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**VIA ELECTRONIC MAIL**

Ms. Renee Purdy, Executive Officer  
California Regional Water Quality Control Board  
Los Angeles Region  
320 W. 4<sup>th</sup> St., Suite 200  
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**Attn: Information Technology Unit**

**Joint Water Pollution Control Plant  
CI No. 1758; Resolution R019-001; NPDES No. CA0053813  
Bivalves as Ecological Indicators (JWSS-19-003)  
Special Study Final Report Submission**

As required under Resolution R019-001, please find the enclosed draft manuscript for submission to the Marine Ecology Progress Series that serves as the final report for the subject special study:

**Detecting Strong Spatial and Temporal Variation in Macroenthic Composition on  
an Urban Shelf Using Taxonomic Surrogates**

This manuscript is a pre-submittal draft and is subject to continued review and editing by the authors prior to after submission for publication. Unless otherwise instructed by the Regional Board or Regional Board staff, this will be the final submission associated with this Special Study. However, a final version of this manuscript and any other reports or peer-reviewed publications resulting from these studies will also be provided to Regional Board staff as they become available.

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Philip Markle  
Senior Environmental Scientist  
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Enclosure

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**Joint Water Pollution Control Plant  
CI No. 1758; Resolution R019-002;  
NPDES No. CA0053813**



**Bivalves as Ecological Indicators  
(JWSS-19-003)**

**Final Report  
March 2021**



**THE UNIVERSITY OF  
CHICAGO**



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**LOS ANGELES COUNTY  
SANITATION DISTRICTS**  
*Converting Waste Into Resources*

## Draft Manuscript for Submission to Marine Ecology Progress Series:

# Detecting Strong Spatial and Temporal Variation in Macrobenthic Composition on an Urban Shelf using Taxonomic Surrogates

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**ABSTRACT:** Surrogates of macrobenthic assemblages, intended to alleviate the effort and taxonomic expertise required for monitoring, can take many forms, such as using coarser taxonomic levels ('sufficiency') or only a subset of the whole fauna ('subsetting'). Here, the power of both surrogacy methods to retain community-level patterns of spatial and temporal variation on an urban continental shelf were evaluated. Using a 45-year infaunal dataset to monitor wastewater impacts on the Palos Verdes Shelf in southern California, four taxonomic sets (whole infauna, polychaetes, bivalves, malacostracans) at five resolutions (species, genus, family, order, functional guilds) were evaluated; the pollution gradient was subdivided into two spatial bins based on proximity to the wastewater outfall (near-field vs far-field) and three temporal bins based on the phases of improved wastewater treatment.

All sets detected flattening of the spatial gradient with improved wastewater treatment, becoming more similar in richness, evenness, and composition through time. Sets are robust to the family level, probably due to mostly mono-specific genera and low-diversity families and phylogenetic conservatism of functional guilds. Polychaetes mirror whole-fauna patterns most accurately, as expected since they constitute the majority of individuals and species. However, bivalves outperform all other sets in distinguishing near-field and far-field stations because their functional diversity spans feeding strategies that exploit and are specialized to both ends of the pollution gradients. Surrogates can thus be very effective in detecting strong, pollution-driven changes over space and time, but different subsets excel at mirroring the whole fauna and at indicating the pollution gradient itself.

**KEY WORDS:** Taxonomic Sufficiency, Taxonomic Subset, Functional Groups, Pollution Gradient, Paleoecology

## 1. INTRODUCTION

Intense urbanization of coastlines exerts an array of anthropogenic stresses on natural systems through resource harvest, landscape modification such as dredging and armoring, and the input of excess nutrients and other contaminants. These inputs include agrochemicals and fertilizers, industrial metals, and polycyclic aromatic hydrocarbons (PAHs) via stormwater, aquaculture, vessels, and municipal wastewater, with the latter usually constituting the largest volume of inputs (Islam & Tanaka 2004). The environmental strain imposed by these human stressors is often evaluated by testing for before-after changes and/or near-far contrasts in the composition and structure of benthic communities, which are sampled as part of sediment quality monitoring (e.g., Warwick 1993, Gray & Elliott 2009, Schiff et al. 2016). Such monitoring maintains a standardized quantitative sampling effort of both organismal abundance and diversity, cover a broad range of taxonomic clades, and identify organisms to the species level or other fine-scale operational taxonomic units. Long-term programs provide invaluable time series of biological responses over the history of environmental stress (or stress alleviation) in a region (e.g., Borja et al. 2006, Stein & Cadien 2009).

However, biomonitoring places a high demand on taxonomic expertise and labor, especially in biologically diverse marine systems. These expectations can also inhibit the establishment of new programs in poorly studied regions where assessment of human impacts for public health and biodiversity conservation may be especially urgent. In principle, these demands can be alleviated by using “surrogates” of species-level data on the whole fauna. Surrogates take many forms (Table 1), but here we focus on two: (a) using genera or other coarser taxonomic levels than species (‘taxonomic sufficiency’ *sensu* Ellis 1985), thereby reducing the taxonomic detail required; and (b) using only a subset of the whole fauna, for example focusing on a single class (‘taxonomic subsetting’), thereby reducing the taxonomic breadth required. Surrogacy is also important in historical ecology and paleoecology, which tend to focus, respectively, on the taxonomic subsets that are most likely to be reported upon (e.g., commercial and sport taxa) or those most likely to be preserved as skeletal death assemblages (e.g., shelled mollusks, ostracods, calcifying foraminifera). “Live-dead” and sediment-core analyses of such clades reveal that naturally time-averaged dead-shell assemblages can provide valuable information about community states that inhabited a given region prior to the onset of biomonitoring (Yasuhara et al. 2012, Kidwell and Tomašových 2013, Albano et al. 2018).

Taxonomic sufficiency has been the subject of numerous tests. Most published studies find that coarser taxonomic resolution correlates with species-level data and suffices to detect both anthropogenic (Warwick 1988, Ferraro & Cole 1992, Buss & Vitorino 2010) and natural (Włodarska-Kowalczyk & Kędra 2007, Bevilacqua et al. 2009) spatial gradients in the diversity and composition of marine ecosystems. Sufficiency has subsequently been evaluated for freshwater (Jones, 2008, Mueller et al, 2013) and terrestrial invertebrates (Pik et al. 1999, Souza et al. 2016). Non-Linnaean classifications such as morphospecies and functional guilds have also demonstrated promising results (Bhusal et al 2014, Brind’Amour et al 2014).

Tests of taxonomic subsetting have had diverse objectives. In most studies, authors sought to identify a single clade with the ability to mirror variation in richness or some other attribute of the whole fauna, that is to serve as a “proxy” for the whole fauna (e.g., Olsgard et al. 2003, Magierowski & Johnson 2006, Fontaine et al. 2015). A subset that emerged as particularly sensitive to a pollution gradient would be designated as an “indicator” group, even if it exhibited poor congruence with the whole fauna (Magierowski & Johnson 2006, Heino 2010). In this work, subset surrogates were subdivided into two types: ‘*proxy subsets*’ (good for mirroring the whole fauna) and ‘*indicator subsets*’ (superior at detecting a particular environment or perturbation; Table 1).

Here, an exceptionally large species-level macrobenthic database was used to test the limits of both taxonomic sufficiency and subsetting to discriminate an anthropogenic pollution gradient over successive phases of abatement. Rather than test only one method or both independently, their interaction (i.e., taxonomic subsets at multiple resolutions) was explored, and was also tested for their ability to detect variation over time rather than only spatial patterns. The dataset spans 45 years of annual infaunal sampling of 11 stations in 60 m water depth along the Palos Verdes Shelf in southern California, encompassing about 600 species from 11 phyla. Previous analyses of the full infaunal dataset, including municipal annual reports, have demonstrated improvement in benthic conditions associated with enhanced wastewater treatment (Stein & Cadien 2009, LACSD 2020). In this study both spatial and temporal gradients in richness, evenness, and community composition were found to be robust to coarsening taxonomic resolution up to the family level. Although polychaetes are the most accurate proxies of patterns in the whole fauna, bivalves were also found to be the most powerful indicators of proximity to the wastewater outfall and of benthic response to remediation over the last four decades.

Table 1. Common aspects of surrogacy as defined in this study.

Term	Definition
Surrogacy	Reducing the effort required to assess biota, via surveys and monitoring
I. Sufficiency	Coarsening the detail (resolution, acuity) of information
A. Numerical Sufficiency	Coarsening the measure of abundance (e.g., presence-absence or rank-abundance rather than number of individuals)
B. Taxonomic Sufficiency	Coarsening the taxonomic units (e.g., species-level data aggregated into higher Linnaean ranks or into functional guilds)
II. Subsetting	Narrowing the scope or breadth of information
A. Numerical Subsetting	Narrowing the number of specimens assessed (e.g., limit to the first 100 individuals processed)
B. Taxonomic Subsetting	Narrowing the taxonomic clades assessed (e.g., limit to a selected clade or functional guild)
i. Proxy Subset	Subset that best reflects the whole fauna
ii. Indicator Subset	Subset that best detects gradient(s) of concern [i.e., <i>indicator taxon</i> ]

## 2. MATERIALS AND METHODS

### 2.1. Study Area

The Palos Verdes shelf in southern California has a long history of receiving wastewater contaminants beginning with the 1937 opening of an ocean outfall in 34 m-deep water at White Point; two Y-shaped outfalls dispersing wastewater at 60 m depth were later installed in 1956 and 1966 (Fig. 1). The 60-m outfalls remain in use and wastewater treatment processes have continually improved since 1970 in anticipation of the passage of the US Clean Water Act in 1972. Wastewater was initially subject only to primary treatment, and emission rates steadily increased with 20<sup>th</sup>-century urbanization, with total suspended solids loadings peaking at approximately 150,000 t yr<sup>-1</sup> (Fig. 2). Emissions of solids (to which most contaminants adhere) began to decrease markedly after the onset of advanced primary treatment in the 1970s, with additional declines in solids and in biological oxygen demand following the onset of partial secondary treatment in the 1980s and 1990s and full secondary treatment starting in the 2000s. Despite a high volume of water outflow to the ocean over the last 50 years, contaminants in the effluent are now well below allowable emission limits (LACSD 2020). This emission history created a strong point-sourced sediment gradient extending mostly northwest of the outfall area, driven by the California Coastal Counter-Current (Fig. 1). The sediments associated with the effluent discharge form a fine-grained, organic-rich mound as thick as 60 cm near the outfall and include numerous contaminants including DDT and PCBs (Stull et al. 1996, Lee et al. 2002). This contaminated sediment layer thins with distance from the outfall. Along the 60-m isobath, the sediment is chemically undistinguishable from stations northwest and southeast of the immediate outfall area.

Long-term monitoring of macrobenthic communities using benthic grabs (described in Section 2.2) were conducted on the Palos Verdes shelf by the Los Angeles County Sanitation Districts (LACSD) starting in 1972. Their sampling grid comprises 44 stations: 11 bathymetric transects each sampled at 30, 61, 152, and 305 m depths (Fig. 1). Infaunal and other data from this standardized effort have revealed a significant and positive benthic response to improved wastewater treatment, including higher macrofaunal species richness and evenness (LACSD 2020, Stein & Cadien 2009). The faunal composition has, throughout the grid, reached or increasingly approached reference condition as defined by the Benthic Response Index (BRI), a metric based on the pollution tolerance and abundances of local species calibrated to regional disturbance gradients (Smith et al. 2001), and as compared to undisturbed areas in the Southern California Bight.

## 2.2. Dataset

LACSD sampled macrobenthic invertebrate communities annually from 1972 to the present, with the dataset encompassing 1972-2019. Samples were collected semi-annually in February and August until 2006, after which the agency switched to annual sampling during the summer. Samples were initially collected using Shipek grabs, which were replaced by Van Veen grabs after 1980. Shipek grab data were transformed to equal the volume of Van Veen grabs by pooling three replicate Shipek grabs taken at each station. Sediments were sieved through 1 mm mesh with seawater on deck, fixed in 10% formalin, and then preserved in ethanol. All live animals were sorted and identified to the species level when possible. Taxonomic identities were standardized to a regional listing compiled and regularly updated by the Southern California Association of Marine Invertebrate Taxonomists (SCAMIT 2013); this reference is used by all regional municipal agencies and in the Southern California Bight Regional Monitoring Program (e.g., Schiff et al. 2016).

The analyses for this study focused only on samples from the 60 m isobath, which coincides with the outfalls' effluent ports that have been active point-sources since the 1950s. Each of the 11 stations along this middle-shelf isobath was categorized as either "near-field" (stations 5-8) or "far-field" (stations 0-4, 9-10) based on sediment chemistry conditions during the first decade of monitoring (Stull et al. 1996), an assignment that reflects physical proximity to the outfall and the prevailing northwest-directed California Countercurrent. Samples collected in February during years 1972-2005 were excluded, yielding a dataset that consisted of one summer-time sample per station per year from 1972 through 2019, for a total of 499 samples.

This 45-year history was subdivided into three temporal phases based on the treatment level of wastewater emissions: primary and advanced primary (Phase 1 in 1972-1983), partial secondary (Phase 2 in 1984-2002), and full secondary (Phase 3 in 2003-2019, Fig. 2). At each station, samples were pooled by these intervals to create three temporal bins (referred to as 'phases' in Results). The final dataset thus consisted of three temporal bins at each of 11 stations, which were assigned to one of the two outfall categories (spatial bins, referred to as near-field and far-field 'areas' in Results). Although seabed conditions clearly improved throughout the Palos Verdes sampling area over these decades of improving wastewater treatment (e.g., LACSD 2020, Stein & Cadien 2009), a decision was made to leave stations in their outfall categories as originally defined based on conditions in 1972, allowing us to test the ability of surrogates to detect weakening of the spatial gradient.

Given the stepwise decrease of emissions across the boundaries of treatment phases (Fig. 2), the robustness of datasets to possible lags in benthic response were tested by omitting the initial one or two years of data immediately following a change in treatment. Omitting these data did not affect results significantly, and so all years of data were retained in analyses.

## 2.3. Data Analyses

All data extraction and analyses were conducted using R with functions supplied by the 'vegan' package (Oksanen et al. 2019). The original dataset was transformed to 20 surrogate matrices (henceforth called 'sets') for coarsened taxonomic levels and selected taxonomic subsets. First, species-level counts for the whole fauna were aggregated into genus, family, order, and functional guild level counts (tests at five levels of taxonomic resolution). Functional guilds were generated by combining guild assignments established by Macdonald et al. (2010), specifically motility, life habit, food source, diet, and feeding mode. New matrices were then extracted from each of these five rank-based matrices for the three most abundant classes represented, namely Polychaeta, Bivalvia, and Malacostraca (three taxonomic subsets, to be compared with the whole-fauna set). These three clades together represent ~90% of individuals in the whole-fauna (Fig. 3). All procedures that follow were applied to each of these 20 matrices.

The distribution of the number of species within the five supra-specific taxa or categories (i.e. those categorized by taxonomic units that are higher than species level, e.g. family. was quantified as the ratio

between the raw number of species (richness  $S$ ) over the number of genera ( $G$ ), families ( $F$ ), orders ( $O$ ), and functional guild ( $FG$ ) (e.g.,  $S/G$ ,  $S/F$ ,  $S/O$ ,  $S/FG$ ). The smallest possible value of any ratio is 1, which indicates that the higher taxon is monospecific.

Richness and evenness were compared between near-field and far-field samples for each treatment phase by comparing the median values and interquartile range (IQR) of one area to the other. Richness was rarefied to the smallest sample size per taxon per treatment phase to account for unequal abundances among the taxonomic sets (3,727 individuals for the whole fauna; 1,783 Polychaeta, 285 Bivalvia, 44 Malacostraca). Evenness is expressed as the probability of interspecific encounter (PIE; Hurlbert 1971), which has low sensitivity to sample size and richness. PIE values range from 0 to 1, with 0 indicating a sample where all individuals are from a single taxon (i.e., the chance of two randomly-selected individuals being different taxa is zero), and a PIE value of 1 indicates that individuals are equally distributed among all taxa.

Compositional variation among samples was assessed using non-metric multidimensional scaling (NMDS) based on Bray-Curtis distances computed with square-root transformed proportional abundances. Bray-Curtis values quantify the compositional dissimilarity among stations on a scale from 0 to 1 (Bray & Curtis 1957). NMDS ranks these distances prior to ordination on a fixed number of axes (here,  $k = 2$ ). Compositional differences among near-field and far-field stations for each treatment phase were also tested using permutational multivariate analysis of variance (PERMANOVA; Anderson 2001).  $R^2$  values generated by PERMANOVA, which measures the amount of variation explained by sample categorization of near-field and far-field conditions, were compared among sets to assess the relative strengths of surrogates to delineate the near-field region of the shelf during each phase of wastewater treatment.

The contributions of individual taxa to the Bray-Curtis dissimilarity between near-field and far-field communities for each set were calculated using the similarity percentage procedure (SIMPER; Clarke 1993). To quantify the proportion of taxa that contribute most to dissimilarity for each set, the number of taxa that met increasing levels of cumulative contribution (25%, 50%, and 75%) were divided by the total number of unique taxa. Higher proportions at contribution thresholds indicate that a higher number of taxa are needed to account for the observed dissimilarity.

### 3. RESULTS

#### 3.1. Taxonomic Structure of the Macrobenthic Fauna

The “whole fauna” dataset comprised 536,056 individual organisms across 1,277 species, 722 genera, 347 families, 120 orders, 34 classes, and 13 phyla (Table 2). Additionally, these taxa were binned into 86 functional guilds. The three focal classes comprised 89% of all individuals (474,653), with polychaetes encompassing 61% (326,888), bivalves 17% (92,922), and malacostracans 10% (54,843) (Fig. 3A). These three classes also comprised 72% of all species; 42% (539 species) for polychaetes, 7% (89) for bivalves, and 23% (288) for malacostracans (Fig. 3B). Seven of the ten most abundant classes were also the highest in species richness.

Species/genus ratios for the three subsets resemble that of the whole fauna ( $S/G = 1.77$ ), averaging 1.78 across the three focal classes (Table 2). Per-family species richness for polychaetes ( $S/F = 11$ ) was approximately three times as high as for other subsets and the whole fauna ( $S/F = 3.07$ - $3.68$ ), and per-order species richness was much higher for both polychaetes ( $S/O = 33.69$ ) and malacostracans ( $S/O = 36$ ). Whole fauna ratios were consistently lower than bivalves and higher than polychaetes, with the magnitude of separation increasing at higher ranks. Malacostracans most closely resembled whole fauna ratios at the genus and family levels.

For the whole fauna, functional guild ratios were greater than those at the order level ( $S/FG = 14.85$ ,  $S/O = 10.64$ ). For each of the subsets, functional guild ratios fell between ratios for the family and order

levels. Polychaete functional guild ratios ( $S/FG = 15.84$ ) were most similar to the whole fauna while those for bivalves ( $S/FG = 7.42$ ) and malacostracans ( $S/FG = 9$ ) were notably smaller.

Table 2. Taxonomic richness (S) at seven hierarchical levels (rows) and the ratio between the number of species and number of supra-specific taxa (S/T) for the whole benthic fauna and for three taxonomic subsets (the three most abundant classes). Higher ratios indicate higher within-taxon diversity.

	Whole		Polychaeta		Bivalvia		Malacostraca		Average
	S	S/T	S	S/T	S	S/T	S	S/T	S/T
Species (S)	1,277	–	539	–	89	–	288	–	
Genus (G)	722	1.77	247	2.18	62	1.44	166	1.73	1.78
Family (F)	347	3.68	49	11	29	3.07	89	3.24	5.25
Order (O)	120	10.64	16	33.69	10	8.9	8	36	22.31
Class (C)	34	37.56							
Phylum (P)	13	98.23							
Functional Guild (FG)	86	14.85	34	15.84	12	7.42	32	9	11.78

### 3.2. Temporal and Spatial Variation in Richness

Temporally, rarefied species richness for all four taxonomic sets – the whole fauna and three subsets – increased with improved wastewater treatment (first column in Fig. 4). The whole fauna, polychaetes, and bivalves exhibited stepwise increases in richness across the three phases – e.g., the whole fauna gained approx. 100 species, polychaetes gained approx. 50, and bivalves gained approx. 10 across each phase boundary. In contrast, malacostracans exhibited a large increase from Phase 1 (1972-1983) to Phase 2 (1984-2002), but there appears to be no change from Phase 2 to Phase 3 (2003-2019).

Spatially, the whole fauna, polychaetes, and malacostracans exhibited lower species richness at near-field stations (close to the outfall source) than at far-field stations, particularly during Phase 1 and 2; these sets all had high richness in both areas during Phase 3 (Fig. 4). In contrast, bivalves exhibited no difference in richness between near-field and far-field stations during any of the treatment phases.

Species-level differences in richness between near-field and far-field stations and temporal increase in richness persist with taxonomic coarsening up to the family level, although family-level polychaete data dampen the magnitude of temporal increase across each phase boundary. Coarsening data to the ordinal level preserves patterns for the whole fauna, but significantly alters patterns for all subsets, particularly for malacostracans (fourth column in Fig. 4). Functional guilds appear to have the opposite effect from orders; functional guilds alter patterns for the whole fauna, but preserve similar, if slightly dampened, patterns as the family level for each of the subsets (fifth column in Fig. 4).

### 3.3. Variation in Evenness

Temporally, species-level evenness generally increased and variation among stations generally decreased (i.e., smaller IQRs) with improved wastewater treatment in all sets with the exception of malacostracans, which maintained consistently high evenness (Fig. 5). Bivalves exhibited the strongest increase in evenness over time – stronger than the whole fauna – and polychaetes most closely resembled the whole fauna, but all sets reached an evenness  $> 0.9$  by Phase 3.

Spatially, during each treatment phase, polychaetes mirrored patterns exhibited by the whole fauna with no significant difference in evenness between near-field and far-field stations. In contrast, bivalves had far higher evenness at near-field than far-field stations during both Phase 1 and Phase 2 (Fig. 5). By Phase 3, these differences among bivalves disappeared, with evenness values from both near-field and far-field stations reaching 0.9-1.0.

As with richness, species-level patterns persisted with coarsening of taxonomic resolution up to the family level (left to right across Fig. 5). Ordinal-level data did not change patterns in the whole fauna but did alter polychaete and bivalve patterns (mostly a decline in maximum evenness). Malacostracans



had greater ranges of evenness and a particularly strong temporal decline at the ordinal level. Functional guilds preserved similar patterns as the family level for the whole fauna, polychaetes, and bivalves, but slightly altered malacostracan patterns.

### 3.4. Temporal Variation in Strength of Spatial Gradient

At the species level, ordination of square-root transformed proportional abundances for each set revealed consistent temporal and spatial separation among samples (Fig. 6; each icon is a station within either the near-field or far-field area during a treatment phase). Generally, successive water treatment phases separate along NMDS axis 1, while near-field and far-field stations within each phase separate along NMDS axis 2. All ordinations also reveal a decrease in multivariate dispersion over time (i.e., the convex hulls become smaller) as well as convergence in the community composition of the two areas over time, thus decreasing beta diversity along the 60-m isobath on the whole Palos Verdes Shelf. These species-level patterns persist for all sets up to the family level. Although ordinal-level data change the relative positions of samples, temporal translation and spatial homogenization are still apparent.

This temporal pattern is also detected by PERMANOVA; the spatial differences in composition between the near-field and far-field areas were high during Phase 1 but declined over successive treatment phases, becoming undetectable during Phase 3 (Fig. 7). Together with NMDS (Fig. 6), PERMANOVA results indicate spatial homogenization in community composition and a loss in strength of the spatial pollution gradient over time.  $R^2$  values for polychaetes and malacostracans were similar to the whole fauna, progressively declining from approx. 0.45 during Phase 1, 0.3 during Phase 2, and  $< 0.2$  during Phase 3. Bivalves demonstrated both the strongest early differences ( $R^2 =$  approx. 0.65 during Phase 1) and the steepest decline across treatment phases (0.4 during Phase 2,  $< 0.1$  during Phase 3). Resolution had little impact on PERMANOVA results up to the family level and for functional guilds. At the ordinal level, the whole fauna pattern was not impacted, polychaetes detected significant differences during Phase 3, bivalves detected even stronger differences during Phase 1 and Phase 2, and malacostracans no longer detected differences during Phase 2. Ordinal-level data thus significantly affected PERMANOVA results.

The two species most responsible for the whole fauna's spatial compositional differences (SIMPER) during Phase 1 are the opportunistic polychaete *Capitella capitata* (9% contribution) and the chemosymbiont-bearing bivalve *Parvilucina tenuisculpta* (7% contribution). All other species had  $< 4\%$  contribution. Abundances of *C. capitata* were much higher in the near-field area during Phases 1 and 2 while *P. tenuisculpta* was more abundant in the far-field area (Fig. 8). Both species declined exponentially in abundance over successive wastewater treatment phases. By Phase 3, neither species was a dominant contributor to spatial dissimilarity, which had also become insignificant for the whole fauna (white bars in Fig. 7).

Richness (total raw count of taxa) increased from Phase 1 to Phase 2 for all sets at all taxonomic resolutions but remained mostly stable from Phase 2 to Phase 3 (Total S; Table 3). However, SIMPER for the whole fauna, polychaetes, and bivalves indicate that spatial homogenization of communities continued from Phase 2 to Phase 3 (parenthetical values; Table 3), with decreasing per-taxon contributions to dissimilarity across all three treatment phases. These patterns persist with coarsening taxonomic resolution up to the ordinal level. Patterns for malacostracans were less consistent; while the number of sub-ordinal taxa increased during each phase, the proportion of taxa that notably contributed to dissimilarity decreased.

Table 3. Summary of SIMPER results for each dataset over three treatment phases, indicating the number of taxa that cumulatively contribute to 25%, 50%, and 75% of total Bray-Curtis dissimilarity. Parenthetical values are the proportion of the total number of taxa (S) in a dataset. Higher proportions indicate that more taxa are required to explain the same amount of dissimilarity among samples, thus dissimilarity is lower.

Cumulative Contribution	Species			Genus			Family			Order		
	Phase 1	Phase 2	Phase 3	Phase 1	Phase 2	Phase 3	Phase 1	Phase 2	Phase 3	Phase 1	Phase 2	Phase 3
<b>Whole Fauna</b>												
25%	6 (0.02)	28 (0.03)	54 (0.06)	4 (0.01)	17 (0.03)	30 (0.04)	3 (0.02)	9 (0.03)	15 (0.05)	2 (0.02)	4 (0.04)	7 (0.07)
50%	28 (0.08)	111 (0.11)	169 (0.18)	21 (0.08)	64 (0.11)	98 (0.14)	12 (0.08)	31 (0.11)	46 (0.16)	5 (0.04)	10 (0.10)	18 (0.17)
75%	91 (0.24)	288 (0.30)	363 (0.38)	67 (0.24)	163 (0.28)	214 (0.30)	37 (0.24)	78 (0.28)	103 (0.36)	14 (0.12)	26 (0.26)	39 (0.37)
Total S	373	975	953	279	579	723	155	282	285	121	99	106
<b>Polychaeta</b>												
25%	4 (0.02)	13 (0.02)	27 (0.06)	3 (0.02)	7 (0.03)	14 (0.06)	3 (0.06)	3 (0.06)	5 (0.11)	2 (0.12)	2 (0.12)	3 (0.20)
50%	16 (0.09)	53 (0.10)	82 (0.19)	12 (0.10)	27 (0.13)	43 (0.20)	7 (0.14)	9 (0.19)	13 (0.28)	3 (0.18)	4 (0.24)	5 (0.33)
75%	50 (0.27)	132 (0.24)	173 (0.39)	36 (0.29)	65 (0.31)	89 (0.40)	15 (0.30)	19 (0.40)	24 (0.51)	6 (0.35)	7 (0.41)	9 (0.60)
Total S	183	540	440	125	211	220	50	47	47	17	17	15
<b>Bivalvia</b>												
25%	2 (0.05)	4 (0.05)	6 (0.10)	1 (0.03)	3 (0.06)	5 (0.08)	1 (0.05)	2 (0.07)	3 (0.12)	1 (0.12)	1 (0.11)	2 (0.20)
50%	4 (0.10)	9 (0.12)	15 (0.25)	3 (0.09)	7 (0.13)	12 (0.19)	3 (0.16)	4 (0.13)	8 (0.31)	2 (0.25)	2 (0.22)	3 (0.30)
75%	8 (0.20)	21 (0.29)	29 (0.48)	6 (0.19)	14 (0.27)	23 (0.37)	4 (0.21)	8 (0.27)	14 (0.54)	2 (0.25)	3 (0.33)	6 (0.60)
Total S	40	73	61	32	52	63	19	30	26	8	9	10
<b>Malacostraca</b>												
25%	4 (0.06)	8 (0.04)	13 (0.04)	3 (0.05)	4 (0.03)	6 (0.04)	3 (0.07)	3 (0.04)	4 (0.04)	2 (0.29)	1 (0.12)	1 (0.12)
50%	9 (0.13)	25 (0.12)	35 (0.12)	7 (0.12)	15 (0.12)	19 (0.11)	6 (0.14)	9 (0.12)	12 (0.13)	3 (0.43)	3 (0.38)	3 (0.38)
75%	23 (0.32)	65 (0.31)	71 (0.25)	15 (0.27)	38 (0.29)	41 (0.25)	11 (0.26)	22 (0.30)	27 (0.30)	4 (0.57)	5 (0.62)	4 (0.50)
Total S	71	213	289	56	130	167	43	74	90	7	8	8

## 4. DISCUSSION

### 4.1. Caveats

The dataset evaluated is itself only a subset of the total macrobenthic fauna in the study area owing to the use of Shipek and van Veen grab samplers, which are most effective at collecting infaunal taxa, especially those living within the upper ~15 cm of the seabed (minimum penetration required to retain a sample; LACSD 2020). Although these data largely exclude mobile epifauna, the suite of taxa collected by these and other point-penetration sampling gear (e.g., 0.01 m<sup>2</sup> box cores) are the basis of almost all quantitative analyses of soft-sedimentary communities by both academics and agencies.

Numerical sufficiency (Table 1) can significantly reduce the effort of counting individuals in samples but limits the analytical utility of data. Presence-absence, ranked abundance, and categorical (abundant, common, etc.) data, for example, will quantify raw richness accurately, but cannot be rarefied to compensate for disparate sample sizes and are unsuitable for evaluating evenness (community structure). Such low-resolution data are also problematic for SIMPER analysis of variation in species composition, which specifies the use of abundance-based Bray-Curtis dissimilarities as opposed to presence-absence based methods such as Jaccard indices (Clarke 1993). For these reasons, the absolute counts of individuals for each sample were used – i.e., density data – in all analyses.

Data transformation (i.e., analytical coarsening) of numerical abundance data constitutes a test of numerical sufficiency, but of course does not reduce processing effort and thus is not a surrogate. Our compositional analyses (NMDS, PERMANOVA, SIMPER) use square-root transformed proportional abundance data, as is common in macrobenthic studies. Up to the family level, our patterns are robust to other transformations of proportional abundances, including no transformation or fourth-root transformation. The main effect of data transformation is on the strength of the spatial difference detected by taxonomic subsets during Phase 1; although differences are significant during Phase 1 for all surrogates,  $R^2$  values decline as the intensity of the transformation increases, and the same trend in the other temporal bins were observed. Coarsening numerical resolution to the extreme of presence-absence data for these analyses makes the patterns robust only to the genus level.

The focused subsetting analyses on the three most numerically abundant classes in the macrofauna is a common practice in surrogacy tests, but it should be noted that the class Gastropoda ranks slightly above Bivalvia in species richness (Fig. 3B). However, gastropods have such low abundance on the Palos Verdes shelf that they did not, on their own, detect any spatial or temporal variation. Thus, in serving as surrogates, taxonomic subsets represented by large numbers of individuals trump subsets with large numbers of species. When gastropods were combined with bivalves into a single analytic group (mollusks), patterns were not significantly different from those achieved using bivalves alone. Therefore, the analyses in this study focused on the three most numerically abundant, rather than most speciose, classes as taxonomic subsets.

### 4.2. Taxonomic Resolution: Genus- and Family-level Data Suffice

Coarsening taxonomic resolution to the genus and family level preserved the spatial and temporal gradients in wastewater contamination that characterize the whole macrobenthic fauna on this shelf, and the same was true for all assessed surrogate subsets. Ordinal-level data also detected the spatial gradient associated with the outfall when that gradient existed (i.e., during Phases 1 and 2; Fig. 7), but altered diversity and compositional patterns across all four faunal sets. Therefore, ordinal data were not a good surrogate for finer taxonomic resolution. These results corroborate previous studies that family-level identification is a good first-order means of reducing the effort of detecting spatial gradients (Jones 2008; Heino 2010; Pitacco et al. 2019). This analysis extends this result to temporal as well as spatial variation and, more importantly, examines the interaction with different taxonomic subsets of the fauna (see next section).

Genus- and family-level data suffice in this southern California setting because S/G and S/F ratios in the whole fauna are low (~2 and 5, respectively; Table 2). Taxonomic sufficiency is commonly found to be inversely related to the ratio of the number of species over the number of higher taxa (S/T) because increasing the number of species per higher taxon increases the probability that these species will differ in their pollution tolerance; this is probably why lower ratios produce stronger sufficiency at a given resolution in other systems (e.g., Bevilacqua et al. 2012, de Oliveira et al. 2020). Some studies postulate that S/T values < 2.5 will generally result in good correlations between taxa- and species-level patterns (Timms et al. 2013, Albano et al. 2016). Although the family and functional guild ratios in this study are greater than this value, particularly for this species-rich polychaete subset, the S/T values on the Palos Verdes Shelf corroborate the growing evidence that the sufficiency of higher taxa is dependent on S/T ratios remaining below a particular threshold.

The unpredictable patterns produced by ordinal data across all faunal datasets probably arise at least in part from the high S/O values (8.9-36, Table 2), although the small number of orders probably also contributes to the low sensitivity of ordinal data. In malacostracans, where diversity and compositional patterns deteriorate most strongly with coarsening resolution, the S/T ratio rises strongly from families (S/F = 3.2) to orders (S/O = 36).

The exceptionally strong, anthropogenic gradient in environmental conditions on the Palos Verdes Shelf, especially during Phases 1 and 2, also favors the practicality of coarser groupings: habitats as distinct as black H<sub>2</sub>S-rich mud and greenish sandy mud are likely to be dominated by different functional guilds rather than simply by different species within a single, consistently dominant functional guild. Functional guilds, including bivalves in particular, have been shown to be conserved within families and genera (Stanley 1970, Collins et al. 2019). As such, coarsening the taxonomic resolution of a dataset will not reduce the ability to differentiate between habitats and temporal changes in areas with known or suspected strong human stressors.

Even in areas with well-resolved macrobenthic systematics such as southern California, species-level taxonomy undergoes revision, challenging the merging of species-level datasets across decades of monitoring. Such revisions will have the greatest consequences for the S/G ratio, but the net effects of splitting and of lumping taxa are likely to balance out. The recognition of new species by splitting older ones creates the greatest complications for historic compilations in the absence of voucher material, which is less of a problem when vouchers are retained for future reference. For example, *Tellina carpenteri* and ‘*Tellina* sp B’ from this dataset were not differentiated prior to the 1990s. Such newly split taxa will increase the S/G ratio, but, fortunately, they constitute a very small minority of taxa in the fauna. Taxonomic revisions such as the upgrading of subgenera to genera and the correction of synonyms are, in contrast, easily applied retrospectively to data and will tend to decrease the S/G ratio. Species that represent known but unresolved taxonomic complexes, that are harboring cryptic species whose distinction is beyond conventional morphologic detection (e.g., the polychaetes *Capitella capitata* and *Scoloplos armiger*), hide per-genus species richness and represent a challenge for many kinds of analysis. Fortunately, they constitute, again, only a small number of taxa in the southern California fauna, and their effect is to amplify the apparent numerical abundance of a named species.

### **4.3. Polychaetes are the best *proxy* of spatial & temporal variation in the whole fauna**

Polychaete patterns resembled the whole fauna most closely, indicating that they are the best proxy subset (Table 1) for characterizing spatial and temporal variation of benthos on the Palos Verdes shelf. This fidelity likely arises from polychaetes constituting the majority of individuals in the whole fauna (61%; Fig. 3, Table 2). This proxy power persists with coarsening of polychaete data to the genus and family levels (Figs. 4-7). To become an effective proxy, a subset probably needs to constitute an absolutely high threshold proportion of the whole fauna in numbers of individuals, not simply a plurality, and certainly more than the 17% of individuals that the second-ranked bivalves represent (Fig. 3). In contrast, constituting a high proportional *richness* of the fauna does not make a clade an inherently

effective proxy (e.g., malacostracans and the species-rich but individual-poor gastropods). Although polychaetes are the most speciose class in our fauna, their proxy power results from their high proportional numerical abundance.

For a spectrum of temperate to subarctic shelves, Olsgard et al. (2003) identified the polychaete order Terebellida as an effective proxy subset for all polychaetes, and to a lesser extent, the whole fauna. In this dataset, Terebellida was the most numerically abundant order (N = 111,616, 34% of polychaetes, 21% of whole fauna), but failed to mirror spatial and temporal patterns of either the full polychaete subset or the whole fauna and it also failed to detect the spatial pollution gradient. Capitellidae, the second most abundant polychaete clade in California (N = 74,523, 23% of polychaetes, 14% of whole fauna), also failed to mirror the full polychaete subset or the whole fauna. However, Capitellidae did rival Bivalvia in its ability to detect the spatial gradient (see section 4.4). The entire class of Polychaeta is therefore an effective proxy subset of the whole fauna in southern California (and elsewhere; e.g., Giangrande et al. 2005; Magierowski & Johnson 2006, Włodarska-Kowalczyk & Kędra 2007) and subsets within Polychaeta may not be suitable on their own.

#### **4.4. Bivalves are the best indicators of spatial & temporal gradients**

Although bivalves did not closely mirror the whole fauna and thus performed poorly as a proxy subset for the whole fauna in this study area, they performed better than other subsets and better than the whole fauna in detecting the outfall gradient and its temporal decline. Effective indicator subsets do not need to correlate to whole fauna patterns: the above-average sensitivity of a clade to environmental change is the primary criterion (Noss 1990, Pearson 1994). Bivalve richness was completely and surprisingly insensitive to spatial variation per treatment phase; it could not differentiate the near-field and far-field areas (Fig. 4). Bivalve richness was, however, very effective at detecting decadal-scale temporal variation, implying that, owing to recovery of benthic communities, the contrast in temporal conditions (between Phase 3 and Phase 1) is greater than that in spatial conditions (near-field and far-field) within Phase 1, the phase with the strongest pollution gradient (Fig. 4). Bivalve evenness and composition – i.e., measures that take numerical abundance into account, not simply a count of species – were powerful at detecting both spatial and temporal variation on this urban shelf (Figs. 5-6).

Much of this observed pattern is driven by the numerical dominance of the bivalve *Parvilucina tenuisculpta* during the height of contaminant emissions in the early 1970s, as previously recognized (e.g., Fabrikant 1984, LACSD 2020). This bivalve, which harbors sulfur-oxidizing chemosymbiotic bacteria, was extremely abundant and large-bodied at stations immediately *outside* the near-field area during Phases 1 and 2 when seabeds were organic- and sulfide-rich. Based on bivalve shell assemblages from <sup>210</sup>Pb-age-dated sedimentary cores, *P. tenuisculpta* populations were significantly lower in the early 20<sup>th</sup> century (before and during the early history of wastewater emissions and before the onset of biomonitoring) and the bivalve community of today, with ~8% *P. tenuisculpta*, appears to be recovering towards these pre-effluent conditions (Leonard-Pingel et al. 2019).

In this dataset, Lucinida (which includes *P. tenuisculpta*) was the most numerically abundant bivalve order (N = 71,685, 77% of bivalves, 13% of whole fauna), followed by Venerida (N = 18,592, 20% of bivalves, 3% of whole fauna). However, neither clade on its own could mirror patterns of the full bivalve subset, and their abilities to detect the spatial gradient were weaker than even the ability of the whole fauna. The entire class of Bivalvia is therefore an effective indicator subset for this outfall gradient, and like the polychaetes discussed above, subsets within Bivalvia are not necessarily suitable on their own.

#### **4.5. The Predictive Power of Functional Guilds for Surrogacy**

Changes in the relative abundance of trophic guilds has been long-appreciated as a key component of benthic response to pollution, especially to nutrients or other organic loading, as observed both over time and along spatial gradients (e.g., Pearson & Rosenberg 1978, Maurer et al. 1999, Gray and Elliott

2009). Species that feed on fresh plankton and other suspended material (filter feeders and photosymbiont-bearing taxa) decline in abundance in favor of those that feed on detritus and/or its microbial communities (many kinds of deposit feeders plus chemosymbiont-bearing taxa). Many detritus-loving metazoans are additionally tolerant of the side effects of organic enrichment, such as hypoxia, soupy mass properties, frequently resuspended fines, and high levels of contaminants, which are preferentially absorbed on fine particles. The relative abundance of trophic guilds – or, more broadly, of functional guilds that additionally consider mobility and life habit – is thus expected to vary significantly along spatial and temporal gradients, and perhaps more strongly than observed among taxonomic clades (Gusmao et al. 2016, Norkko et al. 2019). Our findings on functional guilds are consistent with the general model of benthic trophic response to organic enrichment (Pearson & Rosenberg 1978). Using functional guilds as units of analysis, we find that richness, evenness, and composition all differ more strongly across space during Phase 1 (high enrichment) than during Phase 2 and the spatial difference declines further into Phase 3.

On the Palos Verdes Shelf, functional guild diversity is on par with family- and ordinal-level diversity, depending on which subset is used. The reliability of polychaetes as a proxy subset is possibly tied to its similar functional diversity ( $S/FG = 15.8$ ) as that of the whole fauna (14.9), while the functional diversity of bivalves and malacostracans is considerably lower (7.42 and 9, respectively). Because con-generic and con-familial species often encompass similar functional guilds, functional diversity may be a signal for a good proxy subset even if genus- or family-level diversity is anomalously high. Over time, functional diversity (richness and evenness) increases with improved wastewater treatment, both in the whole fauna and the subsets, especially for bivalves (Figs. 4 and 5). This observed increase is consistent with the decreases in functional diversity observed elsewhere under regimes of deteriorating conditions (Gusmao et al. 2016, Norkko et al. 2019). Future studies on taxonomic surrogacy should regularly include analyses of functional guilds to verify the utility of this often-overlooked means of coarsening taxonomic data.

Beyond numerical diversity of functional guilds, their ecological disparity (that is, the range of life habit and trophic strategies) must be considered. Functional guilds of bivalves that span deep-burrowing chemosymbiosis to free-swimming epifauna are specialized towards each end of the pollution spectrum and may cover a broader environmental response than the numerically larger, but more nuanced, guilds observed in polychaetes and malacostracans. Indeed, the functional response of bivalves to improved water treatment on the Palos Verdes Shelf involves a precipitous decline in chemosymbiont-bearing taxa in the late 1980s and the gradual increase of infaunal suspension and mixed feeders (Stull et al. 1996, Leonard-Pingel et al. 2019, LACSD 2012). The uniquely broad range of functional guilds among bivalves may be a signal for a good indicator subset. A means of quantifying functional disparity among taxonomic subsets would help validate this potential method of subsetting taxonomic data.

#### **4.6. Bivalve Assemblages are Useful Indicators of Ecological Condition**

Biotic indices such as the BRI have been used to assess ecological condition using the abundance-weighted pollution tolerances of taxa. Applying such indices to recent fossil records – e.g., time-averaged death assemblages (DAs) – is a promising method to (1) characterize conditions from before whole-fauna monitoring began, and (2) detect otherwise unappreciated ecological stress in systems using live-dead discordance. However, the robustness of biotic indices when applied to taxonomic subsets, such as shelly fauna, is under-explored.

As revealed in Kokesh et al. 2020, the power of indices calculated from a bivalve-only dataset were compared using the BRI, AZTI's Marine Benthic Index (AMBI, Borja et al. 2003), and BENTIX (Simboura and Zenetou, 2003). All three indices indicated that benthic conditions improved with improving wastewater treatment, with the biggest improvements in condition close to the outfall. Bivalves underestimated whole-fauna AMBI because they only occupy the index's low- and mid-disturbance AMBI groups (I-III), and thus cannot detect the most severely polluted sites. In contrast,

BRI and BENTIX based on bivalves-only correlated strongly with the whole fauna. A driver for this outcome is that the binary group assignment used by BENTIX elevates the influence of bivalves with moderate tolerance to pollution (AMBI group III). As these indices differ in their power to detect impacts, multiple methods should be used in tandem when conducting condition assessments.

Indices for bivalve DAs – which include shells >100s years old on the Palos Verdes shelf – indicate lower stress than was observed in early communities (1970s-80s), and either agree with or overestimate the stress in more recent communities (2000s-10s). This live-dead discordance suggests that time-averaging causes DAs to retain a signal from both pollution and pre-pollution benthic conditions that the shelf benthos is now re-attaining due to ongoing ecosystem recovery.

Bivalves are thus an effective subset of the whole fauna for detecting gradients in benthic conditions using biotic indices. Use of DAs applied to biotic indices can reveal both the existence and direction of change in a community relative to its historic range of variation.

#### **4.7. Implications for Using Dead-Shell, Core, and Fossil Assemblages**

Paleontologists have a long-standing interest in using the “preservable”, i.e., shell-bearing portion, of the benthic community as a surrogate of the entire benthic fauna. That subset, typically dominated by shelled mollusks and echinoderms today, is most likely to be represented in fossil assemblages; species with only soft- or lightly-sclerotized tissues have potential for long-term natural preservation only where sedimentation rates are exceptionally high and/or low-oxygen excludes scavengers and bioturbators. Paleontological interest includes both the power of shelly fauna to serve as proxies, i.e., substitutes for the richness, structure, and trophic complexity of the whole fauna, as well as the power of shelly fauna as indicators of environmental gradients (e.g., Schopf 1978, Staff et al. 1986, Tyler & Kowalewski 2017). Insights from modern systems on the fossilization potential of biological information – called ‘actualistic’ studies, which include live-dead comparisons (Kidwell & Tomašových 2013) – provide guidance and confidence for paleobiological interpretation of fossil records that might preserve only a small portion of all likely fauna.

Rare exceptions to the almost exclusively-skeletal nature of the fossil record are found in Konservat-Lagerstätten – deposits with exceptional preservation of soft tissues often generated by catastrophic burial events in anoxic environments with minimal microbial decomposition (Allison & Briggs 1993, Saleh et al. 2020). Such deposits, exemplified by the 505 million-year old Burgess Shale, serve as windows into broader ecosystem structure otherwise only seen on the modern seabed. The utility of polychaetes as a proxy subset of the whole fauna, especially at coarsened taxonomic (families and functional guilds) and numeric resolutions (rank-abundance or presence-absence, see section 4.1), is encouraging for their potential in approximating broader benthic patterns along comparably strong environmental gradients in ancient systems with soft-part preservation.

Bivalves, on the other hand, are both ubiquitous throughout the fossil record and actively accumulate skeletal material on the seabed under normoxic conditions. Surficial and down-core dead-shell assemblages, which can be sampled in tandem with co-occurring living benthic communities, can extend hundreds to thousands of years before the onset of monitoring efforts, capturing pre-impact conditions and/or historic gradients no longer present. The utility of bivalves as an indicator subset of the pollution gradient on the Palos Verdes Shelf is encouraging for their potential in detecting comparably strong environmental gradients from both modern and ancient systems.

## **5. CONCLUSIONS**

This case study, using an exceptional 45 year-long macrobenthic dataset from the Palos Verdes shelf, demonstrates that coarsening the taxonomic resolution of animal identification and focusing on taxonomic subsets of the whole fauna are both viable techniques to reduce the demands on taxonomic expertise and processing effort of monitoring in regions with strong suspected pollution gradients. The authors found that, with the relatively low ratios of species to higher taxa in temperate southern

California, genus- and family-level identification, as well as functional guilds, are strongly correlated to species-level patterns. Polychaetes, constituting the majority of macrobenthic individuals, are a good *proxy surrogate* for the patterns exhibited by the whole fauna, especially at specific and generic resolutions; the most proportionally abundant taxonomic subset of a fauna would be expected to be the best *mirror of the whole fauna*. Bivalves, on the other hand, are the best *indicator surrogate* of spatial and temporal variation relating to the *environmental stress of concern* (here, wastewater contaminants), despite being only second-ranked in abundance and fourth-ranked in species richness. Using single families and orders within polychaetes and bivalves did not suffice as either proxy, even for the most abundant or speciose clades: class-level taxonomic breadth is apparently required, even where the pollution gradient is very strong, as historically is the case on the Palos Verdes Shelf. This need for class-level breadth, at minimum, may be even stronger in settings with entirely natural, and thus typically less steep, environmental gradients in time and space: although it will be difficult to predict *ad hoc* which families within a class might be ‘best’ for a given region of study, the groups that consist of some species that are specialized to gradient end-members can be most suitable. The indicator power of Bivalvia might be attributed to its impressive trophic breadth, which ranges from pollution-tolerant facultative chemosymbiotic taxa to pollution-sensitive epifaunal species (both distributed across several families) in addition to an array of deposit- and suspension-feeding functional guilds that are also found in other classes. However, guild-level data were effective in every taxonomic subset of the whole fauna (as well as for the whole fauna itself). In each set, the number of guilds were approximately equivalent to the number of orders and thus constitutes a “savings” of effort, but guild assignment requires a high degree of knowledge – or extrapolation – of trophic and other biology.

Long-term monitoring programs are an exceptional means for understanding ecological responses to anthropogenic impacts and assessing the effectiveness of remediation efforts. As demonstrated in this study, insights acquired from the highly-resolved, methodologically-standardized, and broad-scoped data produced by such efforts in well-funded regions like southern California can be used to advise the design of efficient programs for areas where the fauna is less fully documented, local taxonomic expertise and/or funds are scarce, and yet the need for environmental evaluation is still or perhaps especially urgent. The insights presented here, as in the vast majority of other surrogacy tests, are from extratropical regions. The consistency of these findings on the robustness of family-level resolution and of class-level taxonomic subsets with those from other studies suggests, however, that this may be converging on general rules. Comparable case studies are nonetheless needed in fully tropical settings, where regional species pools are commonly an order of magnitude larger. Species/genus ratios are also higher in the tropics (Krug et al. 2008) and thus we suspect that a minimum of genus-level data might be required to sufficiently mirror species-level patterns. Extrapolating from extra-tropical studies, we suspect a similar need for class-level breadth to identify environmental gradients, prioritizing polychaetes and bivalves as the generally most abundant and trophically-diverse subsets of soft-sedimentary communities. The power of Bivalvia as environmental indicators is especially encouraging, given the potential to retrospectively reconstruct historical, pre-impact conditions from their dead-shell assemblages. Surrogate datasets thus hold great promise as an efficient means of launching new monitoring programs, particularly in poorly studied and yet heavily stressed locations.

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## LITERATURE CITED

- Allison PA, Briggs DEG (1993) Exceptional fossil record: distribution of soft-tissue preservation through the Phanerozoic. *Geology* 21:527-530.
- Albano PG, Tomašových A, Stachowitsch M, Zuschin M (2016) Taxonomic sufficiency in a live-dead agreement study in a tropical setting. *Palaeogeogr Palaeoclimatol Palaeoecol* 449:341-348.
- Albano PG, Gallmetzer I, Haselmair A, Tomašových A, and others (2018) Historical ecology of a biological invasion: the interplay of eutrophication and pollution determines the time lags in establishment and detection. *Biol Invasions* 20:1417-1430.
- Anderson MJ (2001) A new method for non-parametric multivariate analysis of variance. *Austral Ecol* 26:32-46.
- Bevilacqua S, Fraschetti S, Musco L, Terlizzi A (2009) Taxonomic sufficiency in the detection of natural and human-induced changes in marine assemblages: a comparison of habitats and taxonomic groups. *Mar Pollut Bull* 58:1850-1859.
- Bevilacqua S, Terlizzi A, Claudet J, Fraschetti S, Boero F (2012) Taxonomic relatedness does not matter for species surrogacy in the assessment of community responses to environmental drivers. *J Appl Ecol* 49:357-366.
- Bhusal DR, Kallimanis AS, Tsiafouli MA, Sgardelis SP (2014) Higher taxa vs. functional guilds vs. trophic groups as indicators of soil nematode diversity and community structure. *Ecol Indic* 41:25-29.
- Borja A, Muxika I, Franco J (2003) The application of a Marine Biotic Index to different impact sources affecting soft-bottom benthic communities along European coasts. *Mar Pollut Bull*;46(7):835-845. DOI: 10.1016/s0025-326x(03)00090-0.
- Borja A, Muxika I, Franco J (2006) Long-term recovery of soft-bottom benthos following urban and industrial sewage treatment in the Nervion estuary (southern Bay of Biscay). *Mar Ecol Prog Ser* 313:43-55.
- Bray JR, Curtis JT (1957) An ordination of upland forest communities of southern Wisconsin. *Ecol Monogr* 27:325-366.
- Brind'Amour A, Laffargue P, Morin J, Vaz S and others (2014) Morphospecies and taxonomic sufficiency of benthic megafauna in scientific bottom trawl surveys. *Cont Shelf Res* 72:1-9.
- Buss DF, Vitorino AS (2010) Rapid bioassessment protocols using benthic macroinvertebrates in Brazil: evaluation of taxonomic sufficiency. *J N Am Benthol Soc* 29:562-571.
- Clarke KR (1993) Non-parametric multivariate analyses of changes in community structure. *Austral Ecol* 18:117-143.
- Collins KS, Edie SM, Gao T, Bieler R, Jablonski D (2019) Spatial filters of function and phylogeny determine morphological disparity with latitude. *PLoS One* 14(8):e0221490.
- Ellis D (1985) Taxonomic sufficiency in pollution assessment. *Mar Pollut Bull* 12:459.
- De Oliveira Jr SS, Ortega JC, dos Santos Ribas LG, and others (2020) Higher taxa are sufficient to represent biodiversity patterns. *Ecol Indic* 111:105994.
- Fabrikant R (1984) The effect of sewage effluent on the population density and size of the clam *Parvilucina tenuisculpta*. *Mar Pollut Bull* 15:249-253.
- Ferraro SP, Cole FA (1992) Taxonomic level sufficient for assessing a moderate impact on macrobenthic communities in Puget Sound, Washington, USA. *Can J Fish Aquat Sci* 49:1184-1188.
- Fontaine A, Devillers R, Peres-Neto PR, Johnson LE (2015) Delineating marine ecological units: a novel approach for deciding which taxonomic group to use and which taxonomic resolution to choose. *Divers Distrib* 21:1167-1180.
- Giangrande A, Licciano M, Musco L (2005) Polychaetes as environmental indicators revisited. *Mar Pollut Bull* 50:1153-1162.
- Gray JS, Elliott M (2009) *Ecology of Marine Sediments: From Science to Management*, 2<sup>nd</sup> edn. Oxford University Press Inc., New York, NY.
- Gusmao JB, Brauko KM, Eriksson BK, Lana PC (2016) Functional diversity of macrobenthic assemblages decreases in response to sewage discharges. *Ecol Indic* 66:65-75.
- Heino J (2010) Are indicator groups and cross-taxon congruence useful for predicting biodiversity in aquatic ecosystems? *Ecol Indic* 10:112-117.
- Hurlbert SH (1971) The nonconcept of species diversity: a critique and alternative parameters. *Ecology* 52:557-586
- Islam MS, Tanaka M (2004) Impacts of pollution on coastal and marine ecosystems including coastal and marine fisheries and approach for management: a review and synthesis. *Mar Poll Bull* 48:624-649.
- Jones FC (2008) Taxonomic sufficiency: the influence of taxonomic resolution on freshwater bioassessments using benthic macroinvertebrates. *Environ Rev* 16:45-69.
- Kidwell SM, Tomašových A (2013) Implications of time-averaged death assemblages for ecology and conservation biology. *Annu Rev Ecol Evol Syst* 44:539-563.

- Kokesh, BS, Kidwell, SM, Tomasovych, A, Walther, SM (2020) The power of bivalve assemblages as indicators of ecological condition over space and time. Paper presented at: GSA 2020 Connects Online. T82. Ecosystem Perspectives on the Marine Fossil Record. *Geol Soc Am Vol 52*, No. 6. Doi: 10.1130/abs/2020AM-356867
- Krug AZ, Jablonski D, Valentine JW (2008) Species–genus ratios reflect a global history of diversification and range expansion in marine bivalves. *Proc Roy Soc B* 275:1117-1123.
- LACSD (Los Angeles County Sanitation Districts) (2012) Joint Water Pollution Control Plant Biennial Receiving Water Monitoring Report 2010-2011. Los Angeles County Sanitation Districts, Whittier, CA.
- LACSD (Los Angeles County Sanitation Districts) (2020) Joint Water Pollution Control Plant Biennial Receiving Water Monitoring Report 2018-2019. Los Angeles County Sanitation Districts, Whittier, CA.
- Lee HJ, Sherwood CR, Drake DE, Edwards BD, and others (2002) Spatial and temporal distribution of contaminated, effluent-affected sediment on the Palos Verdes margin, southern California. *Cont Shelf Res* 22:859-880.
- Leonard-Pingel JS, Kidwell SM, Tomašových A, Alexander CR, Cadien DB (2019) Gauging benthic recovery from 20<sup>th</sup> century pollution on the southern California continental shelf using bivalves from sediment cores. *Mar Ecol Prog Ser* 615:101-119.
- Macdonald TA, Burd BJ, Macdonald VI, van Roodselaar A (2010) Taxonomic and feeding guild classification for the marine benthic macroinvertebrates of the Strait of Georgia, British Columbia. *Can Tech Rep Fish Aquat Sci* 2874.
- Magierowski RH, Johnson CR (2006) Robustness of surrogates of biodiversity in marine benthic communities. *Ecol Appl* 16:2264-2275.
- Mueller M, Pander J, Geist J (2013) Taxonomic sufficiency in freshwater ecosystems: effects of taxonomic resolution, functional traits, and data transformation. *Freshw Sci* 32:762-778.
- Norkko J, Pilditch CA, Gammal J, Rosenberg R, and others (2019) Ecosystem functioning along gradients of increasing hypoxia and changing soft-sediment community types. *J Sea Res* 153:101781.
- Noss RF (1990) Indicators for monitoring biodiversity: a hierarchical approach. *Conserv Biol* 4:355-364.
- Oksanen J, Blanchet FG, Friendly M, Kindt R and others (2019) vegan: community ecology package. R package version 2.5-4. <https://CRANR-project.org/package=vegan>
- Olsgard F, Brattegard T, Holthe T (2003) Polychaetes as surrogates for marine biodiversity: lower taxonomic resolution and indicator groups. *Biodivers Conserv* 12:1033-1049.
- Pearson DL (1994) Selecting indicator taxa for the quantitative assessment of biodiversity. *Phil Trans R soc Lond B* 345:75-79.
- Pearson TH, Rosenberg R (1978) Macrobenthic succession in relation to organic enrichment and pollution of the marine environment. *Oceanogr Mar Biol Ann Rev* 16:229-311.
- Pik AJ, Oliver I, Beattie AJ (1999) Taxonomic sufficiency in ecological studies of terrestrial invertebrates. *Austral Ecol* 24:555-562.
- Pitacco V, Mistri M, Aleffi IF, Lardicci C and others (2019) The efficiency of taxonomic sufficiency for identification of spatial patterns at different scales in transitional waters. *Mar Environ Res* 144:84-91.
- Saleh F, Antcliffe JB, Lefebvre B, Pittet B, and others (2020) Taphonomic bias in exceptionally preserved biotas. *Earth Planet Sci Lett* 529:115873.
- SCAMIT (Southern California Association of Marine Invertebrate Taxonomists) (2013) A Taxonomic Listing of Benthic Macro- and Megainvertebrates from Infaunal and Epifaunal Monitoring and Research Programs in the Southern California Bight, 8<sup>th</sup> edn. SCAMIT, San Diego, CA.
- Schiff K, Greenstein D, Dodder N, Gillett DJ (2016) Southern CalifoBight regional monitoring. *Regional Studies Mar Sci* 4:34-46.
- Schopf TJM (1978) Fossilization potential of an intertidal fauna: Friday Harbor, Washington. *Paleobiology* 4:261-270.
- Simboura, N, Zenetou, A (2003) A new biotic index (Bentix index) for use in ecological quality classification of benthic ecosystems. In *Hellenic Symp on Oceanog and Fish. Abstracts* (p. 56).
- Smail EA, Webb EA, Franks RP, Bruland KW, Sañudo-Wilhelmy SA (2012) Status of metal contamination in surface waters of the coastal ocean off Los Angeles, California since the implementation of the Clean Water Act. *Environ Sci Technol* 46:4304-4311.
- Smith RW, Bergen M, Weisberg SB, Cadien D and others (2001) Benthic response index for assessing infaunal communities on the southern California mainland shelf. *Ecol Appl* 11:1073-1087.
- Souza JLP, Baccaro FB, Landeiro VL, Franklin E and others (2016) Taxonomic sufficiency and indicator taxa reduce sampling costs and increase monitoring effectiveness for ants. *Divers Distrib* 22:111-122.
- Staff GM, Stanton Jr RJ, Powel EN, Cummins H (1986) Time-averaging, taphonomy, and their impact on paleocommunity reconstruction: death assemblages in Texas bays. *Geol Soc Am Bull* 97:428-443.
- Stanley SM (1970) Relation of shell form and life habit of the Bivalvia (Mollusca). *Geol Soc Am Mem* 125:1-256.
- Stein ED, Cadien D (2009) Ecosystem response to regulatory and management actions: the southern California experience in long-term monitoring. *Mar Pollut Bull* 59:91-100.

Tyler CL, Kowalewski M (2017) Surrogate taxa and fossils as reliable proxies of spatial biodiversity patterns in marine benthic communities. *Proc Royal Soc B* 284:20162839.

Warwick RM (1988) The level of taxonomic discrimination required to detect pollution effects on marine benthic communities. *Mar Pollut Bull* 19:259-268.

Warwick RM (1993) Environmental impact studies on marine communities: pragmatic considerations. *Austral Ecol* 18:63-80.

Włodarska-Kowalczyk M, Kędra M (2007) Surrogacy in natural patterns of benthic distribution and diversity: selected taxa versus lower taxonomic resolution. *Mar Ecol Prog Ser* 351:53-63.

Yasuhara M, Hunt G, Breitburg D, Tsujimoto A, Katsuki K (2012) Human-induced marine ecological degradation: micropaleontological perspectives. *Ecol Evol* 2:3242-3268.

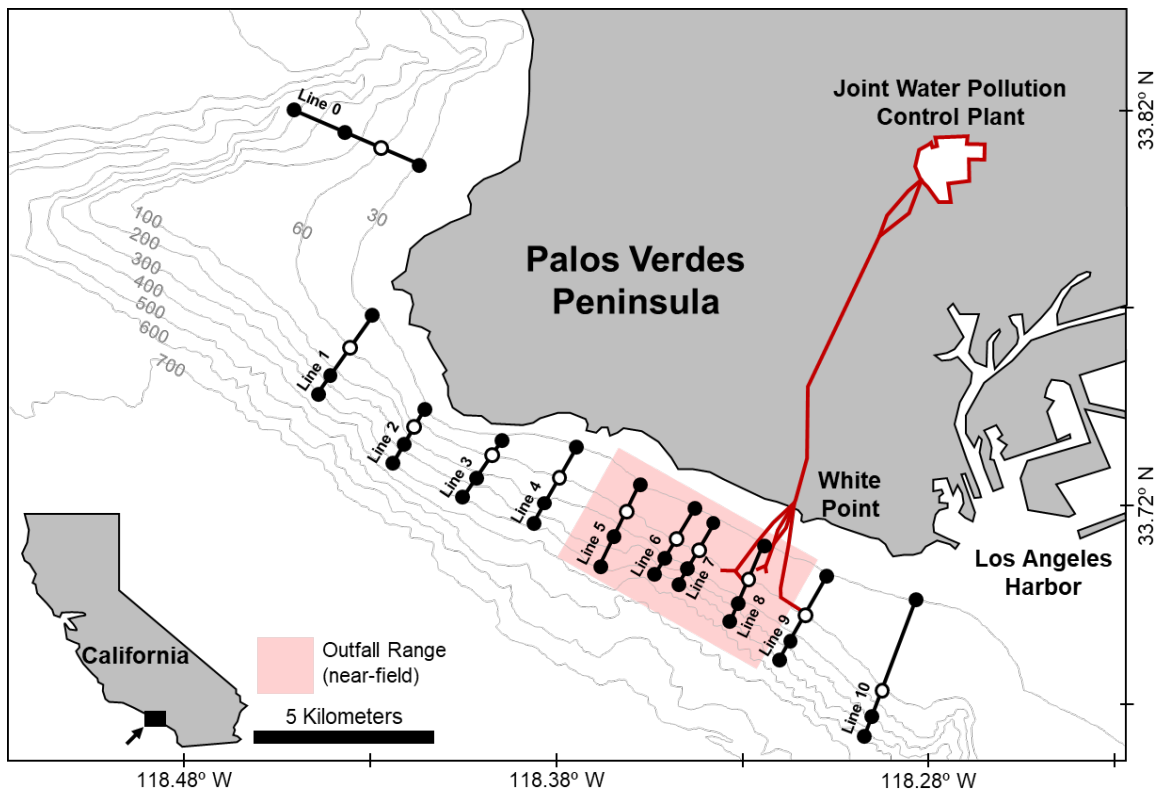


Fig. 1. Study area off the Palos Verdes peninsula on the southern California continental shelf. Annual monitoring of macrobenthos are conducted along 11 bathymetric sampling transects (Lines 0-10) at 30, 60, 150, and 300 m depths. White dots indicate sampling stations along the 60 m isobath used in this study. Gray lines are isobaths and red lines are the outfall pipes extending from the JWPCP to Whites Point. Red area approximates the stations near the outfall source (near-field) defined in this study, encompassing lines 5-8. Modified from LACSD (2020)

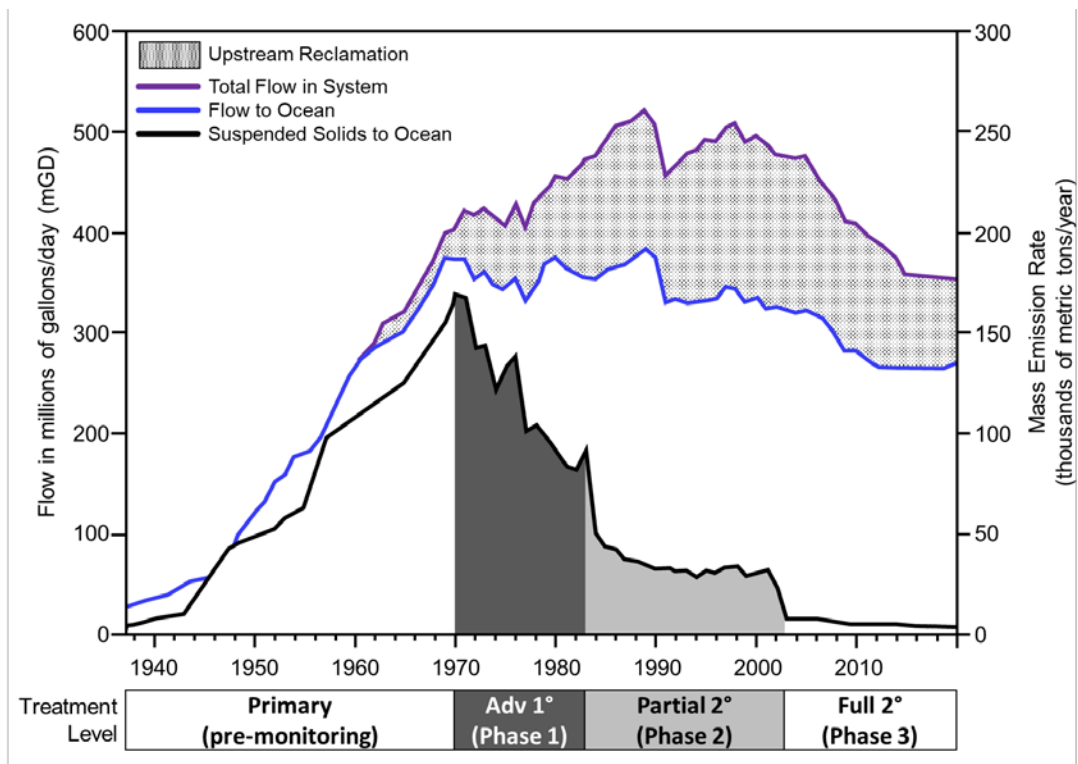


Fig. 2. Discharge history (1 US gallon  $\approx$  3.79 L) from the Joint Water Pollution Control Plant (JWPCP) through the White Point outfall system from 1937-2019. Suspended solid release ( $10^3$  metric tons/yr) increased until the 1970s and declined with advanced primary wastewater treatment (Phase 1), partial secondary treatment (Phase 2), and full secondary treatment (Phase 3). Biological oxygen demand also decreased strongly, by 50% over the first few years of Phase 2 and to  $\sim$ 0 during the initial few years of Phase 3 (Stein & Cadien 2009). Modified from LACSD (2020)

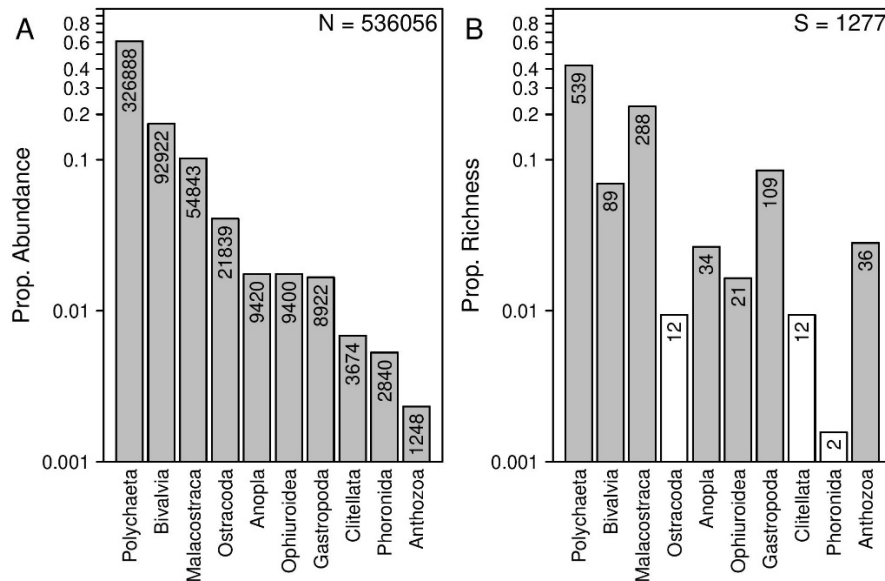


Fig. 3. Proportional abundances (A) and species richness (B) among the ten most abundant faunal classes represented in benthic samples from 1972-2019. Numbers within bars are the raw numbers of individuals or species. The total abundance (N) and species richness (S) for the whole fauna are printed in the upper right corners. White bars in (B) indicate three classes that rank among the ten most abundant (A) but are not among the top ten in richness. Our selected taxonomic subsets (Polychaeta, Bivalvia, and Malacostraca) represent 88% of sampled individuals and 72% of sampled species during the 45 years of monitoring along the 60-m isobath of the Palos Verdes Shelf.

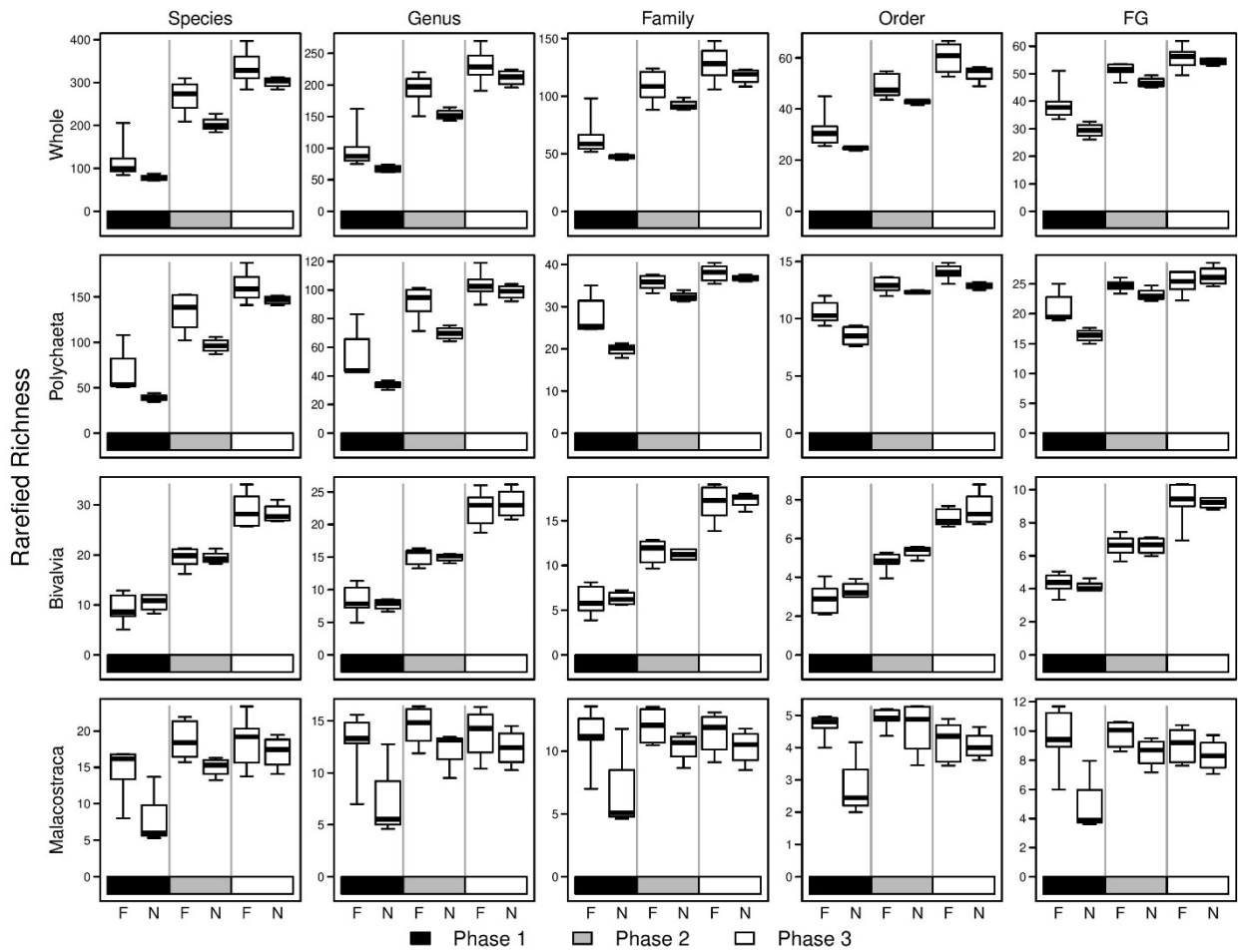


Fig. 4. Box plots of rarefied richness for whole benthic samples and subsets (rows) and coarsened taxonomic resolutions (columns, FG = functional guilds). Heavy line is median, box denotes the interquartile range (IQR), and whiskers denote entire range of values. Paired boxes compare stations at far-field (F; seven 60-m stations) and near-field (N; four stations) areas on the shelf, as judged from sediment chemistry during the 1970s. In each graph, richness was rarefied to the smallest station-level sample size. Richness increases with improved wastewater treatment in all analyses, from Phase 1 (1974-1983) to Phase 2 (1984-2002) and Phase 3 (2003-present; shaded bars along x-axes). Polychaete patterns best mirror the whole fauna and bivalves exhibit the strongest increase across phase boundaries. For all sets except bivalves, richness is higher at far-field stations rather than near-field. This contrast is damped at coarser taxonomic levels.

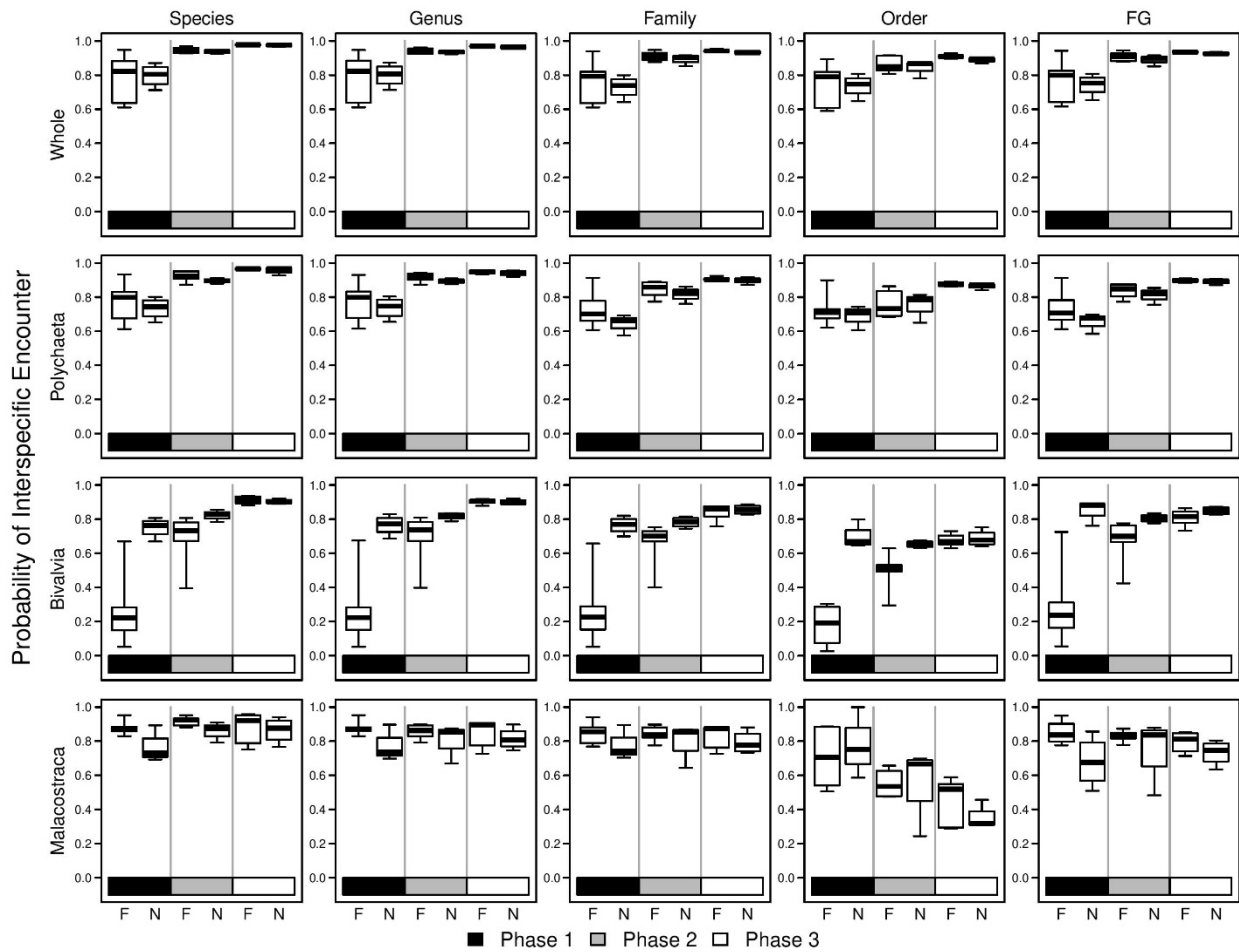


Fig. 5. Box plots of taxonomic evenness (PIE) for whole benthic samples and subsets (rows) at increasingly coarse taxonomic resolutions (columns, FG = functional guilds), with plots organized as in Fig. 4. Evenness increases with improved wastewater treatment, but bivalves exhibit an especially strong trend arising largely from strong contrasts between near-field (N) and far-field (F) stations early in the treatment history. Patterns persist with taxonomic coarsening (left to right within each row) except for malacostracans at the ordinal level.

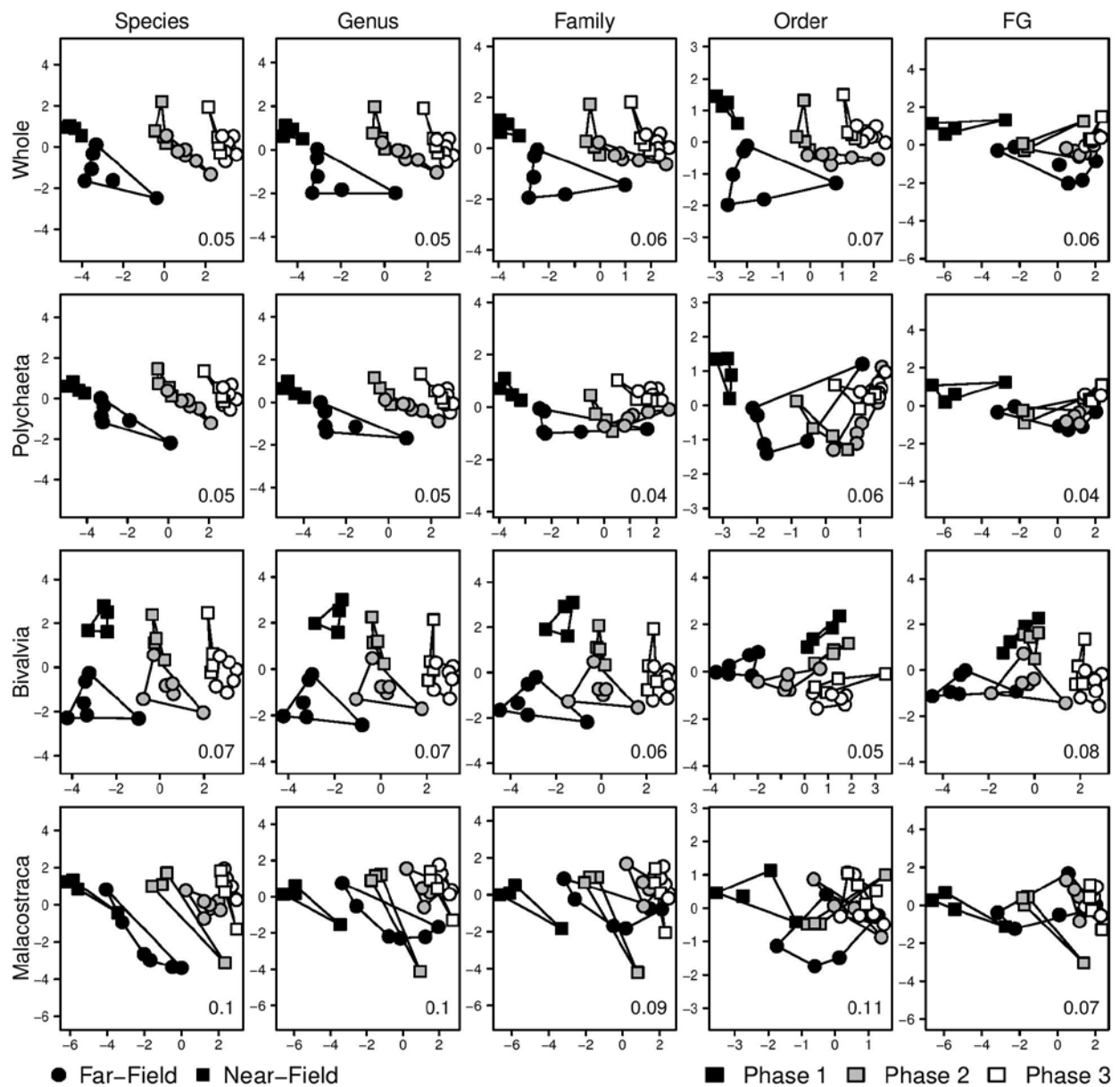


Fig. 6. Non-metric multidimensional scaling (NMDS) plots of Bray-Curtis similarities for whole benthic samples and subsets (rows) at increasingly coarse taxonomic resolution (columns, FG = functional guilds). Distances are based on square-root proportional abundances; convex hulls group samples by water treatment phase (point colors) and outfall proximity (point symbols); ordination stress values printed in lower right corner of each plot. All analyses approximately ordinate successive treatment phases along NMDS axis 1 (horizontal axis) and ordinate the spatial gradient along NMDS axis 2 (vertical axis). The taxonomic compositions of near-field and far-field stations become increasingly similar as wastewater treatment improves, both in the whole fauna (top row) and in each subset.

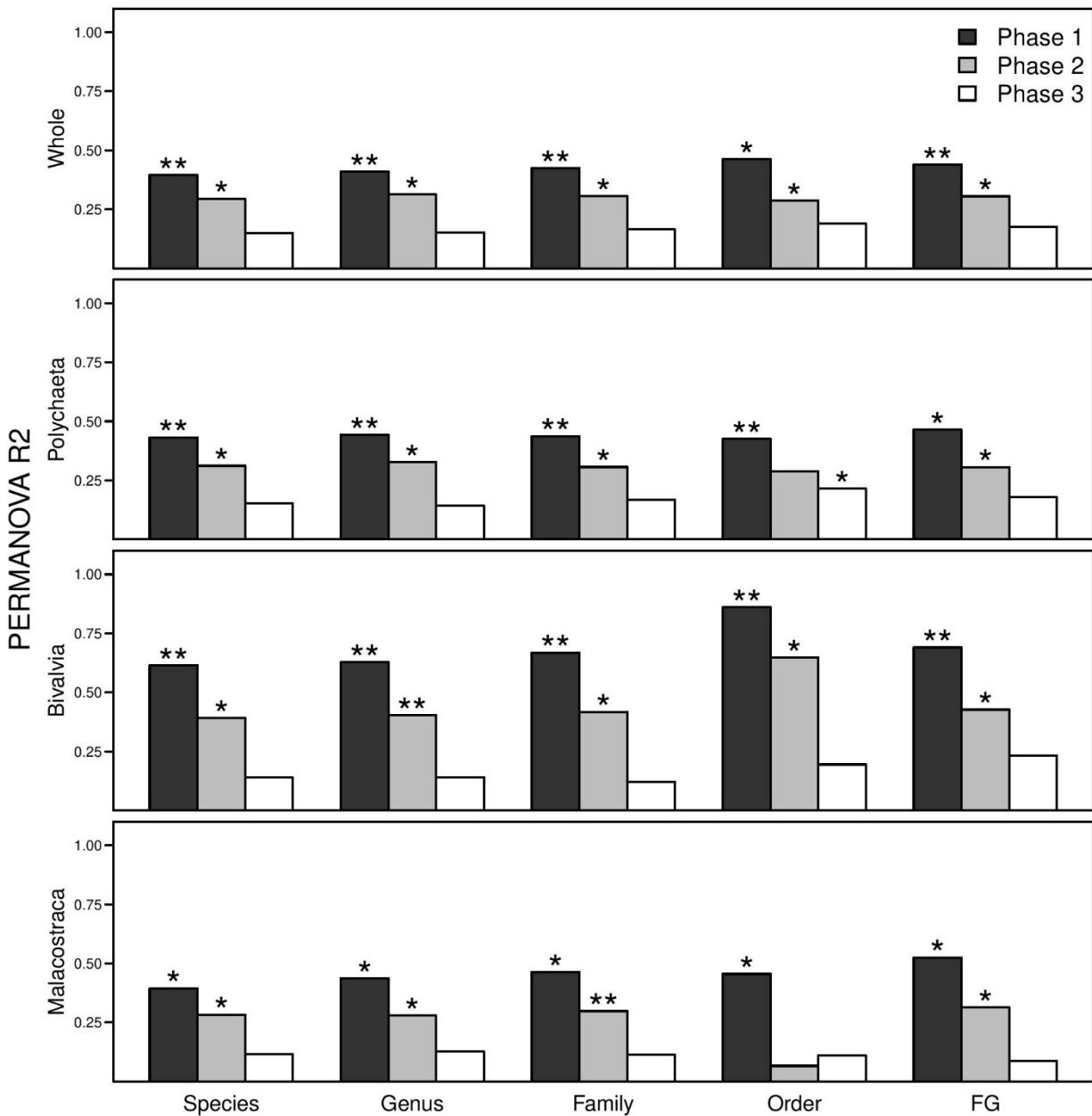


Fig. 7. Bar plots of PERMANOVA R2 values for compositional differences between near-field and far-field stations during each phase of wastewater treatment (bar color) for whole benthic samples and subsets (rows) at increasingly coarse taxonomic resolution (x-axis, FG = functional guilds). Asterisks indicate significant p-values (\* < 0.05, \*\* < 0.01). All taxonomic sets at all taxonomic resolutions detect spatial homogenization of community compositions with improved wastewater treatment. Polychaetes were most consistent with the whole fauna and bivalves exhibited the strongest change in R2 values across treatment phases.



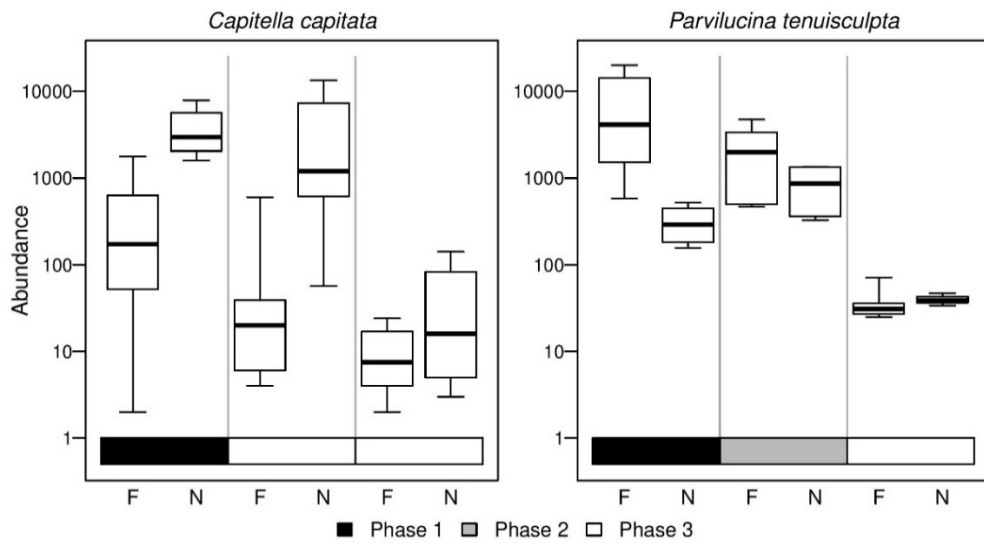


Fig. 8. Raw abundances of the polychaete *Capitella capitata* (left) and bivalve *Parvilucina tenuisculpta* (right). Paired boxes compare near-field and far-field stations as described in Fig. 4. *Capitella capitata* abundance is higher at near-field stations while *P. tenuisculpta* is more abundant at far-field stations. As wastewater treatment improved, the abundance of both species decreased and became more similar spatially.