0.2 cm year^{-1} or higher [32], and so shells from older (pre-twentieth century), epifaunal-rich states can be expected to be buried greater than 10–20 cm at most sites. The functional importance of epifaunal suspension-feeders to pre-twentieth-century community states thus becomes evident in Van Veen samples only at sites with slower sedimentation rates (less than 0.1–0.15 cm year^{-1}). Even under such conditions, epifaunal shells can still be diluted by shells from more recent states, in particular those of chemosymbiotic bivalves that thrived in the 1970s and 1980s in response to wastewater emissions, as seen at SMB, WPV and EPV (figure 2; electronic supplementary material, figures S3 and S4).

We thus interpret the AFD of dead *Laqueus* shells and their spatial and numerical discordance with living populations as the record of a formerly diverse and extensive shell-gravel community state, dominated by suspension feeders, that has become functionally extinct on the southern California mainland shelf. Prior to the nineteenth century, these shell-gravel communities, dominated either by scallops or by *Laqueus* and supporting a suite of other attached suspension-feeding epifauna, had persisted for millennia and coexisted in a mosaic with patches of muddy seabed that were more trophically diverse than their late twentieth and early twenty-first-century counterparts, which have been dominated by infaunal mixed-feeding and chemosymbiotic bivalves. In water depths of 30–50 m where the scallops *Chlamys* and *Leopecten* thrived (electronic supplementary material, figure S1*b*,*c*), infaunal suspension-feeders and siphonate obligate deposit-feeders such as *Nuculana taphria* had, for millennia, been much more abundant (figure 2) [17]. Obligate deposit-feeders depend on microbially conditioned organic matter found in muddy seabeds with well-developed and fairly stable redox profiles, inconsistent with effluent sediment deposition and resuspension, suggesting that modern muddy seabeds are themselves much changed from pre-twentieth-century states. Although our age-dating of *Laqueus* focuses on only three sites within a 100 km segment of the mainland shelf, epifaunal suspension-feeding bivalves and *Laqueus* also occur dead-only in the muddy middle shelves of Santa Barbara and San Diego, indicating that this mosaic formerly characterized the entire approximately 400 km coastline of the Southern California Bight.

Nineteenth-century loss of shell-gravel communities, dominated by epifaunal suspension-feeders, would in itself have altered the functioning of the benthic ecosystem: their living populations and dead shells increase habitat heterogeneity at both local and patch scales, promoting β diversity, and their consumption of food from the water column increases the efficiency of bentho-pelagic coupling and nutrient cycling (as in [36–38]). Extirpation thus represents the collapse of a benthic ecosystem, given the rapidity (less than or equal to 100 years) and thoroughness of their decline following multi-millennial persistence.

(b) Drivers of collapse

Siltation was probably the primary driver of collapse: brachiopods and scallops, like most epifaunal suspension feeders, have low tolerance of high levels of suspended sediments [39,40]; the permanently attached forms are immobile and cannot survive burial; fine-grained seabeds reduce the potential for larval attachment and favour burrowers that can exclude or destabilize epifauna; and the shells of brachiopods and scallops are today buried under or dispersed within muddy sediments. However, several different natural and anthropogenic processes might have led to siltation of the mainland shelf, and factors other than siltation might have contributed to the decline (figure 4).

(i) Wastewater input

Sewage was first discharged to the surf-zone in the late 1890s but was largely re-used on land until the 1920s–1930s, when outfall pipes were extended onto the open shelf (Santa Monica Bay in 1925, San Pedro Shelf in 1927, Palos Verdes shelf in 1937 [41]). Discharges of suspended solids were not significant until the 1950s, peaked in the early 1970s and declined rapidly in the 1990s [21,34] (figure 4*d*). Wastewater emissions to the open shelf, including nutrients and other contaminants, significantly affected mud-dwelling benthos for multiple decades by promoting dominance by chemosymbiotic and facultative deposit-feeding bivalves [34]. However, emissions started too late to have initiated decline of the shell-gravel community.

(ii) Warming

Laqueus and *C. hastata* prefer cool waters and range from the southern edge of the Southern California Bight at the US–Mexico border to the Gulf of Alaska [42,43], and *Laqueus* larvae exhibit abnormal settlement behaviour in waters warmer than 20°C, with very high mortality in waters greater than 25°C [44]. The decline of these species on the mainland shelf and their contraction to the shelf edge thus might be a response to climate warming. However, warming in the Southern California Bight only began in the early twentieth century (by 0.6–1.0°C [35,45]), thus post-dating the decline (figure 4*e*). The persistence of large *Laqueus* populations in middle-shelf depths (30–90 m) of Santa Catalina Island, where the mean annual temperature at 50 m (approx. 12.5°C) is equal to that on the mainland shelf, also strongly argues against a climate-driven decline, as does *Laqueus*'s apparent survival of the full range of inter-annual (ENSO) and multi-decadal climate variability (PDO) that has characterized the Bight over the last 1 kyr [46].

(iii) Marine harvesting

Historically, commercial and sport fisheries on the southern California open shelf have focused on pelagic and predatory finfish, sharks and whales [47], but none are molluscivores, nor are their prey, and thus we have no reason to suspect a top-down dynamic [48]. In addition, habitat destruction by bottom-fishing started too late to have driven the decline, although it might have limited recovery. Southern California was the centre of the California commercial halibut fishery in the early twentieth century, but anchored entangling nets were used almost exclusively during the nineteenth century and are still the dominant gear; drag nets were used only between 1876 and 1911, when they were outlawed [49–51]. California fishermen did not start to use destructive otter trawls until the late 1930s and never in southern California except for a 1-year trial for shrimp on the San Pedro shelf in 1920–1921 [50,51].

(iv) Siltation owing to livestock grazing and farming

Watersheds of the southern California coastal plain have undergone dramatic changes since 1771, when Spanish missionaries introduced cattle, horse, sheep and subsistence gardening. Throughout the Mission Period (1769–1832) and into early statehood (1860s), the regional economy was focused on cattle production, with virtually the entire alluvial plain of modern-day Los Angeles and Orange Counties devoted to unmanaged open-range grazing [52–54]. By 1850, over-grazing had transformed the vegetation from dominance by perennial shrubs and grasses with large areas of thickets and live-oak forest (prairie) to dominance by native and then alien annuals; some observers described the plain as an overgrazed desert by the 1820s (electronic supplementary material). Heavy grazing has many negative effects [54], but most notable in this context is soil compaction from trampling that increases surface runoff of rain and thus the potential for soil erosion. Sediment transport to the sea, always episodic in this semi-arid setting, was thus almost certainly much higher during the nineteenth century than during preceding millennia of occupation by native hunter–gatherers [55,56]. Losses of riparian and coastal wetlands in the late nineteenth century, related to the laying of railroads and creation of Los Angeles Harbor, would have facilitated delivery of sediments to the sea until mid-twentieth-century flood-water controls [52,57].

Quantitatively, our compilation of mission records and US agricultural census reports indicates that livestock on the Los Angeles alluvial plain increased approximately exponentially from 1771 to the early 1800s, approximated carrying capacity by at least 1820–1835, and largely exceeded it for the rest of the century (figure 4*b*; mission records are conservative estimates that ignore feral horses, which were the focus of culls by 1805 [52,53]). By 1900 AD, all approximately 1 million acres had shifted to cultivated crops, although without modern methods of soil conservation. A history of sediment yield computed on the basis of these changes in land use (figure 4*c*,*f*) shows that sediment flux to the sea probably increased approximately 10-fold from pre-European prairie conditions through the nineteenth century, then decreased through the twentieth century with improved range management, soil conservation, river control and a shift to residential and industrial lands with low sediment yields. The conversion of prairie to intense livestock grazing in the early nineteenth century, and the transition to even more erosive cultivation in the late nineteenth century, thus coincides with the onset and steady decline of shell gravel fauna on the mainland shelf.

We hypothesize that extirpation of epifaunal suspension-feeders on the mainland shelf was caused not by sudden, permanent smothering of local populations, but rather by the cumulative effects of an increased frequency and volume of suspended sediment and temporary mud deposits. With progressive compaction of soils by livestock, rain runoff per storm would have increased, thereby increasing the frequency and magnitude of events of sediment delivery to the ocean in the absence of any change in rainfall patterns. This elevated sediment delivery would have been unabated—indeed, further increased—by the late nineteenth-century conversion of rangelands to cultivation and aggravated by the decline of filtering wetlands. At the coast, modern-day studies show that sand is retained near shore, but mud is transported onto the shelf via nepheloid-layer transport at the seabed rather than as a surface plume; most mud resides on the shelf for only a few months to years before it is resuspended and deposited permanently on the slope or basin floor [58,59]. Given the relatively long lifespans of large-bodied *Chlamys* (6 years) and *Laqueus* (12 years), nineteenth-century individuals would have been subject to more frequent debilitating or lethal events of suspended sediment and sediment deposition, and even short-term residence of mud would reduce opportunities for larval settlement and survival. A higher frequency of small-scale, geologically brief siltation events could thus drive demographic decline over an interval of less than 100 years.

The role of siltation in the extirpation of shell-gravel fauna on the mainland shelf is supported by the persistence of dense brachiopod populations on Channel Island shelves, which are sandier (median 21% mud for seabeds greater than 35 m versus 45% on the mainland; electronic supplementary material, figure S8). Grazing occurred on most islands, but mud deposition is highly localized owing to small watersheds and narrow, steep shelves [60]. The siltation hypothesis for the mainland shelf could be tested by information on temporal and spatial variation in sedimentation rates on adjacent slopes and deep basin floors, where cores with high-resolution geological or cultural markers could differentiate changes in sediment accumulation rate among the pre-colonial, nineteenth, twentieth and twenty-first centuries.

5. Conclusion

A greater understanding of the vast shelf biome and of the nature of recent and ongoing changes there is sorely needed. Geological age-dating of shells from time-averaged assemblages preserved in modern shelf seabeds can resolve changes in benthic community composition before the start of scientific monitoring or other historic accounts, providing unique information on the fully natural state of the ecosystem and legacies of past human stresses. For millennia, the coastal ocean of southern California supported a mosaic of epifaunal-rich shell gravels and trophically diverse infaunal-mud communities, an entirely unsuspected former state on the middle and outer mainland shelf. This ecosystem was lost over the course of the nineteenth century, well before urbanization and late twentieth-century benthic sampling efforts, and was most likely driven by increased solid-sediment delivery to the coastal ocean associated with the conversion of prairie to unmanaged livestock grazing and cultivation. Urban nutrients and industrial contaminants carried by wastewater, peaking in the late twentieth century, further altered the benthos, as has secular warming starting in the early twentieth century, but both started too late to contribute to the decline to extinction.

Loss of shell-gravel habitats has several implications for conservation and management. First, from a regional perspective, the nineteenth-century shift to a pervasively soft-bottom infaunal state will probably persist: rates of mud supply have declined by 45% over the last half century owing to damming and paving [56], but natural marine processes are unlikely to remove legacy mud deposits from the shelf on societally relevant time-frames. The similarity of the now-extinct mainland shell-gravel community to communities on Channel Island shelves thus places a premium on their protection there, and argues that remediation success on the mainland shelf should be judged largely on the basis of reattaining trophically diverse mud communities before anthropogenic siltation.

Second, and more generally, the timing of loss of the shell-gravel ecosystem on the open shelf of southern California was primarily from the runoff of solid sediment rather than from dissolved contaminants or climate change. This offshore reach is far beyond the lacustrine, estuarine and near shore settings where anthropogenic siltation stress is commonly detected [7,15,22,61]. Solid-sediment delivered by runoff, especially in regions with soil conservation today, is rarely considered as having potential to negatively affect biota on the open shelf. However, not all rivers have estuarine or other natural coastal traps and even these traps are not 100% efficient. Moreover, sediment yields are typically 10 times higher from unmanaged range and croplands than from well-managed lands and natural watersheds, an extraordinary load if sustained for decades or a century, as in southern California. Land-use legacies thus need consideration as another bottom-up stress on secondary production in offshore seabeds along with the more fully appreciated effects of bottom-trawling, cultural eutrophication and over-harvesting.

This collapse of the southern California shell-gravel ecosystem and its timing would not have been recognized without evidence from death assemblages. Live–dead discordance shows that communities had changed significantly—here, an ecosystem collapse—and dating demonstrates that the change was geologically and culturally recent, in this case driven by siltation and timed with the nineteenth-century introduction of livestock rather than driven by twentieth-century climate change and urbanization. This approach of unmixing time-averaged death assemblages, including making new use of samples acquired for conventional biomonitoring, is a powerful means of differentiating human drivers and determining natural baseline conditions. It will be effective in accessible but understudied coastal regions as well as in logistically challenging biomes such as open shelves.

Data accessibility. The occurrence data and age data are available at Data Dryad: http://dx.doi.org/10.5061/dryad.0r76j [62].

Authors' contributions. A.T. and S.M.K. designed the study, collected data, performed analyses and wrote the manuscript.

Competing interests. We declare we have no competing interests.

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