

Gauging benthic recovery from 20th century pollution on the southern California continental shelf using bivalves from sediment cores

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ABSTRACT: Urbanization of coasts creates stresses on adjacent marine communities, but the full impact is seldom known owing to scarce historical records. Paleoecological analysis of sediment cores can be a powerful means of reconstructing baseline benthic communities, but is particularly challenging for continental shelves where dead-shell assemblages are prone to greater time-averaging than in natural sediment sinks such as deltas, coastal bays, and estuaries. We compared temporal changes in the composition of bivalve shell assemblages collected from box cores on the Palos Verdes (southern California, USA) shelf to a 40 yr time series of annually collected living benthic assemblages in the same area in order to calibrate bivalve core assemblages to known changes in community composition during wastewater remediation. Older (pre-1970) core assemblages were then used to reveal the nature of bivalve communities from the early 20th century and the extent to which present-day communities match, i.e. have recovered to, early urban baselines. Deep bioturbation and only moderate sedimentation rates (0.2 cm yr⁻¹) damp the magnitude and rapidity of changes in core assemblage composition. Despite the geological complexity, bivalve core assemblages (1) detect known late 20th century dynamics in broad outline, (2) reveal the undocumented rise of chemosymbiont-bearing bivalves during the early 20th century, and (3) establish that the present-day community is largely but not fully recovered to its pre-effluent, early urban (1900–1930) baseline. Thus, cores capture the nature, timing, and duration of macrobenthic response to 20th century wastewater, validating this approach for shelf settings with scarce or no historical data.

KEY WORDS: Benthic assemblages · Mollusks · Sediment cores · Urban pollution · Southern California · Functional groups · Nutrient loading

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1. INTRODUCTION

Coastal oceans are strongly pressured by human populations, including bottom-trawling and other resource harvesting, nutrient inputs leading to anoxia and toxic blooms, alien species introductions, and climate change. Such stressors can diminish the capa-

city of ecosystems to provide important goods and services (Vitousek et al. 1997, Worm et al. 2006, Doney et al. 2012). Marine ecosystems near dense urban populations are especially vulnerable (von Glasow et al. 2013, Feist & Levin 2016). Many areas are now protected or subject to remediation, but setting goals for recovery and assessing its success

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[§]Changes were made after publication. For details see www.int-res.com/abstracts/meps/v615/c_p101-119/
This corrected version: April 26, 2019

remain difficult because information about the original community state is typically limited to direct observations of living populations. Such observations are usually sporadic before the onset of human stressors: quantitative monitoring typically begins only after an activity is suspected to have altered the system (e.g. Borja et al. 2010). Where pre-stress baseline data are lacking, species impacts will be undetected, extinction risks underestimated, and recovery goals set too low (Jackson et al. 2001, McClenachan et al. 2012).

Skeletal remains from surficial sediment (naturally accumulated death assemblages), archaeological sites (e.g. midden assemblages), and sediment cores (core assemblages) can be powerful sources of information on community status before the onset or early in the history of human stresses (Kidwell & Tomašových 2013, Rick & Lockwood 2013, Wilkinson et al. 2014). Paleoecological analysis of sediment cores in particular have a long history of use, but this approach usually focuses on coastal lakes, lagoons, estuaries, and back-reef areas that are natural sediment traps (e.g. Finney et al. 2000, Edgar & Samson 2004, Cramer et al. 2015, Armenteros et al. 2016, Wingard 2017). Core-based paleoecological analysis is much rarer on open continental shelves given challenging logistics and concerns of lower sedimentation rates and greater bioturbation, and has further relied almost exclusively on microfossils (e.g. Barmawidjaja et al. 1995, McGann et al. 2003, Rabalais et al. 2007; but see Gallmetzer et al. 2017), despite the diversity and ecological role of macrobenthos as secondary producers and habitat formers.

Here, we used incremental molluscan bivalve assemblages from ^{210}Pb -dated box cores to evaluate the success of remediation efforts on the urban continental shelf of Los Angeles County, southern California, USA. A long time-series of standardized benthic data collected under conditions of decreasing effluent since 1972 (Stull 1995) is available, allowing us to (1) calibrate bivalve core assemblages to the living community over the past 40 yr; older core assemblages can then be used to determine (2) the nature of pre-effluent and rising-effluent bivalve communities from the early 20th century and (3) the extent to which present-day communities match, i.e. have recovered to, those early urban baselines.

Radiocarbon-calibrated age-dating of individual shells from grab samples on this shelf shows that death assemblages from the top 10–15 cm of the seabed reflect extensive, multi-millennial time-averaging (Tomašových et al. 2014), complicating paleoecological inference. Moreover, age-unmixing

of these assemblages shows that the shelf had already been much modified before 1900 by solid-sediment runoff from intense 19th century land use that smothered benthic habitats existing before urbanization (Tomašových & Kidwell 2017). We thus focus here on resolving macrobenthic changes just within the urban 20th century, relevant to judging recovery from a key stressor, i.e. wastewater influx, common to many shelves globally.

2. MATERIALS AND METHODS

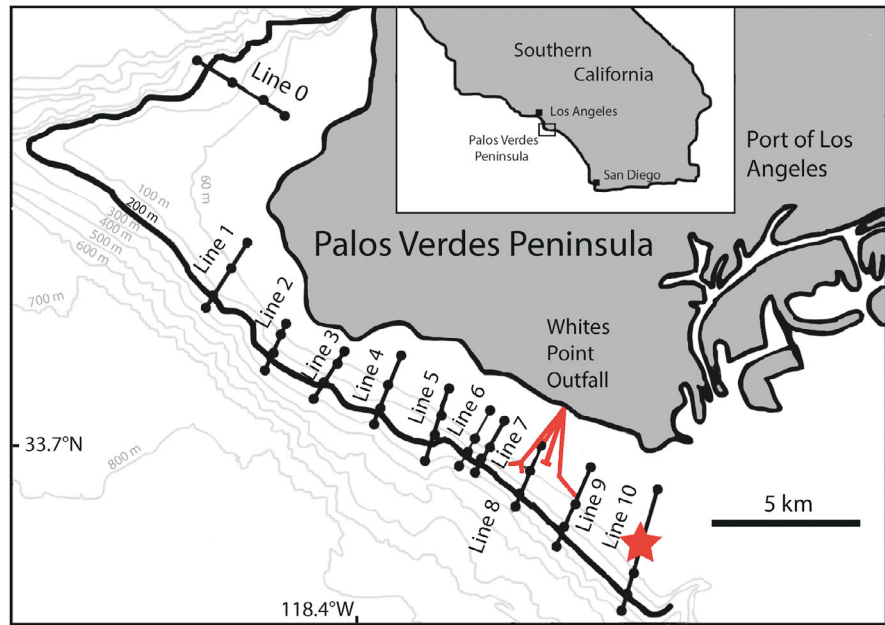
2.1. 20th century history of pollution and benthic response

The open continental shelf off Los Angeles County (Palos Verdes Shelf) has a long history of wastewater emissions (Figs. 1 & 2). Wastewater release via a pipe opening ('ocean outfall') at 34 m water depth started offshore of Whites Point in 1937; 2 Y-shaped outfalls, each 2.3 m in diameter, were opened at 60 m water depth in 1956 and 1966 and remain in use. In this period preceding passage of the US Clean Water Act in 1972, wastewater received primary treatment with intermittent chlorination but still carried a large particulate load, peaking at $\sim 150\,000\text{ t yr}^{-1}$, as well as $\sim 270\text{ kg d}^{-1}$ of DDT and other pollutants (Fig. 2). Emission of contaminants decreased markedly with advanced primary treatment in 1970, despite continued urban and industrial development of the served area. Both suspended-solid emission and biological oxygen demand from nutrient loading decreased sharply in the mid-1980s when half of wastewater received secondary treatment, and became negligible after 2003 when 100% of discharge was treated this way (Lyon & Stein 2009, Stein & Cadien 2009) (Fig. 2).

The majority of discharge was transported northwestward along the Palos Verdes shelf under the California Coastal Countercurrent, producing a historic, elongate mound of clayey, organic- and contaminant-rich sediment that eventually attained $\sim 60\text{ cm}$ thickness proximal to the outfall and still covers $\sim 40\text{ km}^2$ of the shelf and adjacent slope (Stull et al. 1996, Lee et al. 2002). Sediment deposition also extended southeastward, but by Line 10, located 4 km up-current from the outfall and the site of our cores, the effluent layer as identified by sediment chemistry is $< 5\text{ cm}$ thick (Stull et al. 1996, Alexander & Lee 2009).

Monitoring of infauna since 1972 on the Palos Verdes shelf documents benthic response to the

Fig. 1. Study area on the southern California continental shelf off the Palos Verdes peninsula. Lines 0 to 10 are sampling transects used by the Los Angeles County Sanitation Districts (LACSD) for annual biomonitoring of living macrobenthos; dots denote sampling stations at 30, 61, 152, and 305 m; star is our 50 m coring site PVL10-50 along Line 10, which is outside the effluent-affected area. Heavy black isobath: 200 m; red lines: outfall pipes. Modified from LACSD (2005)



multi-decadal history of wastewater remediation (Stein & Cadien 2009). Semi-annual to annual sampling on a grid of sites in waters 30–305 m deep along the entire length of the Palos Verdes shelf (Fig. 1) shows that macroinvertebrate species richness and evenness have increased several-fold since 1972, and the density and dominance of pollution- and hypoxia-

tolerant benthos decreased strongly. By 1994, only a few sites on the slope directly offshore of the outfall showed depressed biodiversity compared to reference conditions. Bivalves played a large role in these macrobenthic changes (e.g. Stull et al. 1986, Swartz et al. 1986) and are key components of an abundance-weighted regional 'benthic response index' (Smith et al. 2001). Of the 477 infaunal taxa that Smith et al. (2001) ordinated against sediment chemistry, the chemosymbiont-bearing lucinid *Parvilucina tenuisculpta* and mixed (facultative deposit) feeding tellinid *Macoma carlottensis* anchor the polluted extreme, and bivalves also help anchor the 'reference condition' extreme, especially suspension-feeders such as the cardiid *Nemocardium centifilum*. During the peak-effluent phase (1970s and early 1980s), huge populations of the bivalve *Parvilucina* occurred across much of the shelf outside the depauperate outfall zone itself (Fabrikant 1984, Swartz et al. 1986). These populations decreased in density and extent with secondary treatment in the early 1980s, providing a first-order prediction of late 20th century changes in the composition of bivalve core assemblages.

In contrast, data on macrobenthic community composition for the rising, early-20th century limb of the emissions peak are extremely scarce, limited to 2 surveys conducted in the 1950s, each with only a few

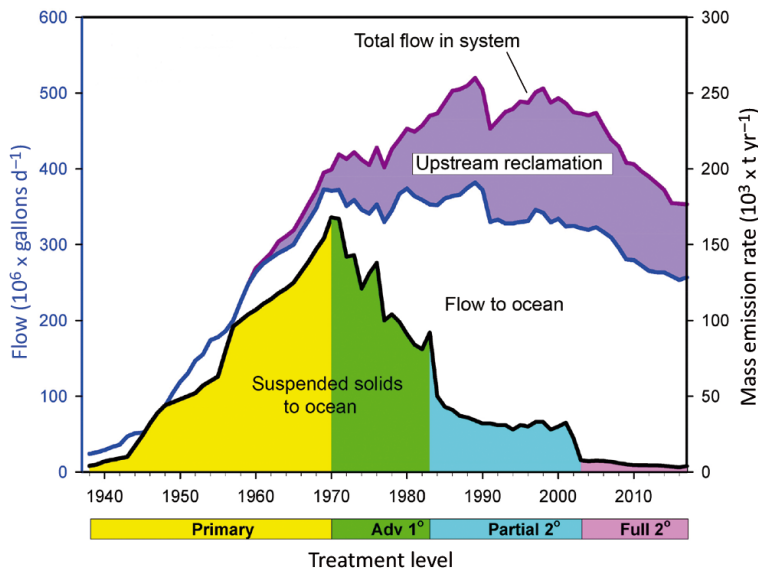


Fig. 2. Wastewater emissions (1 US gallon \approx 3.79 l) from the Los Angeles County ocean outfall off Whites Point from its opening in 1937. Suspended solids released to the shelf started to decline from their peak in 1972 with the Clean Water Act, dropped again in the mid-1980s and early 2000s as half and then roughly all water received secondary treatment, and have continued to decline since then. Monitoring of benthic infauna and other sedimentary indicators started in 1972. Adapted from LACSD (2018)

sampled sites in <200 m water depth (AHF 1965, Hartmann 1966). These and other environmental data from the 1950s (Rittenberg et al. 1958, Bandy et al. 1964) nonetheless recognized that the shelf was already severely polluted, a dead zone of H₂S-rich black muds that extended up-current almost to Line 10. Core-based analysis indicates that this dead zone may have emerged by ~1940 (Eganhouse & Pontolillo 2000). The zone with the highest contaminant concentrations expanded bathymetrically from 15–45 m in the early 1950s when the 34 m outfall operated (Bandy et al. 1964) to ~50–100 m with the 1956 opening of the new discharge pipe at ~60 m depth and closure of the original 34 m outfall in 1958 (Lee et al. 2002). H₂S-rich sediments still existed on the middle shelf by the early 1970s when biomonitoring began (Stull et al. 1986).

Emissions were thus unlikely to have had a macrobenthic signature on the middle shelf at Line 10 until at least the mid-1940s, based on the initially slow rise in outflow at the original 34 m outfall (Fig. 2). However, neither qualitative nor quantitative benthic data are available from anywhere on the shelf from this early-effluent (1940s) phase, nor from the pre-effluent (pre-1937) phase.

2.2. Core sample collection and processing

We focus on new cores, acquired in September 2012, at a station in 50 m water depth (PVL10-50) along Line 10 of the Los Angeles County Sanitation Districts (LACSD) biomonitoring grid (Fig. 1), a spot that is largely outside the area historically affected by effluent deposition and anoxia but was still within the range of nutrient-rich waters (Stull et al. 1996). We collected 5 large box cores (50 × 50 cm cross-section) and 6 vibracores (8 cm diameter aluminum barrels) while onboard the RV 'Melville' (cruise MV1211).

For radiochemistry, one 15 cm diameter PVC sub-core of a box core (BC2, 26 cm long) and the top 1.5 m of a vibracore (VC1, 502 cm long) were sectioned at 1 cm intervals in the first 10 cm and at 2 cm intervals thereafter, stopping at 35 cm in the vibracore. The ages of core increments were estimated using the short-lived radioisotopes ²¹⁰Pb and ¹³⁷Cs, which were analyzed using gamma spectroscopy as described by Alexander & Lee (2009). ²¹⁰Pb, with a half-life of 22.3 yr, is supplied at steady state from the atmosphere (excess ²¹⁰Pb) and adsorbed onto mud-sized particles, which are buried via both sediment accumulation and bioadvection. In both cores, the surficial activity of excess ²¹⁰Pb (4–6 disintegrations

min⁻¹ g⁻¹) is within the range previously observed in southern California continental shelf sediments, where excess ²¹⁰Pb activity declines to levels below instrumental detection within ~100 yr (Alexander & Venherm 2003, Alexander & Lee 2009). Bomb-generated ¹³⁷Cs usually has peak abundance in 1963, when fall-out from atmospheric weapons testing peaked, but the timing on the Palos Verdes shelf is delayed by ~10 yr (peak in 1971; Santschi et al. 2001) owing to the semi-arid climate, which causes a delay between its rainout on the upland and discharge to the sea.

Bivalve shells (core assemblages) were acquired by incrementally subsampling 2 box cores collected at the same station (BC3 and BC4), each 24 cm long. Each box core was subsampled using transparent Plexiglas subcores of our design, with a 15 × 15 cm square cross-section. After photography and description of core stratigraphy, sediment was extruded (3 subcores from BC3, 4 from BC4) in 2 cm increments up to 20 cm sediment depth, below which increments increased to 4 cm thickness. Subcore increments (e.g. 0–2 cm, 2–4 cm, etc.) were gathered from all subcores in that box core and wet-sieved on deck using seawater and a 1 mm mesh. This procedure yielded core assemblages from ten 2 cm thick core increments and a single 4 cm thick sample. Compiling material from both BC3 and BC4, a total of ~3 l of sediment was processed per 2 cm increment, comparable to the volume of sediment from a single Van Veen grab such as used in biomonitoring. The box cores provided abundant visual evidence of bioturbation: open 1 cm diameter burrows and biogenic topography at the sediment–water interface; an upper ~10 cm of homogeneous brownish silty sand reflecting 'complete' reworking; and both open and shell-packed burrows to ~20 cm core depth produced by callianassid shrimps and other 'non-local' infaunal feeders, as also observed on this shelf by others (Swift et al. 1996, Wheatcroft & Martin 1996, SAIC 2005).

Sieve residue from the top 10 cm was processed immediately for live animals. Although samples were too small for quantitative analysis of living fauna, this sorting permitted immediate air-drying of the remaining residue. That residue was dominated by the calcareous shells of macrobenthos and was sorted for taxonomically identifiable bivalve individuals at the University of Chicago. To be counted as a dead bivalve individual, a fragment had to retain at least one-half of its hinge line or the umbo. All valves were counted using a conventional, maximum-number-of-individuals procedure that assumes each valve comes from a different living bivalve individual (Gilinsky & Bennington 1994). This processing yielded,

from BC3 and BC4 combined, 6556 individuals and 61 species (see Table S3 in the Supplement at www.int-res.com/articles/suppl/m615p101_supp.xlsx).

2.3. Data on bivalve living assemblages

The LACSD has surveyed infaunal macrobenthos on the Palos Verdes shelf since 1972, sampling the seabed at 4 sites along each of 11 bathymetric transects (Fig. 1). Surveys were semi-annual (February and August) until 2006 and annual (summer) since then, using Shipek grabs until 1980 and Van Veen grabs since then (0.1 m², with 10–15 cm penetration; 1–1.5 l sediment volume per grab). Each sample was sieved on deck through a 1 mm mesh with seawater, fixed in 4% formalin seawater, and later transferred to 70% ethanol for preservation. In the lab, all live animals from all phyla were picked, counted, and identified to species level using a standardized regional taxonomy (SCAMIT 2013).

We compiled the bivalve subset of these data from the years 1972–2012 at the 2 shallowest stations along LACSD's Line 10 (Station C at 61 m and Station D at 30 m) to approximate the composition of living bivalve assemblages at the intervening 50 m depth of our coring site. We used only the first replicate from the summer sampling of each site; species abundances per year reported here are thus the density of living bivalves in a single 0.01 m² summer sample; up to 1980, we pooled 3 Shipek grabs into a single living assemblage for analyses of raw abundances so that they could be compared with later samples collected using Van Veen. To reduce noise from small sample sizes and better approximate the lower temporal resolution of naturally time-averaged core assemblages, we pooled annual counts to 10 yr assemblages (i.e. 1972–1981, 1982–1991, etc.). Pooling data from Stations 10C and 10D, the bivalve dataset from 1972–2012 comprises ~20 000 live-collected individuals and 59 unique bivalve taxa (Table S1).

2.4. Data treatment and analysis

Core-assemblage data from equivalent sediment depths in the 2 box cores BC3 and BC4 were pooled, yielding 10 core assemblages from 2 cm thick increments and 1 core assemblage from the bottom ~4 cm increment. Using SCAMIT (2013), 92% of bivalves from core assemblages could be identified to the species level. Combining core assemblages from PVL10-50 and 40 yr of live data from the 10C and

10D biomonitoring stations, the bivalve fauna on the Line 10 middle shelf totals 84 unique bivalve taxa, of which 25 occurred only in core assemblages and 23 occurred only in living assemblages. Raw species richness, species richness rarefied to $n = 50$ specimens, and the probability of interspecific encounter as a metric of evenness (Hurlbert's PIE) were calculated for annual living bivalve assemblages, for living assemblages pooled to 10 yr bins, and for each core assemblage using the iNext package (Hsieh et al. 2016).

Species were assigned to 1 of 7 functional groups differentiated by life habit and trophic group using ecological insights from Todd (2000) and Coan et al. (2000): infaunal chemosymbiont-bearing (lucinids, thyasirids, solemyids), infaunal mixed feeders (facultative deposit-suspension; tellinids, psammobiids, solecurtidids, and the asiphonate carditid *Cyclocardia* per Jones & Thompson 1987), infaunal obligate deposit feeders (siphonate nuculanids and yoldiids; asiphonate nuculids), epifaunal suspension feeders (mytilids, pectinids, chamids, limids; includes nestling hiattellids preferring coarse debris and semi-infaunal byssate Modiolinae), infaunal suspension feeders (cardiids, venerids, pharids, corbulids, thraciids), commensals (inside the burrow of or attached to the body of another animal; lasaeids), and predators (cuspidariids). Commensal and predatory bivalves were rare in core assemblages (each constituting <2% of bivalve shells) and were also either very erratically abundant (commensals, depending on whether a sample intersected with a burrow; up to 24% but median 1.5%) or consistently rare (few occurrences of single individuals) in living assemblages, and thus were excluded from further functional-group analysis.

Trends in both the raw (numbers of individuals) and proportional abundances of species and functional groups were compared between the core and living assemblages, both qualitatively and quantitatively, to address the following 3 questions. (1) Since the early 1970s, when inputs of solid sediment and contaminants were at peak values (Fig. 2), do core assemblages exhibit a qualitatively and quantitatively similar decline in pollution-tolerant species and functional groups? (2) Do core increments between 1900 and 1970 exhibit the increase in pollution-tolerant bivalves expected from the onset and increase in emissions to the Palos Verdes shelf? (3) Which pre-1970 core increments do the core-top (2010) and modern-day living assemblages most closely resemble, as a gauge of the extent to which macrobenthic communities have recovered under remediation?

The 40 yearly living assemblages, the four 10 yr pooled living assemblages (1972–1981, etc.), and the 11 core assemblages (each separated by ~10 yr on the basis of the age model below, but each representing more than 10 yr) were compared in terms of their functional group and species composition. They were plotted on linear time-axes for comparison using 95th confidence intervals on functional group proportional abundances. Species-level data were ordinated on the basis of square-root transformed proportional abundance with nonmetric multidimensional scaling (NMDS). Using Bray-Curtis distances, we tested (1) whether multivariate dispersions of decadal-pooled living and core assemblages differed using a test of homogeneity of multivariate dispersions (Anderson et al. 2006), (2) whether the composition of core assemblages differed from the composition of living assemblages, i.e. whether distances between core assemblages and the centroid of living assemblages were larger than the distances between living assemblages and their centroid (Tomašových & Kidwell 2011), and (3) whether the composition of core assemblages shows any relationship to temporal separation among increments with the Mantel test (Anderson & Walsh 2013). All analyses are based on Bray-Curtis distances, and were conducted in R using the 'vegan' package (Oksanen et al. 2018).

3. RESULTS

3.1. Age-model for core assemblages

Excess ²¹⁰Pb is constant within the upper 9–10 cm of both the box and vibracore, indicating complete biomixing on yearly to decadal time scales, and then declines monotonically to levels below detection by 33 cm core depth in vibracore VC1, producing an apparent sedimentation rate of 0.23 cm yr⁻¹ (95% confidence intervals = 0.19–0.26 cm yr⁻¹; Fig. 3). The decay profile from the shorter (26 cm) box core BC2 is consistent (Fig. 3), including 2 outlier (enriched) values from 20 to 26 cm, probably representing a zone affected by downward piping of sediment by non-local feeding infauna. The activity of bomb-generated ¹³⁷C shows a clear peak in the vibracore at 9 cm, suggesting 0.22 cm yr⁻¹ (assuming it corresponds to ~1971), but multiple peaks in the box core, also indicating smearing and displacement by bioturbation (open burrows to 18 cm core depth).

These estimates of ~0.2 cm yr⁻¹ for the middle shelf of Line 10, located at the up-current edge of the effluent-affected zone, are consistent with previous esti-

mates of 20th century sediment accumulation on this shelf for periods before effluent release (e.g. Gorsline 1992, Swift et al. 1996, Alexander & Lee 2009). Effluent deposition increased sediment accumulation rates closer to the outfall in the late 20th century (between Lines 3 and 9; Lee et al. 2002), but Line 10 remained largely unaffected.

We used this apparent sedimentation rate of 0.2 cm yr⁻¹ to estimate that the box cores (BC3 and BC4) sieved for bivalves capture ~110 yr of deposition. The 11 box-core assemblages are binned into decadal-scale age groups that differ in their central tendency; the upper ten 2 cm increments have 'mean' ages extending from 2010 back to 1920, and the bottom 4 cm thick increment represents 1900–1910 (Fig. 3). Differences in slope estimates derived from the box and vibracore radioisotopic data (ranging from 0.20–0.23 cm yr⁻¹) can shift the estimated mean age of a sedimentary increment by 5–10 yr, and uncertainty in slope estimation itself can shift the age based on the upper 95% confidence interval by 10–40 yr.

These uncertainties, combined with burrows and signs of non-local bioturbation in ²¹⁰Pb profiles, suggest that, although sedimentary increments differ in mean age, the age range of particles in 1 core increment (or of shells in 1 core assemblage) likely overlaps that of adjacent or additional core increments. This inference is supported by our radiocarbon-calibrated age-dating of shells of 2 bivalve species from these same box cores (A. Tomašových et al. unpubl.): consistent with extensive bioadvection, (1) the age ranges of shells in consecutive increments strongly overlap, including shells that are several thousand years old, and (2) the median age of shells per increment is consistently '20th century,' and does not increase monotonically down-core within the uppermost 24 cm of these box and vibracores.

To convey the complexity of age modeling in such a bioturbated record, ²¹⁰Pb-based age values based both on the slope and on its 95% confidence interval are scaled in Fig. 3, where only the core depth (cm, left edge) is fully determined.

3.2. Bivalve living assemblages 1950s to 2012

Bivalve communities from the middle shelf along Line 10 from 1972–2012 changed in raw numbers of individuals, species diversity, and functional-group composition (Fig. 4) that are consistent both with ecological recovery in response to increased wastewater treatment (Fig. 2) and with changes observed in the

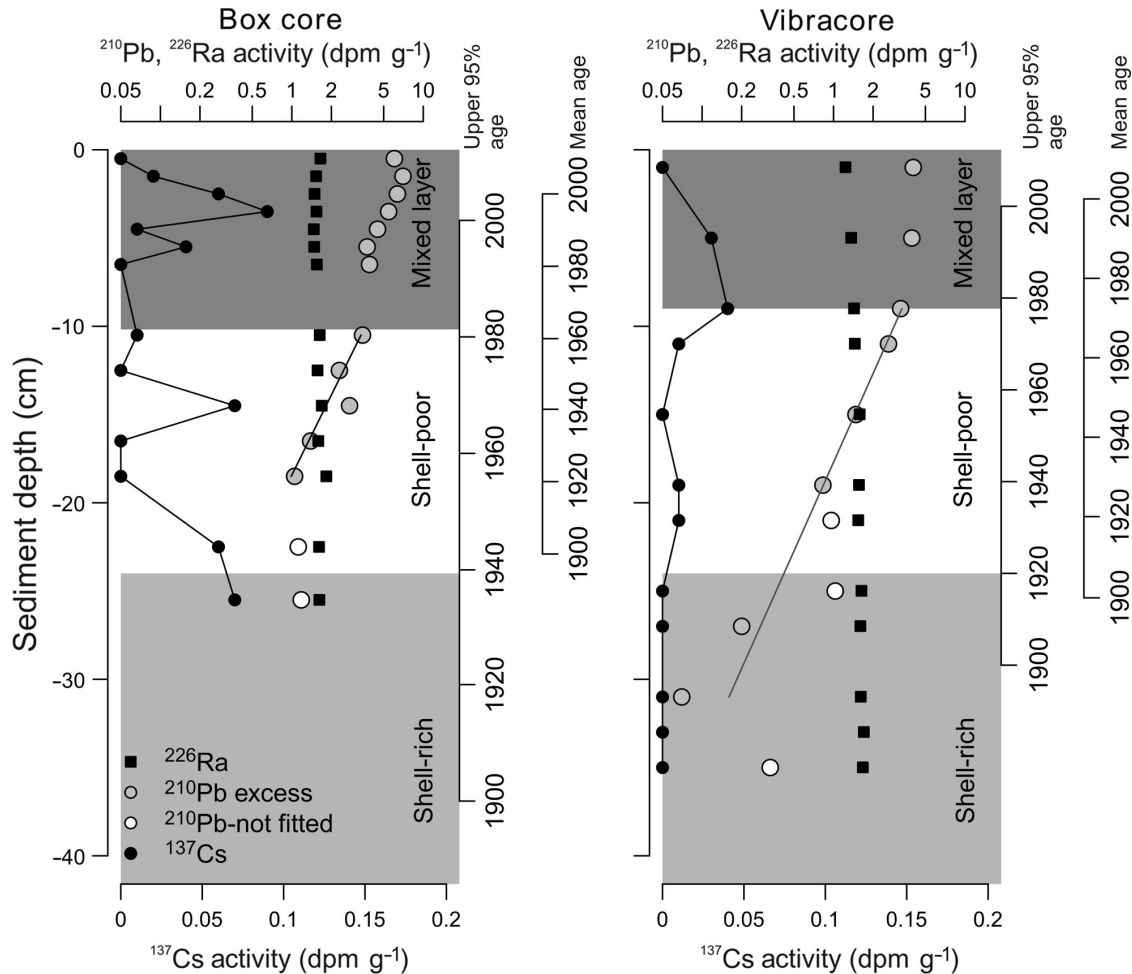


Fig. 3. Radiochemical profiles for a box core (BC2; left column) and the upper part of a vibracore (VC1; right column) at site PVL10-50. Core sample depths are raw depths, uncorrected for a 4.4% core shortening due to compaction. Calendar dates represent mean predicted ages of ^{210}Pb -carrying grains and the upper 95% age bounds on those mean ages based on the Constant Flux–Constant Sedimentation model. Age binning is based on excess ^{210}Pb in VC1

entire macrobenthos and other routine sediment monitoring (Stein & Cadien 2009). Both raw and sample-size standardized richness increase, as does living assemblage evenness, especially once secondary treatment began in the mid-1980s (Fig. 4A). Total numbers of bivalve individuals (hereafter reported as individuals per 0.1 m^2) were exceptionally high in the 1970s–80s during peak emissions (thousands of individuals), declined by an order of magnitude in the late 1980s with remediation, and continued to decline to only 50–100 ind. in the 2010s (Fig. 4B), with the last phase overlapping with the 1994 introduction of the carnivorous gastropod *Philine auriformis* (Cadien & Ranasinghe 2001) and the 2003 transition to 100% secondary treatment (Fig. 2).

Bivalve community composition also changed dramatically, driven largely by order-of-magnitude changes in the raw abundance of chemosymbiont-

bearing bivalves, especially the pollution-tolerant lucinid *Parvilucina tenuisculpta* (Fig. 4B,C). Populations of *Parvilucina* at 10C (61 m depth) fluctuated between 240 and 810 ind. during peak emissions (1972–1979); increased abruptly to >1500 in 1980 and 1981, and then remained at 400–1000 in 1982–1984, all during advanced primary treatment with still relatively high emissions (1979–1985). They declined abruptly to <100 ind. by 1990 and decreased to <20 from 1991 onward as secondary treatment became complete. Raw abundances of *Parvilucina* at the shallower station 10D (30 m) were consistently smaller, mostly <20 ind., peaking at 51 in 1985. *Parvilucina* consistently and overwhelmingly dominated the bivalve community (85%) during the 1970s and early 1980s when emissions were highest. Their average body size also nearly tripled under high nutrient enrichment near the outfall (Fabrikant 1984). The entire

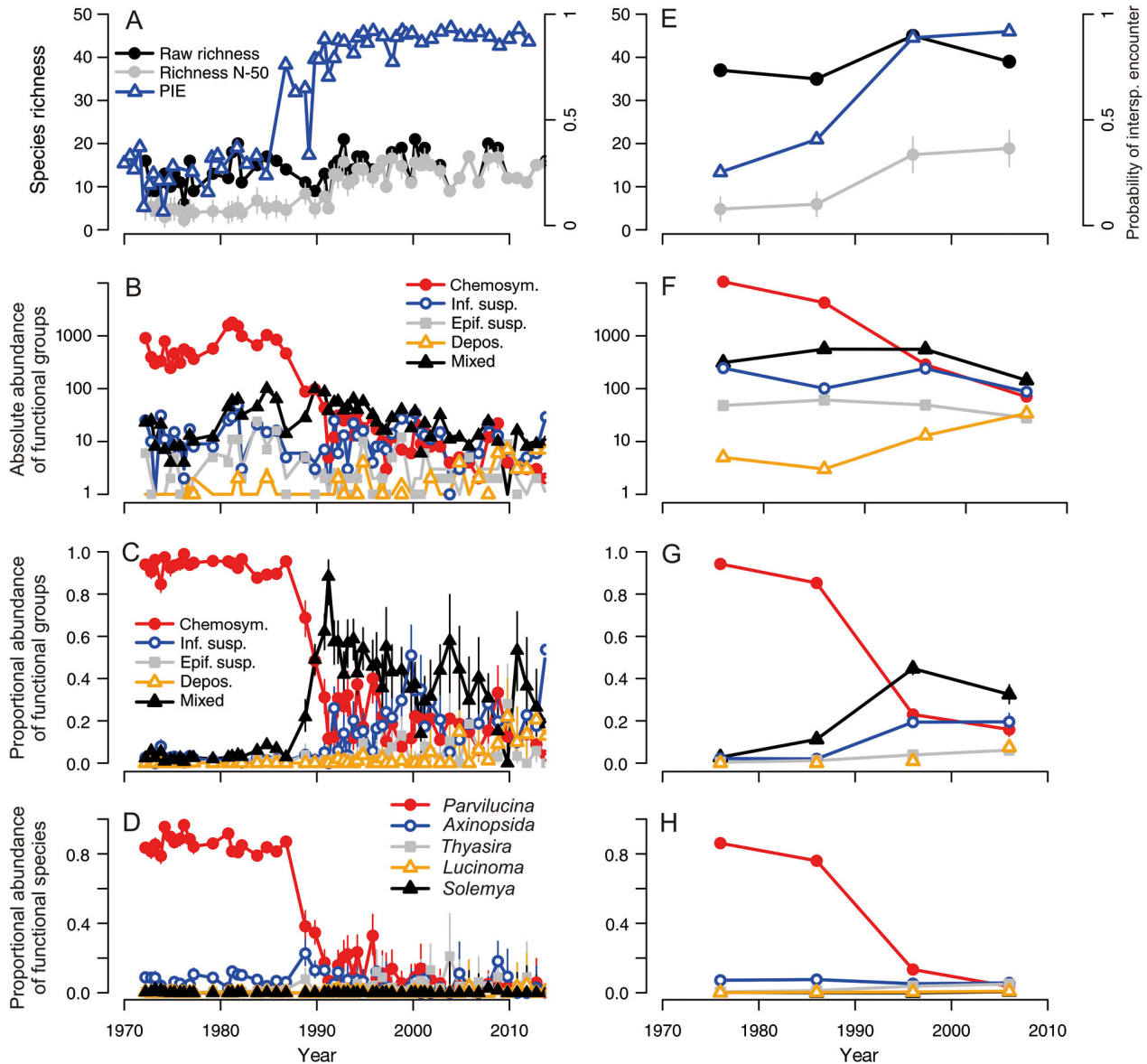


Fig. 4. Data on living bivalves collected since 1972 near coring site PVL10-50, based on pooling annual data from 2 sites (10D at 30 m and 10C at 61m) into annual (left column) and 10 yr time bins (right column, to simulate time averaging). (A,E) Species richness and evenness (probability of interspecific encounter, PIE) of living bivalve assemblages increased dramatically in the late 1980s after the start of secondary wastewater treatment. (B,F) Raw number of living individuals in the 5 most abundant functional groups (see Table S2 in the Supplement), showing a dramatic decrease in chemosymbiont-bearing bivalves in the 1980s. (C,G) Proportional abundance of functional groups (see Table S2) documents the steep decline in chemosymbiont-bearing bivalves and concomitant rise to dominance of mixed (facultative deposit) feeders in the 1980s, with increasing equitability of trophic groups though the 1990s and 2000s. Error bars are 95% confidence intervals. (D,H) Proportional abundance of the main constituent species of the chemosymbiont-bearing functional group, showing dominance by the lucinid *Parvilucina tenuisculpta* during maximum emissions in the 1970s–80s and increasingly equitable numbers of *Parvilucina* and the thyasirid *Axinopsida serricata* since the on-set of secondary treatment

functional group of chemosymbiont-bearing bivalves, by contrast, comprised <40% of the living assemblage by the 1990s and <20% in the 2000s (Fig. 4C), by which time *Parvilucina* became roughly co-abundant with the thyasirids *Axinopsida* and *Thyasira* (Fig. 4D). Those and other chemosymbiont taxa had

been present throughout the peak emissions period at relatively steady but low densities; *Axinopsida* seems to have thrived best, but only *Parvilucina* had exceptional densities under peak emissions (Fig. 4D).

With the decline of *Parvilucina* in the late 1980s, mixed feeders (especially *Macoma*) rose to domi-

nance, increasing from fluctuating densities of 10–100 ind. during peak emissions to a steady ~100 in the early 1990s. Mixed feeders have declined in abundance since then (only a few tens of individuals in the 2010s), but they remain the top-ranked functional group at ~30% (Fig. 4B,C). Infaunal suspension feeders maintained relatively steady, albeit low, densities throughout the 1972–2012 interval (tens of individuals); epifaunal suspension feeders have also been steady but at much lower densities (0–10 ind.); obligate deposit feeders (mostly nuculanids) have increased modestly in occurrence and density since the 1990s (to 10 ind.), becoming co-abundant with epifaunal suspension feeders (Fig. 4B). The community has thus changed (Fig. 4C) from (1) overwhelming dominance (95%) by chemosymbiont-bearing taxa during the 1970s–80s interval of peak emissions to (2) dominance by mixed feeders during the 1990s following the onset of secondary wastewater treatment and (3) increasing equitability of these and suspension- and deposit-feeding groups to the present day (complete secondary treatment of wastewater), all concomitant with dramatically dropping raw abundance (density) of bivalves. The high taxonomic evenness and rarefied richness in the bivalve living community today (Fig. 4A) comes from the collapse of the *Parvilucina* populations that had so strongly dominated the community during peak emissions and the tailing off of the 1990s bloom of mixed feeders that followed the chemosymbiont collapse, producing a trophically more equitable composition.

Survey data of the Palos Verdes shelf from the 1950s, when primary wastewater treatment was inefficient, are only semi-quantitative. The Allan Hancock Foundation (AHF) survey of the late 1950s (AHF 1965) indicated that bivalve abundances probably did not exceed 100s of individuals and numbers of *Parvilucina* were rather low (maximum 10 ind. >1 mm per ~50 l grab). However, chemosymbiont-bearing bivalves were already dominant (56–100% range, median 76%, of all bivalves in 4 middle-shelf samples from 1957; AHF stations 5086, 5027, 5029, 5502) and *Parvilucina* was already important, with *Axinopsida* and *Thyasira* as common co-dominants. Suspension feeders were the second most numerous and frequently occurring functional group. Dominance by chemosymbiont-bearing taxa on the middle shelf at Line 10 thus appears to have been underway by the late 1950s (AHF samples), but raw population sizes were still small.

Earlier samples (Hartmann 1966; collected in 1952–53) were processed primarily for polychaetes; samples with at least genus-level data on mollusks

are exclusively from the inner shelf down-current of the then-active 34 m outfall (Hartmann's samples 27, 28, 45, 45b). The inner shelf then was shelly and locally rocky but nonetheless supported a detritus-based bivalve community, with a mix of living and dead chemosymbiont-bearing *Thyasira*, obligate deposit feeders (nuculid, nuculanid, and yoldiid bivalves), mixed feeders (tellinid *Macoma* and solecurtid *Tagelus*), and infaunal suspension feeders (venerid *Pitar*), although never more than a few specimens >1 mm per ~50 l sample.

3.3. Bivalve core assemblages and live-core comparisons

Core assemblages show a down-core increase in total bivalve abundance, even after compensating for the thicker bottom increment (Fig. 5B), which is notably shellier than the rest of the core. A small peak in the raw abundance of chemosymbiont-bearing species occurs at 10–14 cm (mid-20th century according to the age model). This and most other functional groups then decline in raw abundance to the present, with chemosymbiont-bearing taxa dropping out of the top rank, resembling the pattern in the living assemblages since 1972 (Fig. 5B). The scale of the decline in raw numbers is about an order of magnitude lower (compare with log-scale for living assemblages, Fig. 4B).

Raw richness is highest at the bottom of the core (43 species), where the sample size is largest, and declines to ~30 species in the core top (Fig. 5A), about twice the raw richness of annual samples of living bivalves (Fig. 4A). Sample-size standardized richness is roughly constant through the core at ~15 ($N = 50$), which is comparable to the rarefied richness in bivalve living assemblages (Fig. 4A) in the 1990s to present (secondary treatment) and much higher than that observed alive (~5 species) during the 1970s–80s peak emissions interval. Core assemblage evenness is constant and very high (PIE ~0.9) throughout the core (Fig. 5A), closely approximating the living assemblage evenness from the present secondary treatment phase but failing to detect the low evenness of peak emissions (living PIE 0.25–0.35 in the 1970s–80s; Fig. 4A). Core assemblages from the 1970s–2010s thus do not exhibit the increase in richness and evenness that living assemblages exhibit over the same interval of decreasing nutrient loading.

In proportional abundance, chemosymbiont-bearing bivalves are the top-ranked functional group in the 3 mid-core increments (8–14 cm, early half of

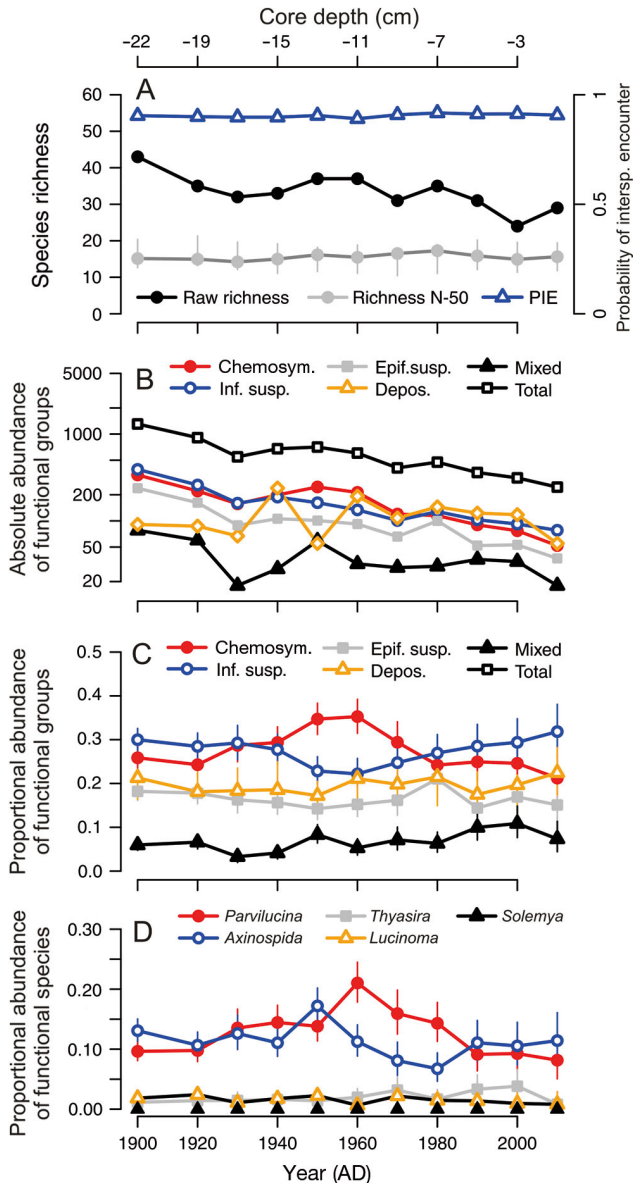


Fig. 5. Data on bivalve core assemblages. (A) Species evenness (probability of interspecific encounter, PIE) is high throughout the core, and species richness is steady when rarefied to a standard sample size. (B) Raw number of dead individuals in functional groups, and strong decline in total numbers of bivalves to a minimum of 196 specimens in the top 0–2 cm increment (mean age 2010). (C) Proportional abundance of functional groups, showing equitable proportions of infaunal suspension feeders, obligate deposit feeders, and chemosymbiont-bearing bivalves in the pre-effluent early 20th century, a rise to dominance by chemosymbionts for multiple decades in the peak-effluent mid-20th century, and a decline back to equitability with late 20th century remediation. Error bars are 95% confidence intervals. (D) Proportional abundance of the main constituent species of the chemosymbiont-bearing functional group, showing dominance by the lucinid *Parvilucina tenuisculpta* during the group's mid-20th century peak; *Parvilucina* and *Axinopsida serricata* were co-dominant in the early 20th century and in the 1990s to present

the late-20th century) (Fig. 5C), dominated by *Parvilucina* (Fig. 5D). The timing of this peak corresponds approximately to the well-documented top-ranking of living chemosymbiont-bearing bivalves in the 1970s to early 1980s (Fig. 4C) and their likely high proportional abundance in the 1960s. Considering the upper 95% confidence interval of the ²¹⁰Pb age-model prediction, the central tendency of the 10–12 cm increment might be as young as 1974 (VC-based model) or 1982 (BC-based model; Fig. 3).

The peak abundance of the chemosymbiont-bearing group is strongly damped in core assemblages, with a maximum of 35% versus >95% in bivalve living assemblages (Figs. 4C & 5C). However, the temporal pattern of switching among dominant taxa within the chemosymbiont group is consistent with data on living assemblages: the lucinid *Parvilucina* and thyasirid *Axinopsida* were co-dominant in core increments from the early 20th century (14–24 cm), comparable to the co-dominance observed in the oldest living assemblages from the 1950s; *Parvilucina* constitutes the majority of chemosymbiont-bearing bivalves at 8–14 cm, corresponding to the early half of the late-20th century, as also seen in living assemblages. *Parvilucina* decreases to once again become co-abundant with *Axinopsida* and *Thyasira* in the uppermost core increments, as seen in living assemblages in the 1990s–2010 (Fig. 5D). The core-based record of chemosymbiont-bearing taxa, individually and as a group, thus conforms to a damped version of that known directly from living assemblages.

Mixed feeders (tellinids, mostly *Tellina* sp. B and *Macoma yoldiformis*) maintain a low and steady proportional abundance (at ~5%) in core assemblages in the lower half of the core (10–24 cm), but double at 2–6 cm (latest 20th century) and decline back to ~5% in the 0–2 cm core top (early 21st century; Fig. 5C). The decline is qualitatively similar to mixed feeders in living assemblages, which were subsidiary in the 1950s, 1970s, and early 1980s (7–8% in Hartmann and AHF samples from the 1950s; 2–9% in LACSD data from the 1970s and early 1980s), bloomed in the late 1980s–90s (to ~50%; mostly *Macoma yoldiformis*, *Tellina cadieni*, and *Tellina* sp. B along Line 10), and have since declined, although only to ~20% (Fig. 4C). Core assemblages thus capture the qualitative trend in living assemblages of a small peak following the collapse of chemosymbiont-bearing taxa as emissions declined, but, although its timing is correct, the maximum proportional abundance of the mixed-feeder functional group is strongly damped from that observed in living assemblages.

Infaunal suspension feeders, mainly represented by the venerid *Compsomyax* and cardiid *Nemocardium*, are the second most abundant functional group overall in the core. The group is top-ranked at ~30% at 16–24 cm (early 20th century), dips in proportional abundance to ~20% in the early late-20th century during the peak of the chemosymbiont-bearing group, and then returns to ~30% at 0–8 cm (latest 20th century; Fig. 5C). This pattern resembles, in damped but well-timed form, the relatively low abundance of infaunal suspension feeders in living assemblages during the 1950s–80s (a few percent), and their increase during the 1990s to ~20%, remaining stable to the 2010s (Fig. 4C).

Epifaunal suspension feeders (mostly the small scallop *Leptopecten latiauratus*, and secondarily the large scallop *Chlamys hastata* and mussel *Modiolus*) constitute 15–20% of assemblages throughout the core (Fig. 5C), in contrast to their very low abundance in living assemblages, where they have increased above a few percent (to ~10%, mostly the mussel *Solamen*) only within the last 15 yr (Fig. 4C). Shells of *C. hastata* are consistently present throughout the core (a few percent), although this species has never been sampled alive along Line 10 nor elsewhere on the Palos Verdes since sampling began in the 1950s (Tomašových & Kidwell 2017).

Obligate deposit feeders (mostly asiphonate nuculanids, especially *Nuculana taphria*) constitute 18–22% of core assemblages at 14–24 cm (early 20th century), dip slightly to ~17% in the mid-20th century

during the peak of the chemosymbiont-bearing group, and generally increase in abundance since then toward 22% in the core top (early 21st century; Fig. 5C). Their increase in recent decades thus has the same trend as in living assemblages. However, deposit-feeder abundance in core assemblages during peak emissions was much higher than the zero to few percent abundances observed in living assemblages (Fig. 4C). Deposit feeders have increased to 10–20% in living assemblages only since 2004, and only in scattered years (Fig. 4C, see annual data versus 10 yr binned data; mostly *N. taphria*). Variation in deposit-feeder abundance in the cores is thus much smaller than observed in living assemblages (a few percentage points rather than ~20%), and core abundances are consistently higher (Figs. 4C & 5C).

3.4. Multivariate comparison of living and core assemblages

NMDS of square-root transformed species proportional abundance data for unpooled yearly living assemblages, living assemblages pooled to 10 yr bins, and naturally time-averaged core assemblages show, first, that core assemblages cluster tightly in ordination space and differ significantly in composition from living assemblages ($F = 46$, $p < 0.001$, Fig. 6A). Second, living assemblages binned by decade exhibit greater separation, i.e. are more different from each other, than are core assemblages: their multi-

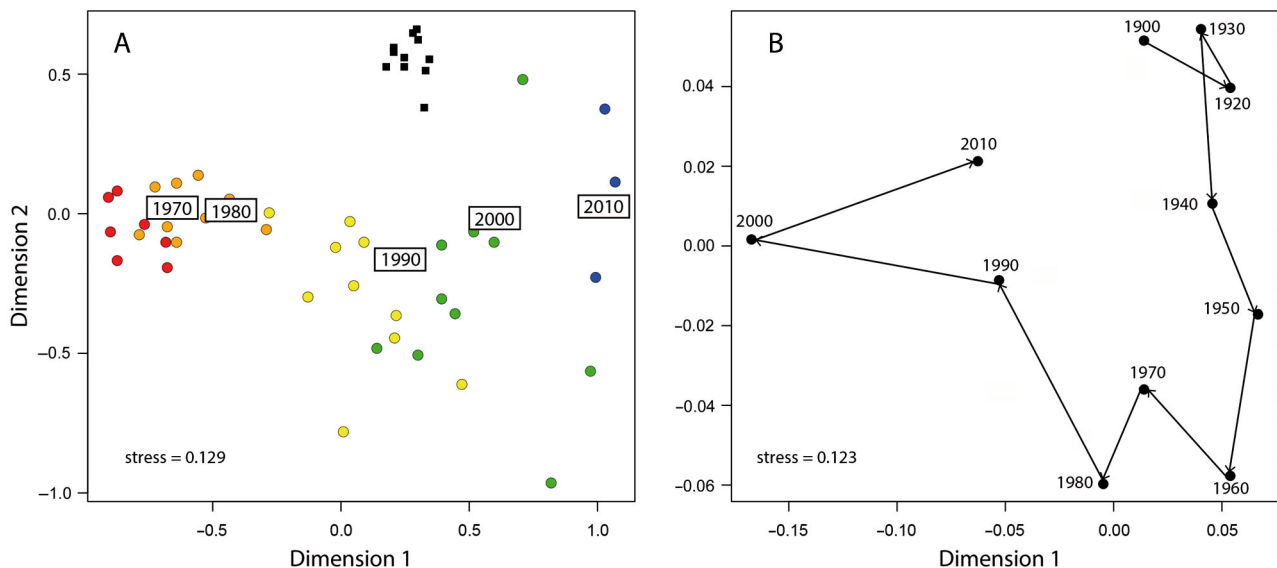


Fig. 6. Non-metric multidimensional scaling (NMDS) performed on square-root transformed species proportional abundances. (A) NMDS using both living and core assemblage data; circles denote living assemblages, colored by their decadal age midpoint (numbers). Black squares denote core assemblages. (B) NMDS using core assemblages only, denoted by their midpoint calendar age

variate dispersion (mean Bray-Curtis dissimilarity among the group centroid and assemblages = 0.32) significantly exceeds dispersion among core assemblages (mean Bray-Curtis dissimilarity = 0.11; $F = 70.7$, $p < 0.0001$). The increasing dispersion in NMDS space of annual living-assemblage samples starting in the 1990s and continuing to today (Fig. 6A) reflects the increased inter-annual variability in their functional group abundances, in contrast to the highly stereotyped and almost monotypic living assemblages of the 1970s to early 1980s (Fig. 4B,C).

The species most responsible for the large compositional separation between living and core assemblages (NMDS axis 2) is the deposit feeder *Nuculana taphria*, which attains 15–19% of bivalves in every decadal core assemblage but is absent or rare in living assemblages (0 to 1% in the 1970–1990s, increasing to 6% by the 2000s and 12% by the early 2010s). Epifaunal suspension-feeders (the scallops *Leptopecten latauratus* and *Chlamys hastata* and mussel *Modiolus* sp.) and infaunal suspension feeders (mostly *Compsomyx subdiaphana* and *Nemocardium centifilosum*) are also over-represented in core assemblages. In contrast, mixed-feeders are under-represented in cores, comprising at most 11% rather than ~50% at peak abundance. Chemosymbiont-bearing bivalves and *Parvilucina* in particular are the most severely under-represented, achieving 35% (21% *Parvilucina*) at maximum in cores in contrast to 95% (85% *Parvilucina*) in the 1970 and 1980 decadal living-assemblage bins.

Living assemblages show temporal structure in NMDS space with a major gradient along the first axis, reflecting the proportional decline in *Parvilucina* from its peak abundance in the 1970s and the increasing equitability of the chemosymbiont-bearing group with other trophic groups in the 1990s and 2000s, despite higher inter-annual variability (Fig. 6A). Living assemblages from the 1970s and early 1980s during the primary treatment phase of high effluent are thus clearly separated from living assemblages collected in the 1990s and 2000s during remediation.

Core assemblages preserve this temporal structure despite much smaller dispersion (Mantel test rank-correlation of temporal separation between 10 yr increments against their Bray-Curtis dissimilarities, $\rho = 0.64$, $p < 0.001$). Core assemblages show a nearly circular trajectory in NMDS space (Fig. 6B), although differences in Bray-Curtis dissimilarity are very small. Core assemblages from 16–24 cm (the pre- to early-effluent early 20th century) are closely spaced in the upper right quadrant; core assemblages from 8–16 cm (the high-effluent state of the mid to early

part of the late 20th century) shift down into the lower half of the diagram; and assemblages from 0–8 cm (the reduced-effluent and remediated latest 20th and early 21st century) reverse that trajectory, shifting back into the upper but left quadrant.

Bivalve core assemblages from the remediated shelf thus do not overlap with those from the pre-effluent shelf (Fig. 6B). However, the nearest neighbors of the core-top 2010 assemblage in NMDS space (other than the immediately preceding, likely auto-correlated decadal increments) are the pre-effluent assemblages at the base and next-to-base of the core (18–24 cm, Fig. 6B). These assemblages have the same 6 taxa in their top ranks, with the deposit-feeder *Nuculana* top-ranked (at 18% and 17–21% of the top and bottom core assemblages, respectively) and the chemosymbiont-bearing *Parvilucina* bottom-ranked among these 6 taxa (at 8% and 10–11%). In contrast, *Parvilucina* is top-ranked in core assemblages from the rising-effluent (1940s–1960s) and peak-effluent (1970s) decades, and is 6–21% more abundant there than in the core-top assemblage (2010s).

4. DISCUSSION

4.1. Detecting bivalve community response to 20th century wastewater history

Core assemblages from the eastern Palos Verdes middle shelf, embedded in mud that carries a 20th century ²¹⁰Pb signature, capture the broad outline of change in bivalve community composition in response to a known multi-decadal increase and decrease in wastewater emissions.

First, the timing of the peak in the proportion of pollution-tolerant species and functional groups at 10–12 cm (i.e. ~1960) is comparable to the timing of their peak documented by annual sampling of living assemblages at the same site (1970s) (Figs. 4C & 5C). That unimodal trend in composition is preserved despite the intense bioturbation evident visually from the radioisotopic profile (Fig. 3), and from between-increment overlaps in the age distributions of bivalve shells (A. Tomašových et al. unpubl.), and despite only modest sediment accumulation (~0.2 cm yr⁻¹). The paleoecological signal is strongly damped, as seen both in time-series of the proportional abundances of species and functional groups (Fig. 5C,D) and in ordination of assemblages based on species composition (Fig. 6). Chemosymbiont-bearing bivalves, which comprised >90% of all living bivalves for at

least 15 yr leading up to the initiation of remediation in the mid-1980s (Fig. 4C), dominate mid-20th century core assemblages but have a peak abundance of only 35 % (dated as 1960s, but the increment might be as young as 1972 or 1984, using 95 % CIs of the age model). Mixed feeders, which bloomed to dominance (40–50 %) in the 1990s, increase in proportional abundance in the appropriate core increments but never dominate.

Second, core assemblages at 12–24 cm (from the earliest 20th century to ~1960) reveal an increase in pollution-tolerant bivalves, as expected from the onset of nutrient loading in 1937, providing empirical, local-evidence-based insights to an undocumented phase of ecological history. Core assemblages indicate that benthic response to effluent and H₂S buildup was primarily in the increasing proportional abundance of chemosymbiont-bearing taxa, that is, mirroring the late 20th century decline of those groups during wastewater remediation (Fig. 4C). The rise to dominance was probably underway along Line 10, 4 km up-current of the 34 m outfall, by the 1940s (14–16 cm core increment), a decade before the first benthic surveys and 30 yr before regular monitoring. Release of organic-rich dredge spoil at the nearby, up-current LA-2 dumpsite on the San Pedro shelf during World War II deepening of the Los Angeles Harbor might have contributed to this impact.

Third, core assemblages record key, otherwise undocumented species-level responses during the early 20th century. For example, *Parvilucina*, which dominated the mid-century peak-effluent period in both core and biomonitoring data, was only co-dominant with the chemosymbiont-bearing thyasirid *Axinopsida* in the pre- and early-effluent periods (Fig. 5D). It became co-dominant with *Axinopsida* again during the 1990s extending up to the present day, as also supported by biomonitoring data (Fig. 4D). In time-averaged assemblages, co-dominance can be produced by admixing shells from 2 species that alternate in dominance, e.g. seasonally or inter-annually, and/or that are spatially patchy on a fine (within-habitat) scale; co-dominance in a time-averaged assemblage does not necessarily indicate the co-occurrence of 2 equally abundant taxa (Peterson 1977, Fürsich & Aberhan 1990, Tomašových & Kidwell 2009, 2010). For our study system, co-dominance in pre- and early-effluent (and late-remediation) core assemblages probably reflects temporally variable populations of *Parvilucina* and *Axinopsida*, much as documented by biomonitoring in the last few decades (Fig. 4D).

4.2. Absence of a diversity trend

The rarefied richness and evenness of the core-top (2010) assemblage is very similar to that of living assemblages today (~15 species, PIE ~0.9; Figs. 4A & 5A), but core assemblages maintain those values even during the peak-effluent phase, when living assemblages were low (~5 species, PIE 0.25; Figs. 4A & 5A). Core assemblages thus do not detect the first-order diversity increase in diversity with remediation, known also from the entire microbenthic assemblage (Stein & Cadien 2009), nor the diversity decline that is expected during the late early-20th century, based on general models of benthic response to the rise of nutrient loading and anoxia (e.g. Diaz & Rosenberg 1995, Borja et al. 2010). Within-habitat time averaging is predicted to produce dead-shell assemblages with higher richness and evenness than in a single sampling of the source living community (Tomašových & Kidwell 2009, 2010), and the effect is stronger when time-averaging sums across multiple successive community states (as here). Such between-habitat time-averaging of shells—here, from upward and downward mixing of pre- and post-effluent shells with peak-effluent shells—almost certainly accounts for the high rarefied richness and evenness of core assemblages whose mean age is ‘peak effluent’ (and see A. Tomašových et al. unpubl.).

4.3. Modification of assemblage composition by bioadvection of legacy shells

The strongly damped mid-century peak of chemosymbiont-bearing bivalves in core assemblages (a maximum of 35 % rather than >90 % of all bivalves; Figs. 4 & 5) and their much smaller multivariate dispersion in community composition (Fig. 6) are consistent with the abundant evidence for strong bioturbation, including open burrows through most of the 24–26 cm core lengths, the irregular profiles of radionuclides (Fig. 3), and the overlapping age distributions of shells (Tomašových et al. unpubl.). Bioturbation can move shells both upward and downward, thereby diluting the abundance of *Parvilucina* and other chemosymbiont-bearing taxa in increments dating to their peak abundance alive. This smearing and attenuation of a signal, known from observations and models of geochemical tracers and microfossils (e.g. Johannessen & Macdonald 2012, Steiner et al. 2016), almost certainly contributed to reducing the abundance of chemosymbiont-bearing bivalves in core increments from their known peak decades.

By shifting particles vertically, bioturbation also tends to broaden the peak of a pulsed input, i.e. increase its apparent temporal duration, creating lead and lag effects. Here, the duration of the peak in chemosymbiont-bearing taxa in the cores (30–40 yr) has probably been only slightly coarsened from its true duration. Biomonitoring documents ~15 yr of dominance by chemosymbiont-bearing bivalves (Fig. 4C) since 1972, and an additional 10 (1960s) to 20 yr (1950s) before that would be assumed from the history of effluent quality and from benthic surveys in the 1950s.

The most obvious bias is a more prolonged decline than is true, which is also the most common asymmetry arising from bioadvection (e.g. Steiner et al. 2016). However, although the late 20th century decline of chemosymbiont-bearing taxa evident in the core (Fig. 5C) is definitely slower than that documented by annual sampling of living assemblages (occurs within a few years), it is comparable to the apparent rate of decline using decadal binned live data (Fig. 4B,C,F,G). Thus, considering history with decadal resolution, the core record is quite good.

A second significant divergence in the composition of core assemblages from living assemblages, seen most dramatically by their separation in NMDS space (Fig. 6A), is the unexpectedly high abundance of deposit feeders (principally *Nuculana taphria*) at ~20% throughout the core (Fig. 5C). In living assemblages, deposit feeders, especially *Nuculana*, have risen to constitute ~20% of all living bivalves only in the last decade (Fig. 4C), aided by declines in the density of chemosymbiont-bearing taxa and mixed feeders; they constitute only a few tens of individuals per 0.1 m² even today, and only a few individuals in the 1970s–80s. Our age-dating of *N. taphria* shells from grab samples of the upper 10–15 cm on the Palos Verdes shelf reveals that in fact very few *N. taphria* shells were produced there in the 20th century: their median age is 447 yr, in contrast to a median age of 36 yr (before 2003) for *Parvilucina* shells in the same samples (Tomašových et al. 2014). Age dating of shells from our PVL10-50 box cores yields median ages between 1800 and 2400 yr for *N. taphria*, in contrast to median ages of 40–50 yr for *Parvilucina* (A. Tomašových et al. unpubl.).

These results from shell dating are consistent with the low abundance of *N. taphria* in living assemblages of the Palos Verdes shelf over the last 50 yr (Tomašových et al. 2014, summarizing LACSD and other survey data), and its preference for the somewhat sandier substrates of other southern California mainland shelves (especially San Pedro and San

Diego; Bandy 1958, Zmarzly et al. 1994). Species of the genus *Nuculana* in southern California are also more sensitive to pollution than the dominant chemosymbiont-bearing species *Parvilucina* and *Axinopsida* (Smith et al. 2001). Thus the disproportionately high abundance of *N. taphria* in core assemblages, contributing to damping of the *Parvilucina* peak, most likely reflects the inclusion in time-averaged core assemblages of shells dating to periods when pollution and fine-grained sedimentation on the Palos Verdes shelf were lower, i.e. prior to the onset of wastewater pollution in the 20th century or even prior to siltation induced by the onset of European land use in the 19th century (Tomašových & Kidwell 2017).

Therefore, although deposit feeder (especially *N. taphria*) populations and proportional abundances were likely higher in the pre-effluent 20th century benthos, more like or even exceeding those sampled today (12% of living assemblages in 2010–2012), their high abundance throughout the core probably derives in large part from the inclusion in 20th century muds, via upward reworking, of shells from older and much larger pre-20th or pre-19th century populations. The abundance of these legacy shells shifts the composition of box-core assemblages away from that of living assemblages (Fig. 6A), diluting the more exclusively 20th century record of *Parvilucina*.

We suspect a similar dynamic for infaunal suspension feeders (e.g. pollution-intolerant *Compsomyx subdiaphana* and *Nemocardium centifilosum*). This group was proportionally rare as living individuals during the peak abundance of *Parvilucina* in the 1970s and early 1980s but is quite common in core assemblages from that interval; like *Nuculana taphria*, they were probably also reworked upward, and belonged to an important component of more deeply historical Palos Verdes shelf communities. Their abundance has not, however, been modified as strongly as that of deposit feeders because they were not as rare during peak emissions: infaunal suspension feeders were living in 30–60 m along Line 10 for the entire biomonitoring period at ~tens of individuals per 0.1 m² (Fig. 4B). Their top-rank in core-bottom (20–24 cm) assemblages (Fig. 5C) is thus probably a reasonable characterization of their importance in pre-effluent living communities, given that upper core assemblages (0–6 cm, latest 20th century and earliest 21st century) correctly capture that infaunal suspension feeders are becoming higher ranked than chemosymbiont-bearing and deposit feeders in living assemblages on the remediated shelf (Figs. 4C & 5C).

A more extreme version of this dynamic of upward advection of legacy shells applies to epifaunal suspension feeding bivalves such as the large scallop *Chlamys hastata*, which comprises 15–20% of most core assemblages but, like the co-occurring dead shells of the terebratulid brachiopod *Laqueus*, has not been sampled alive on this and other mainland southern California shelves for the last 50 yr (LACSD and other data compiled by Tomašových & Kidwell 2017). Our age-dating of *Laqueus* shells from nearby surface grabs (station 10C in 61 m) show that it went into decline in the early 1800s and disappeared by ~1900 (Tomašových & Kidwell 2017).

4.4. Adjusting the core record for poor preservation

Bioturbational smearing, combined with dilution by upward-advection of pre-20th century shells, reduced the magnitude of variation in the core of all functional groups (above), but the strongly damped abundance trajectory of mixed feeders, with a peak of only 11% in decades when they attained ~50% of living assemblages (Figs. 4C & 5C), is probably further affected by preservational bias caused by their relatively thin and fragile shells. Tellinid bivalves, the dominant mixed feeders in the bivalve fauna, do exhibit higher frequencies of broken shells than the other functional groups. Analytically excluding them from the dataset, a common strategy for groups with low preservation potential, does not substantively alter pale-

oecological trends: the mid-20th century peak in chemosymbiont-bearing taxa is increased only slightly from 35% to 37–38% (Fig. 7A).

Analytically amplifying the allegedly poorly preserved group to compensate for under-representation is another option. Here we found through iteration that, by multiplying the raw abundances of mixed feeders in each core assemblage by 3, we can restore a key feature of known ecological response to wastewater remediation, namely the decadal-scale replacement in the 1990s of chemosymbiont-bearing taxa by mixed feeders (Fig. 7B). In this ‘taphonomically adjusted’ record, mixed feeders dominate the upper core assemblages from the latest 20th and early 21st century (25–27%), as observed in bivalve living assemblages (26–52% in 2010–2012). The chemosymbiont peak is lowered to 32% (from 35%), but persists and is (correctly) higher than the subsequent mixed-feeder peak. Mixed feeders in the pre-1990s part of this adjusted record exhibit strong variations in proportional abundance because multiplication has exaggerated small-scale variation in mixed-feeder abundance among core increments, which is typical of a poorly preserved group and probably not biologically meaningful. The rank of the adjusted mixed feeders there is (correctly) lower than that of infaunal suspension feeders and chemosymbionts, and is mostly higher than deposit feeders and epifaunal suspension feeders, both during the peak-effluent period when that ranking can be confirmed by biomonitoring and during the pre- and rising-effluent phases (Fig. 7B).

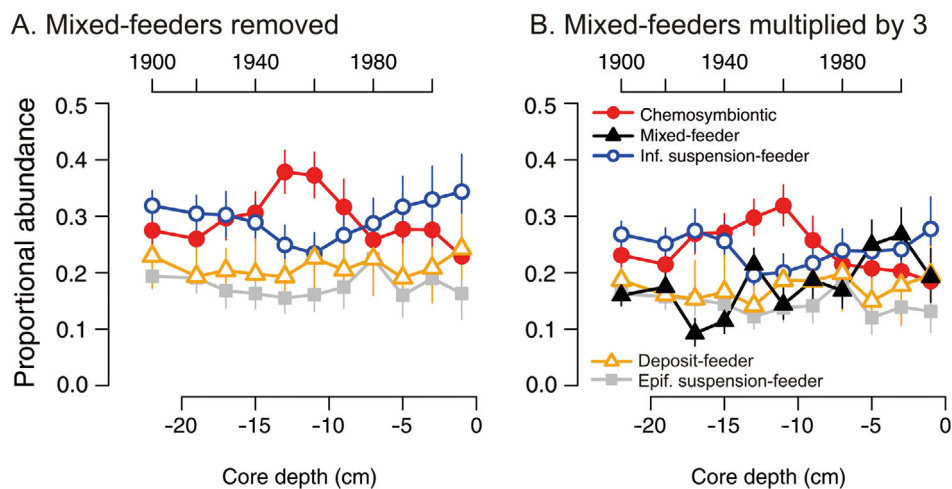


Fig. 7. Proportional abundance of functional groups in core assemblages after adjusting to compensate for the low preservation potential of very thin-shelled mixed feeders; same conventions as Fig. 5C. (A) Recalculated proportional abundances after removing mixed feeders from the analysis, a common strategy. (B) Recalculated proportional abundances after multiplying the raw numbers of mixed feeders by 3, which restores the temporary dominance by mixed feeders during the late 20th century as observed in living assemblages, following the decline of chemosymbionts

4.5. Gauging ecological recovery from pre-effluent core assemblages

Comparing among core assemblages, rather than comparing core assemblages with living assemblages, circumvents the challenges of possible preservational bias among species (suspected for mixed feeders, as above) and differential time-averaging, here with substantial numbers of pre-20th century shells retained in mud bearing a 20th century ²¹⁰Pb signature. We find that, as a gauge of the extent to which macrobenthic communities have recovered under remediation, the core-top assemblage—a proxy of the modern-day shelf macrobenthos (2010s)—most closely resembles the core assemblage from the pre-effluent lowermost core increment (earliest 20th century), based on NMDS distances (Fig. 6B). The circular temporal trend of core assemblages within NMDS space suggests that the macrobenthic community on the eastern Palos Verdes shelf, as judged by bivalves, is on the recovery trajectory towards its pre-effluent state. This NMDS pattern is qualitatively robust to using core data adjusted for likely underrepresentation of mixed feeders. All of these early 20th century assemblages are pre-effluent excepting the 1940 assemblage, which should be considered to be part of the rising-effluent phase, especially given the 95 % CIs of the age model.

Given bioturbation, we prefer to remain conservative in interpreting these cores, stating at this point only that modern-day communities are very close to but not yet fully recovered to their early urban, pre-effluent state, without specifying target abundances that particular species or functional groups should attain for recovery to be deemed complete. We will nonetheless point out that, between 2012 and 2017, bivalve communities have continued to show an increase in the proportional abundance of deposit feeders, a decline in chemosymbiont-bearing taxa, and thus an increase in trophic equitability. These changes further increase the similarity of present-day living assemblages to pre-effluent core assemblages (Fig. 5C), excepting the poorly preserved mixed feeders, and are a further indication that recovery is still ongoing (i.e. not yet complete). Given additional stressors over the same period, including invasives such as the predatory snail *Philine* arriving in 1994 (Cadien & Ranasinghe 2001) and secular warming starting in the early 20th century (Bringué et al. 2014), continued change in living assemblages need not owe exclusively to the final stages of their recovery from wastewater remediation. Core assemblages from the early 20th century pre-effluent de-

cedes, such as here, and from native sediments from earlier centuries (our longer vibracores S. M. Kidwell et al. unpubl. progress) will be the best measure of recovery from wastewater itself.

5. CONCLUSIONS

We find that, notwithstanding strong vertical mixing from bioturbation and only moderate rates of sedimentation (0.2 cm yr⁻¹), core assemblages from the Palos Verdes shelf correctly register the broad outline of known changes since the onset of secondary wastewater treatment in the late 1980s, namely a strong decrease in pollution-tolerant, chemosymbiont-bearing species and an increase in the proportional abundance of mixed (facultative-deposit) feeders, although the magnitudes of both peaks are strongly damped. Core assemblages from the earliest 20th century to ~1960 reveal, for the first time, that benthic response to the onset of emissions in 1937 was primarily via the increasing proportional abundance of the chemosymbiont-bearing functional group and the growing dominance of a single species within it, in contrast to the shifting dominance of multiple species on the pre-effluent shelf, thus mirroring late 20th century changes during remediation, one of several paradigms for recovery (cf. Duarte et al. 2015). Bivalve community deterioration had started by the 1940s even at our relatively distant coring site, a decade before the first benthic surveys and 30 yr before the onset of biomonitoring. Finally, recovery, while definitely underway since the 1990s as tracked by biomonitoring, is not yet complete: as shown by NMDS, the core-top assemblage (2010s) most closely resembles but does not match the core-bottom (1900–1910s) and other early 20th century, pre-effluent core assemblages.

Bioadvection, which both blurs 20th century peaks in populations and injects older legacy shells to the 20th century mud record, combined with poor preservation of the mixed-feeding group, strongly damps the magnitude of ecological changes registered by these cores. Core assemblages thus underestimate both the magnitude of community deterioration during peak-effluent conditions and the rapidity of benthic response to remediation. The shells of the chemosymbiont- and mixed-feeders that dominated the mid- to late-20th century community are diluted by those of the obligate deposit feeders and suspension feeders that age-dating shows had previously thrived on this shelf (Tomašových et al. 2014) and that have been bioadvected upward into 20th century

muds under conditions of modest sedimentation rates and deep bioturbation (A. Tomašových et al. unpubl.). Sedimentary records accumulated under conditions like those of the southern California shelf will thus, in general, be conservative measures of the actual ecological changes occurring during the rise and the remediation of anthropogenic stressors.

Longer cores that penetrate older strata and extensive shell age-dating that permits the unmixing of legacy shells within core increments will help resolve the quantitative composition of early-urban shelf communities, distinguishing them from earlier community states under agrarian (19th century) and pre-European watershed conditions. However, notwithstanding the geological challenges, and relevant to both management and academic uses, the qualitative nature, mid-20th century timing, and multi-decadal duration of known wastewater-linked changes in bivalve community composition are all captured by our short, 24 cm box cores. Macrobenthic core assemblages can thus provide a useful, decadal resolved record of benthic history for shelves where direct observations are scarce or absent. Even on the exceptionally well-monitored Palos Verdes shelf, they provide new insights into the otherwise undocumented early-20th century phase of community deterioration and provide the first empirical gauge of macrobenthic recovery to an early-urban baseline.

Acknowledgements. Research supported by NSF grants EAR-1124189 (S.M.K and A.T.) and EAR-1124318 (C.R.A.); A.T. was also supported by the Slovak Agency for Research and Development (APVV 17-0555) and the Slovak Scientific Grant Agency (VEGA 0169/19). For valuable assistance on the cruise, we thank University of Chicago volunteers S. Edie, N. Bitler Kuenle, K. Jenkins Voorhies, A. Mine, and M. Baris, and, from UCSD, J. Moore; undergraduates from both the University of Chicago and Savannah State University; and professional colleagues R. Cipriani (Santa Monica); L. DeLeo, M. Robinson, and C. Venherm (Skidaway); B. Edwards (US Geological Survey); C. Hintz (Savannah State); C. McDonald and T. Parker (LACSD); J. McNinch and H. Wadman (US Army Corps of Engineers); and the crew of the RV 'Melville.' We thank LACSD for release of biomonitoring data, loan of their sluice-sieving equipment, and other facilitation of fieldwork; J. McNinch and H. Wadman for loan of their vibracoring equipment; and M. LaBarbera (U Chicago) and San Diego Plastics Inc. (National City) for assistance with the design and fabrication of other coring equipment.

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*Editorial responsibility: Romuald Lipcius,
Gloucester Point, Virginia, USA*

*Submitted: November 1, 2018; Accepted: March 4, 2019
Proofs received from author(s): April 4, 2019*